Allelopathy

FUNDAMENTAL CONCEPTS

- Allelopathy is a form of plant interference that occurs when one plant, through living or decaying tissue, interferes with growth of another plant via a chemical inhibitor.
- Allelopathy may be present in many plant communities.
- Allelopathy has a potential but largely unexploited role in weed management.

LEARNING OBJECTIVES

- To know the definition of *allelopathy*.
- To understand the complexity of research to discover true allelopathy.
- To understand the complexity of allelopathic chemistry.
- To understand how allelochemicals enter the environment.
- To know the application of an analogous form of Koch's postulates to allelopathy.
- To know some examples of allelopathic interference.

The Three Princes of Serendip was published in Europe in 1557 by the Venetian author Michele Tramezzino. Horace Walpole, a British statesman, read the story as a child and coined the word *serendipity* in a 1754 letter to Horace Mann, the British envoy to Florence. The story is based on an ancient Persian tale in which the characters make fortunate, unexpected, wonderful discoveries. In the story, the three princes, each vying for the hand of a princess, are assigned impossible tasks by the princess. Each failed to accomplish the assigned tasks, but wonderful, serendipitous things happened to them as they tried to do what they had been asked to do. Serendipity is an apparent aptitude to make fortunate discoveries accidentally; unexpected, good things happen. Serendipity may be available to weed science if the presence of allelopathy can

be used to control weeds. Organisms from microbes to mammals find food, seek mates, ward off predators, and defend themselves against disease via chemical interactions. Allelopathic interactions are chemical, and discovery of the cause and mechanism of these interactions may yield a treasure of biological and chemical approaches to control weeds. At least 25% of human medicinal products (see Chapter 4) originated in the natural world or are synthetic derivatives of naturally occurring substances. Many natural interactions are chemical interactions, and some of them could influence the course of weed science.

Interference is the term assigned to adverse effects that plants exert on each other's growth. Competition is part of interference and occurs because of depletion or unavailability of one or more limiting resources. Allelopathy, another form of interference, occurs when one plant, through its living or decaying tissue, interferes with growth of another plant via a chemical inhibitor (Figure 8.1). Allelopathy comes from the Greek *allelo*, meaning "each

Interference = Competition + Allelopathy

FIGURE 8.1.   Components of plant interference.

other," which is similar to the Greek *allelon*, meaning "one another." The second root is the Greek *patho* or *pathos*, meaning "suffering, disease, or intense feeling." Allelopathy is therefore the influence, usually detrimental (the pathos), of one plant on another by toxic chemical substances from living plant parts through their release when a plant dies or their production from decaying tissue.

There is a subset of allelochemicals known as *kairomones* (from the Greek *kai*, meaning "new," and *hormaein*, meaning "to set in motion, excite, stimulate") that have favorable adaptive value to organisms that receive them. A natural kairomone from waterhyacinth is a powerful insect attractant for a weevil (*Necochetina eichhorniae*) and the waterhyacinth mite (*Orthogalumna terebrantis*). The kairomone is liberated when waterhyacinth is injured by surface wounding or by the herbicide, 2,4-D. The kairomone enhances control of waterhyacinth by attracting large numbers of weevils and mites to the area of the plant's wound (Messersmith and Adkins, 1995). Thus, the kairomone has favorable value to the insects but not to the waterhyacinth. Control of waterhyacinth is enhanced when insect damage is combined with herbicide stress.

For weed management purposes, allelopathy is considered a strategy of control. Corn cockle and ryegrass seeds fail to germinate in the presence of beet seeds. If tobacco seeds germinate and grow for six days in petri dishes, and then an extract of soil, incubated for 21 days with timothy residue, is added, the root tips of tobacco blacken within one hour, while radicle

elongation is unaffected. If an extract of soil that is incubated with rye residue is added, the symptoms are reversed (Patrick and Koch, 1958). Residues of timothy, maize, rye, and tobacco all reduce the respiration rate of tobacco seedlings (Patrick and Koch, 1958).

Kooper (1927), a Dutch ecologist, observed the large agricultural plain of Pasuruan on the island of Java, Indonesia, where sugarcane, rice, and maize grew. After harvest, the fallowed fields developed a dense cover of weeds. Kooper observed that the postharvest floristic composition of each community was stable year after year. He found that floristic composition was determined at the earliest stages of seed germination, not by plant survival rate or a struggle for existence but by differential seed germination. He showed that seeds of other species were present but could not germinate unless removed from their environment. Competition for light, nutrients, or water did not cause the consistent floristic composition. Kooper (1927) concluded that previous vegetation established a soil chemical equilibrium (an allelopathic phenomenon) and determined which seeds could germinate and, subsequently, which plants dominated.

The word *allelopathy* was first used by Molisch (1937), an Austrian botanist. He included toxicity exerted by microorganisms and higher plants, and that usage has continued. The phenomenon, however, had been observed much earlier by several scientists (Putnam, 1985). A classic example of allelopathy is found in the black walnut forests of Central Asia (Stickney and Hoy, 1881). Few other plants survive under the forest plant canopy because of the presence of juglone, a quinone root toxin derived from black walnut trees (Massey, 1925). The effect of juglone couldn't be reproduced in the greenhouse because some plant metabolites, including phenolics, require ultraviolet light for their biosynthesis (Davis, 1928).

Another classic study is the work by Muller and Muller (1964) in California, who observed that California chaparral often occurred near, but not intermixed with, California sagebrush. Neither species grew in the zones of contact between the respective communities; other species grew between the communities. They found terpenes, particularly camphor (a monoterpene ketone) and cineole (a terpene ether) produced by the chaparral, were responsible for the no contact zones. They concluded that plants, in this case the chaparral, are fundamentally leaky systems. Other studies are described by Rice (1974, 1979) and Thompson (1985).

One plant does not consciously set out to affect another, but rather the effect occurs as a normal, perhaps serendipitous, ecological interaction with evolutionary implications. Allelopathic species have been selected by evolutionary pressure because they can outcompete neighbors through energy-expensive biochemical processes that produce allelochemicals. The energy expense is not a waste of resources because no species evolves successfully

by wasting resources. Exploration of the phenomena will lead to better understanding of plant evolutionary strategies and, possibly, provide clues for herbicide synthesis and development.

Reviews of allelopathy are found in Putnam (1985, 1994) and the proceedings of the American Chemical Society symposium on the chemistry of allelopathy (Thompson, 1985). Putnam (1985, 1994) lists 50 weeds alleged to interfere with one or more crops (Table 8.1). Allelopathy has also been explored with a number of crops, and there have been attempts to find crop cultivars with a competitive allelopathic edge (Putnam, 1983, 1985; Rice, 1979; Thompson, 1985). Residues of several crops have phytotoxic activity on other plants (Table 8.2).

Laboratory studies have often demonstrated allelopathy, but the evidence produced should not be regarded as conclusive of the existence of allelopathy in the environment until it is confirmed by field studies. Field studies are essential to obtain ecologically relevant data (Foy and Inderjit, 2001; Inderjit

TABLE 8.1.   Some Weeds with Alleged Allelopathic Activity in Agroecosystems (Putnam, 1983, 1994; Duke et al., 2002).*

Weed	Susceptible species
Barnyardgrass	rice, wheat
Bermudagrass	barley, coffee, soybean
Bluegrass	tomato
California peppertree	cucumber, wheat
Canada thistle	several
Catnip	peas, wheat
Cogongrass	corn, cucumber, rice, sorghum, tomato
Common chickweed	barley
Common lambsquarters	cabbage, cucumber, corn, sugarbeet, wheat
Common milkweed	sorghum
Common purslane	alfalfa, durum wheat, tomato
Common ragweed	several
Corn cockle	wheat
Crabgrass	cotton, trailing crownvetch
Diffuse knapweed	ryegrass
Dock	corn, pigweed, sorghum
Field bindweed	wheat
Flaxweed	flax

(*Continues*)

TABLE 8.1. (*Continued*)

Weed	Susceptible species
Giant foxtail	corn
Giant ragweed	peas, wheat
Goosegrass	bean, corn, sorghum
Goldenrod	several
Hairy beggarticks	several
Heath	red clover
Italian ryegrass	oats, brome, lettuce, clover
Jimsonweed	several
Johnsongrass	barley, cotton, soybean, trailing crownvetch
Ladysthumb	potato, flax
Large crabgrass	several
Leafy spurge	peas, wheat
Mayweed	barley
Mugwort	cucumber
Mustard	several
Nutsedge, purple	barley, black mustard, broccoli, Brussels sprouts, cabbage, carrot, collards, cotton, cucumber, onion, radish, rice, sorghum, soybean, strawberries, tomato
Nutsedge, yellow	corn
Prince's feather	mustard
Prostrate spurge	several
Quackgrass	several
Redroot pigweed	soybean, wheat
Russian thistle	several
Spiny amaranth	coffee
Sunflower	barley, garden cress, jimsonweed, lettuce, redroot pigweed, tomato, wheat
Syrian sage	wheat
Velvetgrass, common	barley
Velvetleaf	several
Western ragweed	several
Wild cane	wheat
Wild garlic	oats
Wild marigold	several
Wild oats	barley, flax, wheat

*Complete citations for several weeds can be found in Duke et al., 2002.

TABLE 8.2.   Some Crops Whose Residues Have Been Reported to Be
Phytotoxic (Putnam, 1994; Duke et al., 2002).

Crop	Affected species
Alfalfa	alfalfa
Apple	apple
Asparagus	tomato, asparagus, fescue spp.
Barley	white mustard
Bean	pea, wheat
Black walnut	tomato
Cabbage	mustard, lettuce, spinach, tomato
Clover, red	several
Clover, white	radish
Coffee	several
Corn	several weeds
Crambe	wheat, velvetleaf
Cucumber	several weeds
Jackbean	Brazilian satintail
Lentil	wheat
Oats	several
Pea	several
Rice	barnyardgrass, lettuce, rice
Rye	common lambsquarters
Ryegrass	several
Smooth bromegrass	several
Sorghum	fescue
Sunflower	barley, clover, garden cress, jimsonweed, lettuce, redroot pigweed, tomato, wheat
Wheat	several weeds

et al., 2001). Lab studies provide clues but are not sufficient without field
confirmation. For example, Norsworthy (2003) demonstrated the allelopathic
potential of aqueous extracts of wild radish in controlled environment studies.
The evidence indicated that aqueous extracts of wild radish or incorporated
wild radish residues suppressed seed germination, radicle growth, seedling
emergence, and seedling growth of "certain crops and weeds," but subsequent
field confirmation is essential to establish the reality of allelopathy as an eco-
logical phenomenon.

I. ALLELOPATHIC CHEMISTRY

Plants produce a myriad of metabolites of no known utility to their growth and development. They are often referred to as secondary plant metabolites and are defined as compounds that have no known essential physiological function. The idea that these compounds may injure other forms of life is not without a logical base. However, proof is questionable because most allelochemical effects occur through soil, a complex chemical matrix. Conclusive studies require extraction and isolation of the active agent from soil. Any allelopathic chemical may be chemically altered prior to or during extraction. That which is extracted, isolated, and studied may not be what the plant produced.

Secondary plant metabolites, also known as natural products, are regarded by many as "a vast repository of materials and compounds with evolved biological activity, including phytotoxicity" (Duke et al., 2002). It is proposed that some of these compounds may be useful directly as herbicides or as templates for herbicide development. According to Duke et al. (2002), they often have unique molecular target sites in plants but have not been developed or used much in agriculture or herbicide development. Several reviews of this area of research are available (Dayan et al., 1999; Duke et al., 1998, 2000a, 2000b, 2002; Hoagland, 2001; Hoagland and Cutler, 2000). Acetic acid, the primary component of vinegar, is a contact, burning herbicide that can be used selectively in some crops (e.g., onion and sweet corn). Martan 2 is a clove oil product that also shows promise as a natural product herbicide (Evans and Bellinder, 2006). In both cases, success depends on the time of application and the growth stage of the crop and weeds. Both require high active ingredient application (acetic acid 34 to 68 gallons per acre), and both are expensive (up to several hundred dollars per acre) (Evans and Bellinder, 2006).

Allelochemicals vary from simple molecules, such as ammonia, to the more complex quinones, juglone, and the terpenes camphor and cineole, to very complex conjugated flavonoids such as phlorizin (isolated from apple roots) or the heterocyclic alkaloid caffeine (isolated from coffee) (Putnam, 1985; Rice, 1974; Thompson, 1985). Putnam (1985) lists several chemical groups from which allelopathic agents come: organic acids and aldehydes, aromatic acids, simple unsaturated lactones, coumarins, quinones, flavonoids, tannins, alkaloids, terpenoids and steroids, a few miscellaneous compounds such as long chain fatty acids, alcohols, polypeptides, nucleosides, and some unknown compounds. Some of the diversity and complexity of allelopathic chemistry are shown in Table 8.3. The diversity suggests several mechanisms of action, a multiplicity of effects, and is one reason for the slow emergence of a theoretical framework. The chemistry of allelopathy is as complex as synthetic herbicide chemistry, but it is a chemistry of discovery as opposed to one of synthesis.

TABLE 8.3.   Allelopathic Compounds Isolated from Plants (Putnam, 1983).

Common name	Chemical class	Natural source
Acetic acid	aliphatic acid	decomposing straw
Allylisothiocyanate	thiocyanate	mustard plants
Arbutin	phenolic	manzanita shrubs
Bialaphos	amino acid derivative	microorganisms
Caffeine	alkaloid	coffee plants
Camphor	monoterpene	*Salvia* shrubs
Cinnamic acid	aromatic acid	guayule plants
Dhurrin	cyanogenic glucoside	sorghum plants
Gallic acid	tannin	spurge plants
Juglone	quinone	black walnut trees
Patulin	simple lactone	*Penicillium* fungus on wheat straw
Phlorizin	flavonoid	apple roots
Psoralen	furanocoumarin	*Psoralea* plants

There is little doubt that allelopathy occurs in plant communities, but there are questions about how important allelopathic chemicals are in nature and if they can be exploited in cropped fields. It has been reported for many crop and weed species (Putnam, 1983, 1985, 1994), but proof of its importance in nature is lacking (Foy and Inderjit, 2001). Proof will require something similar to the application of Koch's (1912) postulates that were proposed for plant pathology in 1883 and amended by Smith (1905).

These are the analogous postulates applied to allelopathy (Aldrich, 1984; Putnam, 1985):

1. Observe, describe, and quantify the degree of interference in a natural community.
2. Isolate, characterize, and synthesize the suspected toxin.
3. Reproduce the symptoms by application of the toxin at appropriate rates and times in nature. [Koch's (1912) postulates called for reisolation of the bacterial agent from the experimentally infected plant—an inappropriate criterion for allelopathic research.]
4. Monitor release, movement, and uptake, and show that they are sufficient to cause the observed effect(s).

These four steps describe difficult, expensive, complex scientific research. Rigorous proof has rarely been applied to any ecological interaction, but such proof is vital if allelopathic research is to move from description to causation.

In short, it is insufficient to make an observation and suspect a toxin. It is insufficient to demonstrate the toxin is produced by one plant. Specific cause and effect must be demonstrated through chemical and plant studies. It may not be necessary to prove that plant X is the source of allelochemical Y. If an allelochemical, effective as a natural herbicide, can be isolated and identified, in theory, it might be useful without absolute proof of its plant origin or physiological mode of action. The basic chemistry and biology would remain a scientific challenge, but it might be possible to exploit the activity. Proceeding with partial knowledge is more risky but not impossible. For example, medical science still doesn't know exactly how aspirin relieves pain, and weed science doesn't know exactly how 2,4-D kills a plant, but both can be used productively and safely.

II. PRODUCTION OF ALLELOCHEMICALS

Production of allelochemicals varies with environment and associated environmental stresses. It can occur in any plant organ (Rice, 1974), but roots, seeds, and leaves are the most common sources. Source becomes important for exploitation of allelochemicals for weed control. For example, an allelochemical found in flowers or fruits would have less potential value than if it were concentrated in roots or shoots (Putnam, 1985). (A statement about availability, not allelochemical potency.) For control, soil incorporation of whole plants might create proper distribution regardless of which plant part produced the chemical. The amount is important for control purposes, and if specific effects are to be predicted in the field, total quantity and concentration must be determined (Putnam, 1985).

There is evidence that allelochemical production may be greater when plants suffer from environmental stress (Putnam, 1983, 1985; Rice, 1979). Production is influenced by light intensity, quality, and duration, with a greater quantity produced with high ultraviolet light and long days (Aldrich, 1984). Weeds, commonly understory plants, might be expected to produce lower quantities of allelochemicals because UV light is filtered by overshadowing crop plants. This, of course, assumes that crops provide shade and that shade effectively suppresses allelopathic activity. Quantities of allelochemicals produced are also greater under conditions of mineral deficiency, drought stress, and cool temperatures, as opposed to more optimal growing conditions. In some cases, plants affected by growth regulator herbicides may increase production of allelochemicals. Because stress frequently enhances allelochemical production, it is logical to assume that stress accentuates the involvement of allelopathy in weed-crop interference and that competition for limited resources may increase allelopathic potential or sensitivity of the weed, the
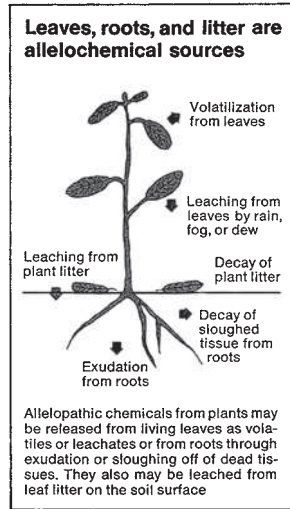
FIGURE 8.2. Sources of allelochemicals (Putnam, 1994).

crop, or both. Thus, weed-crop competition and allelopathy should be regarded as intimately related components of interference in a crop ecosystem.

Allelochemicals enter the environment in a number of ways at different times, and mode and time of entry can alter their effects (Figure 8.2). Although chemicals with allelopathic activity may be present in many species, presence does not mean that allelopathic effects will ensue. Even after a chemical has been isolated and identified, its placement in the environment after plant release or its time of release may preclude expression of potential activity.

Allelochemicals enter the environment through volatilization or root exudation and move through soil by leaching (Figure 8.2). These entry paths are usually regarded as true allelopathy. Toxins also result from decomposition of plant residues, properly regarded as functional allelopathy—that is, environmental release of substances that are toxic as a result of transformation after their release by the plant.

Allelochemicals can be produced by weeds and affect crops, but the reverse is also true, although it has not been as widely studied (Putnam, 1994). It is probably true that some crop cultivars produce allelochemicals. Therefore, it is theoretically possible that such cultivars could be planted to take advantage of their allelochemical potential. It has been suggested that crops with allelopathic potential could be planted as rotational crops or companion plants in annual or perennial cropping systems to exert their allelopathic effect on weeds. Rye and its residues have been shown to provide good weed control in

a variety of cropping systems (Barnes and Putnam, 1983). Rye residues reduced emergence of lettuce and proso millet by 58 and 35%, respectively. Rye shoot tissue inhibited lettuce seed germination 52%. It also was phytotoxic to barnyardgrass and cress (Barnes and Putnam, 1986).

III. ALLELOPATHY AND WEED-CROP ECOLOGY

Aldrich (1984) suggested allelopathy was significant for weed-crop ecology in three ways:

1. As a factor affecting changes in weed species composition
2. As an avenue of weed interference with crop growth and yield
3. As a possible weed management tool

Allelopathy should not always be implicated when other explanations do not suffice, but it should not be overlooked because of the difficulty of establishing causality.

A. Effects on Weed Species

Why one species succeeds another is a question that has intrigued ecologists for many years. Weed scientists are interested in the same question but often only for the life-span of an annual crop. Weed scientists accept that plants change the environment and are changed by it. It is generally agreed that many early colonizers succeed by producing large numbers of seeds, whereas late arrivals succeed through greater competitive ability. This is true in old-field succession and in annual crops. Ecologists have shown that successful plants may change the environment to their advantage by subtle means, such as changes in soil nitrogen relationships caused by release of specific inhibitors of nitrogen fixation or nitrification (Putnam, 1985; Thompson, 1985).

B. Weed Interference

Weed seeds survive for long periods in soil, and chemical inhibitors of microbial decay have been implicated in their longevity, but specific identification of inhibitors from weed seeds has not been accomplished. Allelochemicals have been implicated in the inability of some seeds to germinate in the presence of other seeds or in the presence of crop residues in soil. Although neither phenomenon has been exploited for weed management, there is little doubt

that both occur. Eventual exploitation may depend on discovery of specific chemicals and their mode(s) of action. Because of the mass of plant residue and its volume compared to the volume of seed (even though the number of seeds may be large), the possibility of effects from plant residues is greater than that of effects from seed.

The problems with replanting the same or different crops in a field have been cited (Putnam, 1985; Rice, 1974) to show the effect of allelochemicals on crop growth. Putnam (1983) showed that the allelopathic potential of sorghum residues has been exploited for weed control in subsequent rotational crops. While there is little doubt that allelochemicals inhibit crop growth, a research challenge still exists to separate allelopathic effects from competition. Most greenhouse studies cannot be directly translated to the field because of different climatic, edaphic, and biological conditions, and possible effects of soil volume. Allelopathy awaits adequate experimental methods for independent but related field and greenhouse studies.

A fundamental assumption of biological control of weed is that damaged plants are less fit and compete poorly and therefore they will fail in the struggle for survival. That assumption, like so many in science, often is not borne out by research. When, as a management strategy, spotted knapweed is intentionally attacked by the larvae of two different root-boring biocontrol insects and a parasitic fungus, its allelopathic potential increases significantly, and it has "more intense effects on native" vegetation (Thelen et al., 2005). The authors conclude that while biological control can be very effective, it can often be less effective or fail. Without a detailed understanding of the basic ecology of the area and the plants, it is not possible to know why success or failure occurred. "An invasive species that inhibits natives via unusually deep shade might be a more appropriate target for biological control than allelopathic invaders."

C. Weed Management

A living cover crop of spring planted rye reduced early season biomass of common lambsquarters 98%, common ragweed 90%, and large crabgrass 42% compared to control plots with no rye (Barnes and Putnam, 1983). Wheat straw has reduced populations of pitted morningglory and prickly sida in no-tillage culture. It was suggested the wheat produced an allelochemical that inhibited emergence of several broadleaved species (Liebl and Worsham, 1983). Inderjit et al. (2001) studied the allelopathic potential of wheat and perennial ryegrass. They showed in a laboratory study that root length of perennial ryegrass was suppressed by wheat and was dependent on the density of wheat seeds in a petri dish. Ryegrass shoot growth was unaffected by wheat,

and ryegrass density had no effect on wheat seedling growth. The allelopathic potential of wheat straw has been demonstrated in the laboratory (Guenzi and McCalla, 1962; Guenzi et al., 1967; Hamidi et al., 2001) but not in the field.

It is reasonable to assume that many plants have allelopathic potential or some susceptibility to allelochemicals when they are presented in the right amount, form, and concentration at the appropriate time. It is equally reasonable to assume that allelopathy may have no role in the interference interactions of many species. However, enough work has been done to conclude that allelopathy could be utilized for development of new weed management strategies. Trials in South Dakota showed that fields planted to sorghum had two to four times fewer weeds the following year than similar fields planted to soybean or corn (Kozlov, 1990). It was proposed, although not proven, that reduced weed seed germination was due to phenolic acids and cyanogenic glucosides given off by sorghum. Suppression of weeds by sorghum has been reported by Guenzi and McCalla (1966) and Hussain and Gadoon (1981). Sunflower has been reported to have an allelopathic effect against grain sorghum (Schon and Einhellig, 1982) and against other weeds (Leather, 1983). Guenzi and McCalla (1966) found allelopathic phenolic acids in oats, wheat, sorghum, and corn residues, and Lodhi et al. (1987) discussed the role of allelopathy from wheat in crop rotations. Other sources are available to describe and summarize the major findings of allelopathy research and their application in weed management (Putnam, 1983, 1985, 1994; Rice, 1974, 1979; Thompson, 1985; and the reviews previously cited). A few examples follow to illustrate the research and its potential.

Walker and Jenkins (1986) were the first to demonstrate that sweet potato residues inhibited growth of sweet potato and cowpea. Decaying residues reduced uptake of calcium, magnesium, and sulfur by other plants (Walker et al., 1989). Additional studies showed that after one growing season, shoot dry weight of yellow nutsedge growing with sweet potatoes was less than 10% of the weight when yellow nutsedge was grown alone. Moreover, remaining yellow nutsedge had no effect on sweet potato growth (Harrison and Peterson, 1991). Allelochemicals were present in the tuber periderm that is continually sloughed off during root growth. Proso millet was susceptible to all extracted fractions but other plants showed differential susceptibility, indicating that several allelochemicals may be present (Peterson and Harrison, 1991).

Plant pathogens and allelochemicals from plant pathogens and other soil microorganisms can be used as bioherbicides. This possibility has been studied for more than three decades (Hoagland, 2001). Numerous pathogens and microbial allelochemicals have been isolated and studied for their bioherbicidal potential. A good example of a microbial product is the herbicide bialophos (active ingredient phosphinothricin). It is manufactured by fermentation as a metabolite of the soil microbe *Streptomyces viridochromogenes* (Auld and

McRae, 1997). It is available in Japan (as Herbiace) but not in the United States. The second example is the ammonium salt of phosphinothricin, glufosinate (see Chapter 13). A gene coding for the enzyme phosphinothricin acetyl transferase was isolated from the nonpathogenic bacteria *Streptomyces hygroscopicus* and cloned into several crops. The enzyme converts the herbicide glufosinate to a nonphytotoxic metabolite and the genetically engineered crop is thus resistant to glufosinate. Another example began with a study of the root parasitic damping of fungus (*Pythium* spp.) in turf. Christians (1991, 1993) wanted to establish the fungus in the soil of a new golf course green at Iowa State University. Pythium was cultured in the laboratory on cornmeal, a standard procedure. The culture was placed on field plots, and other plots were treated with the same amount of fresh cornmeal. The attempt to establish Pythium failed, but seeded cultivars of creeping bentgrass did not germinate well on plots that had received fresh corn gluten meal, a by-product of the wet-milling process of corn grain. This was unexpected. Further study showed potential for selective control of crabgrass in Kentucky bluegrass turf. Liu et al. (1994) demonstrated that enzymatically hydrolyzed corn gluten meal was more herbicidally active than corn gluten. Corn gluten hydrolysate completely inhibited germination of crabgrass and creeping bentgrass seed and root emergence of perennial ryegrass seed. Corn gluten meal is used for preemergence weed management and fertilization (Bingamen and Christians, 1995; Christians, 1993; Gough and Carlstrom 1999).

Pollen can also be allelopathic. Pollen can release toxins that inhibit seed germination, seedling emergence, sporophytic growth, or sexual reproduction (Murphy, 2001). Two crops (timothy and corn) and four weeds (orange hawkweed, ragweed parthenium, yellow hawkweed, and yellow-devil hawkweed) are known to exhibit pollen allelopathy (Murphy, 2001). There may be others. Pollen allelopathy might be useful in biological weed management because the allelochemical is active in very low doses (as little as 10 grains of pollen per mm^2 on stigmas) and pollen is a small, naturally targeted distribution system. Murphy (2001) points out that pollen allelopathy has potential but is not a confirmed weed management technique. Disadvantages include weed adaptation to pollen toxicity and possible threats of toxic pollen to crop plants.

Few researchers recommend that allelopathy is a dominant way plants interact. Many argue that it is present and that nonresource competitive mechanisms should regularly be considered to account for the success of weeds and other invading species (Hierro and Callaway, 2003). Diffuse knapweed is an invasive Eurasian weed in western North America. Research and general observations suggest that diffuse knapweed produces virtual monocultures and that allelopathy may be an important component of its success. Hierro and Callaway (2003) suggest that allelopathy "may be more important in recipient communities than in origin communities because the former are more likely

to be naive to the chemicals possessed by newly arrived species." They do not suggest that allelopathy is a unifying theory or a dominant way that plants interact or the only way to explain diffuse knapweed's dominance. They do suggest that such nonresource mechanisms should not be dismissed as irrelevant.

With this kind of evidence one is inclined to agree with Putnam's (1985) suggestion that not believing in allelopathy, now, is like not believing in genetic inheritance before DNA's structure was known. One area to explore might be testing for suppression of weed seed germination and seedling emergence by potential allelopathic species. Work to date has shown this to be an inconsistent effect, and, if developed, it could be used with other methods of weed management. Allelopathy isn't, and will never be, a panacea for all weed problems. It is another weed management tool to be placed in the toolbox and used in combination with other techniques. It is not a technique that will finally solve all weed problems or make the hoe obsolete.

The second strategy where allelopathy may be used is weed suppressing crops. This can be realized by discovering, incorporating, or enhancing allelopathic activity in crop plants. This technique would be most useful in crops maintained in high-density monocultures, such as turf grasses, forage grasses, or legumes. Olofsdotter (2001) notes that while allelopathy has been demonstrated with varying success, it has been much more difficult to use the principle in crop production. She suggests that if genetic mapping of quantitative traits can be linked to understanding of allelopathic mechanisms, it may lead toward optimization of a plant's allelopathy and production of more competitive crops—crops with an allelopathic advantage. It may be possible with modern techniques to transfer (genetically modify) the ability of any plant to produce a weed-controlling allelochemical to a crop plant (for example, the work on rye done by Barnes and Putnam, 1983, 1986). Much more physiological and chemical knowledge is required before this can be done successfully, but it is an enticing possibility—a crop that does more, perhaps all, of its own weed control because it has a chemical advantage.

The third area for allelopathic research and development includes the use of plant residues in cropping systems, allelopathic rotational crops, or companion plants with allelopathic potential. Many crops leave residues that are regarded as a necessary but not a beneficial part of crop production, except as they contribute to soil fertility or tilth. Research (Putnam, 1985, 1994; Rice, 1979) indicates that plant residues have allelopathic activity, but the nature of this activity has not been explored sufficiently to permit effective use. Rotation, a neglected practice in many agricultural systems, is being studied because of its potential for weed management through competition and allelopathy. Companion cropping is a new and interesting technique for agricultural systems in developing countries. Multiple cropping is common in many

developing countries where allelopathy may be operational without being obvious and defined. These systems may hold valuable lessons for further agricultural development of allelopathy as a useful weed management tool.

Weed scientists need to look beyond the immediate assumption that interference is always competition and see what they may not be looking for: an allelopathic effect, which can be an unexpected, but good, thing. Perhaps there are expressions of allelopathy before our eyes that we don't see because we're not looking for them. If there are compounds in nature with such great specificity, they should be examined. The patterns of herbicide development point to greater specificity, and nature may have solutions in natural products if we recognize them, learn how they work, and exploit their capabilities.

One of the first and quite potent phytotoxins found in higher plants was 1,8-cineole released by sagebrush species (Muller and Muller, 1964). Cinmethylin was developed as an herbicide for weed control in rice, cotton, soybeans, peanuts, some vegetables, vine crops, and ornamentals. It is not sold in the United States. Chemically, it is a structural analog of 1,4-cineole, which inhibits asparagine synthetase, the enzyme responsible for biosynthesis of the amino acid asparagine (Romagni et al., 2000). Cinmethalin controls many annual grasses and some broadleaf weeds and sedges. It is produced synthetically, but the thought behind it was probably derived from the known phytotoxicity of the allelopathic cineoles.

A second and clearer example of a natural herbicide is AAL-toxin, a natural metabolite produced by *Alternaria alternata* f. sp. *Lycopersici*, the pathogen that causes stem canker of tomato (Abbas et al., 1995). The phytotoxic effects of AAL-toxin were tested on 86 crop and weed species (Abbas et al., 1995). Monocots were generally immune to its effects. Black nightshade, jimsonweed, all species of tomatoes tested, and several other broadleaved plants were susceptible at low doses. Other broadleaved species were susceptible but only at higher doses. Abbas et al. (1995) proposed that the differential susceptibility of species to AAL-toxin could be exploited for selective weed control. There may be other potentially valuable chemicals hidden from us because we are looking for something else. Promising observations await the good observer?

However, Duke et al. (2002) present five problems associated with natural products, including allelochemicals, that describe why there has not been more research and development of these potent chemicals. Perhaps the most important reason is that natural products that have or potentially have phytotoxic activity are usually structurally complex and therefore expensive to manufacture. Second, these chemicals often have high mammalian toxicity (AAL-toxin is toxic to mammalian cells; Abbas, 1996), which makes them undesirable from a public health standpoint. Many potentially beneficial natural products (phototoxins, pharmaceuticals, etc.) are derived from plants found only or mainly in developing countries. These countries have charged, with adequate

justification, that developed nations have exploited their resources with inadequate or no compensation. Laws have been passed in many countries to prevent exploitation of indigenous natural resources and to retain some level of ownership. The cost of compound identification (discovery), isolation, structural identification, and manufacture has been very high, with no assurance of a return to justify the initial costs. Finally, many natural products have relatively short environmental half-lives. This is desirable from a nontarget species view but not from a weed management view, where some persistence in time is a good thing.

THINGS TO THINK ABOUT

1. What is the present role of allelopathy in weed management?
2. What is the potential role of allelopathy in weed management?
3. Why has so little research been done on allelopathy?
4. What are the essential ingredients of a research program to discover allelochemicals?

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