

Chapter 1

Allelopathy: Current Status and Future Goals

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The phenomenon of allelopathy encompasses all types of chemical interactions among plants and microorganisms. Several hundred different organic compounds (allelochemicals) released from plants and microbes are known to affect the growth or aspects of function of the receiving species. Many new allelochemicals have been identified in recent years and it has become clear that the actions of allelochemicals are important features characterizing the interrelationships among organisms. These compounds influence patterns in vegetational communities, plant succession, seed preservation, germination of fungal spores, the nitrogen cycle, mutualistic associations, crop productivity, and plant defense. Allelopathy is tightly coupled with competition for resources and stress from disease, temperature extremes, moisture deficit, and herbicides. Such stresses often increase allelochemical production and accentuate their action. Allelopathic inhibition typically results from a combination of allelochemicals which interfere with several physiological processes in the receiving plant or microorganism. Other than the autecological study of specific species, there are persistent challenges in allelopathy to determine the mechanism of action of compounds, isolate new compounds, evaluate environmental interactions, and understand activity in the soil. New frontiers will focus on ways to capitalize on allelopathy to enhance crop production and develop a more sustainable agriculture, including weed and pest control through crop rotations, residue management, and a variety of approaches in biocontrol. Other goals are to adapt allelochemicals as herbicides, pesticides, and growth stimulants, modify crop genomes to manipulate allelochemical production, and better elucidate chemical communications that generate associations between microorganisms and higher plants.

systems. We cannot ignore this reality, and we are challenged to capitalize on the opportunities that these chemical interactions present.

Most systems of the world face serious environmental problems, and a portion of these evolve from a heavy reliance on herbicides and pesticides in agricultural production. Efforts toward a more sustainable agriculture have recently taken into account the adaptive mechanisms that have evolved in several of certain plants, and these include the allelochemicals they produce. The insights in this book illustrate that a better understanding of the allelopathic phenomenon can help in progress toward a more sustainable agriculture worldwide. To this end, this book is timely, and we hope it will stimulate the thinking of young scientists to take up some of these challenges.

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The writings of some natural philosophers that date back more than two millennia show that they recognized chemical influences in nature (1). However, it is the evidence accumulated over the last several decades which has established that external roles for biochemicals, meaning roles that do not directly affect the basic physiology of the producing organism, are pervasive themes characterizing the interrelationships among organisms. This realization does not diminish the respective importance that competition for resources has on the relative success of an organism or a species. Instead, chemical ecology extends our dimensions of understanding and provides new insights into the intricacies of interchanges that occur in an ecosystem, community, or population.

Allelopathy, a subset within the broader scope of chemical ecology, is concerned with effects that chemicals of plant or microbial origin have on growth, development, and distribution of other plants and microorganisms in natural communities or agricultural systems. The aims of this overview chapter are to provide a synthesis of the scope of allelopathy, suggest general principles, illustrate some complications in this field, and project future opportunities for study and application.

Scope of Allelopathy

Background. The definition of allelopathy has not been static and the term continues to be applied in slightly different ways. It was first used by Molish (2) to indicate all effects that are either directly or indirectly the result of chemicals transferred from one plant to another plant. At that time more than half a century ago, the accepted parameters of the plant kingdom included algae, fungi, and the various microorganisms as well as higher plants. It also is clear that Molish intended allelopathy to encompass both inhibitory and stimulatory activity. When Rice (3) wrote the first comprehensive treatise on allelopathy, he limited the term to inhibitory effects in keeping with most of the available information. However, Rice (4) revised his view and the second edition of *Allelopathy* embraced the original definition of the term which included stimulatory as well as inhibitory effects (1).

Both Waller (5) and Rizvi and Rizvi (6) included the plant-insect and plant-higher animal interactions in the terms allelopathy and allelochemicals as used in the books they edited. Lovett (7,8) has been articulate in pointing out that many of the same plant-produced chemicals that affect associated plants also influence other organisms, and he has called for expanding the context of allelopathy. He has focused on allelopathy as the complex of subtle communications between plants and also between plants and other organisms. In referring to the scope of biological activities that arise because plant-produced chemical messengers are added to the environment, Lovett (8) has adopted a perspective that broadens the parameters of allelopathy to include some aspects of plant defense. There has been no other umbrella terminology to encompass chemical defenses of plants, so Lovett's usage may eventually become established in the literature.

Most of the investigators in the field of allelopathy have adopted the original definition of Molish (2). However, terms do not set the limits on the actions of plant allelochemicals and it is useful to recognize that some of the same compounds active in plant-plant interactions also impact insects and other animals.

Interference. Theories in classical ecology assumed that competition for space and resources such as water, nutrients, and light was responsible for the mythical "balance of nature" and the relative success of an individual or species in plant communities. Allelopathic effects can not be considered a part of competition since they do not rely on removal of resources. To avoid confusion and recognize that both competition and allelopathy are often involved, Muller (9) designated the collective effects of one plant on another as interference. Interference is a term now widely used in the literature, especially in the literature of weed biology where the perspective has generally focused on the deleterious effects of a weedy species on a crop.

Communications. There has been considerable recent work on chemical communications or signals between plants, including those involving the plant-microbe interface. Many bacteria and fungi in the soil form mutualistic or symbiotic associations with plant roots, and evidence exists for roots excreting specific chemical signals which influence microbial activity (10-14). Initiation of *Rizobium*-legume symbiosis involves a complex series of steps wherein the bacteria and plant each influence each other. *Rhizobium* are chemotactic toward plant roots and root colonization, growth, and nodulation by rhizobia inoculants are stimulated by seed and root exudates which include certain flavonoids (11,15,16). Recent studies show that both plant growth-promoting rhizobacteria and vesicular-arbuscular mycorrhizal fungi produce chemical signals that mediate root growth (14,17,18).

Volatile flavor compounds from fungal spores, seeds, bacteria, and plant tissue have been implicated in a number of bioregulatory actions (19). Stem rust of wheat urediniospores (*Puccinia graminis* var. *tritici*, causal agent of wheat stem rust) are stimulated to germinate by nonanal at levels as low as 0.01 ppm (20). These volatile compounds are not found alone and an array of compounds may be active stimulators of fungal spores. French and Leather (21) found nonanal and several related compounds stimulated germination in some weed seeds. Exposure to octyl thiocyanate as low as 1 ppm/v stimulated *Rumex crispus* germination.

Likewise, host signals are required for stimulating germination and several stages of development in witchweed (*Striga asiatica*) parasitism of *Sorghum bicolor* and several other crops (22,23). Another type of communication is seen from the evidence that insect feeding on one plant may result in biochemical changes in neighboring plants as the result of an airborne cue originating in the damaged tissue (24). Although the picture is not clear, recent work suggests that when insect or mechanical damage occurs, volatile methyl jasmonate released from one plant may signal defense responses in another plant (25,26). The

biology of these communications fits within the parameters of the original definition of allelopathy.

Allelochemical Release and Transfers

A key concept in allelopathy is that chemicals transfer through the environment from one organism to another. As illustrated in Figure 1, Grummer (27) proposed specific designations for the agents of allelopathy based on the type of producing plant and the type of plant affected. However, with the exception of antibiotic, these designations have not received wide usage. Most investigators have opted to use the general terminology of allelopathic chemicals, or allelochemicals. I feel there are several reasons for the lack of promulgation of the more specific terms. Often the immediate source of a compound involved in allelopathy is obscure. For example, compounds released from higher plants may be altered by microorganisms before the altered substance is contacted by another higher plant. Similarly, it is very difficult to establish the source when a compound of any origin is contacted through the soil medium. A further complication is that the same compound is likely to have multiple roles, affecting different kinds of recipient plants. Alternative usage of these terms has added to the confusion, with antibiotic sometimes designated to encompass any allelopathic chemical (28).

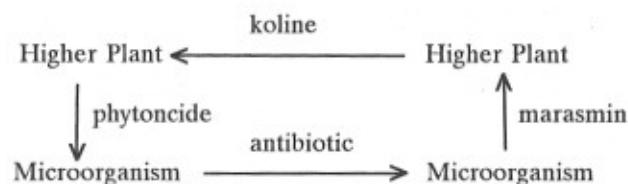


Figure 1. Terms for chemical agents that indicate the type of donor and receiver plants, as shown by the arrows.

While investigators in allelopathy refer to the organic agents that affect the receiving plant as allelochemicals, this term is applied throughout chemical ecology. The active agents in the interorganismic chemical effects involving insects are routinely referenced as allelochemicals. As stated by Reese (29), the context of allelochemicals includes the array of nonnutritional chemicals produced by living organisms that affect the growth, health, behavior, or population biology of other species.

Modes of Release. Higher plants regularly release organic compounds by volatilization from their surfaces and through leaf leachates and root exudates. Since the pioneer work on leaf leachates and root exudates (30-35), an array of literature confirms that plants lose many metabolites as well as allelochemicals. There is compelling evidence that a wide range of allelochemicals present in

seeds contribute to the prevention of seed decay (1,36), and a few experiments illustrate that inhibitors may leach from seeds (37-41). Likewise, even during their limited life span, the various microorganisms do not retain all that they produce. Toxic releases are the mechanisms of action of many fungal pathogens, antibiotic zones improve the success of certain bacteria, and microbial signals lead to some associations.

Eventually, the chemical constituents of all organisms are released to the environment through the processes of decomposition. These decomposition products are often added to the soil matrix. Some are volatile compounds that permeate the air environment of the soil as well as having some solubility in the aqueous phase. Allelopathic effects of *Amaranthus palmeri* residue result from an array of volatile methyl ketones and alcohols (42-46). There is evidence that volatile seed germination inhibitors that include $C_2 - C_{10}$ hydrocarbons, alcohols, aldehydes, ketones, esters, and monoterpenes arise from a variety of weed and crop plants (47,48). The most inhibitory volatile to seed germination tested by Bradow and Connick (48) was (*E*)-2-hexenal, an emission from purple nutsedge (*Cyperus rotundus*) residue.

In addition to allelochemicals, organic releases include many chemicals which either have no negative or positive impacts on an associated plant or these possibilities have not been investigated. For example, methanol appears to be a volatile routinely released from plant leaves and it probably is a carbon source for methylobacteria that colonize leaf surfaces (49,50), yet we have no information about its effects on adjacent plants. In contrast, volatile phytotoxic monoterpenes such as cineole, piene, and camphor have long been reported as allelopathic inhibitors (51-54).

Very little is known about the cellular mechanisms involved in the release of allelochemicals from living tissue, including any modes of regulation or environmental influences on these processes. This area should eventually be a focus of investigation. It will be particularly important to determine the role of environmental factors on the type and quantity of compounds released. Sterling et al. (55) showed that the toxicity of exudates from velvetleaf (*Abutilon theophrasti*) glandular trichomes was twice as high in temperature-stressed plants compared to plants grown under more moderate temperatures, yet the volume of exudate production remained fairly constant. Alsaadawi et al. (56) reported that gamma irradiation of grain sorghum increased the allelopathic activity of future root exudates. A variety of factors appear to affect the amount and chemical content of root exudates (57,58), but generalizations as to how various stresses affect losses of allelopathic compounds into the rhizosphere are premature. Tang and Young (59) developed a trapping system for root exudates that allows collection and subsequent identification of small quantities of novel compounds in the exudate. Coupling techniques like this with a manipulation of plant conditions should provide a better understanding of the interplay between environmental stress and the release of allelochemicals.

In most cases, it is an open question whether escaping allelochemicals are actively exuded or simply passive leakage. Even in chemically influenced mutualism or parasitic associations, little is known about regulation. Parasitism of crop plants by members of the genus *Scrophulariaceae* has been shown to be

facilitated by small amounts of germination stimulants in root exudates, yet whether these exudate compounds are regulated releases is unknown (60). Another challenge is that substances are released from plants which cannot be isolated from the tissue, implicating a transforming role of membrane enzymes. Inhibitory *p*-benzoquinones, known as sorgoleone, are abundant in *Sorghum* root exudates but have not been found in the root tissue (61).

Distance of Transfer. Allelochemical transfers from one higher plant to another in a terrestrial community can be either through volatiles, aqueous leachates, or various exudates. Volatiles may move through the atmosphere from a donor plant to a receiving species; alternatively, these compounds are adsorbed on soil particles and solubilized in the soil solution. Water-soluble allelochemicals leach from shoot tissue into the soil matrix and exudates from roots are a regular occurrence. Hence, spacial movements of allelochemical can be of some distance and they often infer that the soil acts as an allelochemical pool (62). Roots of a receiving plant take up allelochemicals from the soil solution or lipid-soluble compounds adsorbed on soil particles can partition directly into root tissue. As pointed out by Patrick (63), plant residues decomposing in the soil will result in localized regions of higher allelochemical concentrations and the impact of allelochemicals in the soil on a receiving plant often depends on the chance encounters of the root system with such regions.

Our perspective also must be one that recognizes the importance of microclimates and microdistances involved in many interfaces between organisms. This is the case in the rhizosphere where antibiotic effects occur between bacteria that interact for space in colonizing root tissue (10,64,65). Although allelopathy is not a common term in the literature of plant pathology, the actions of disease organisms are frequently mediated by toxins they release that cause chlorosis, necrosis, wilting, or modification of growth (66). The distance of chemical transfer is obviously minute for the numerous pathogenic fungi whose deleterious action comes by release of phytotoxic substances.

Allelochemicals of Allelopathy

Origin and Diversity. With a few exceptions, the allelopathic agents reported from higher plants are secondary compounds that arise from either the acetate or shikimate pathway, or their chemical skeletons come from a combination of these two origins (Figure 2). This is not to suggest that the details of biosynthesis are always known. These compounds do not appear to have central metabolic functions and the more novel ones have limited occurrence throughout the plant world, being absent from the majority of species. Hence, the genetic capacity for their biosynthesis is important to explaining their roles in a plant community.

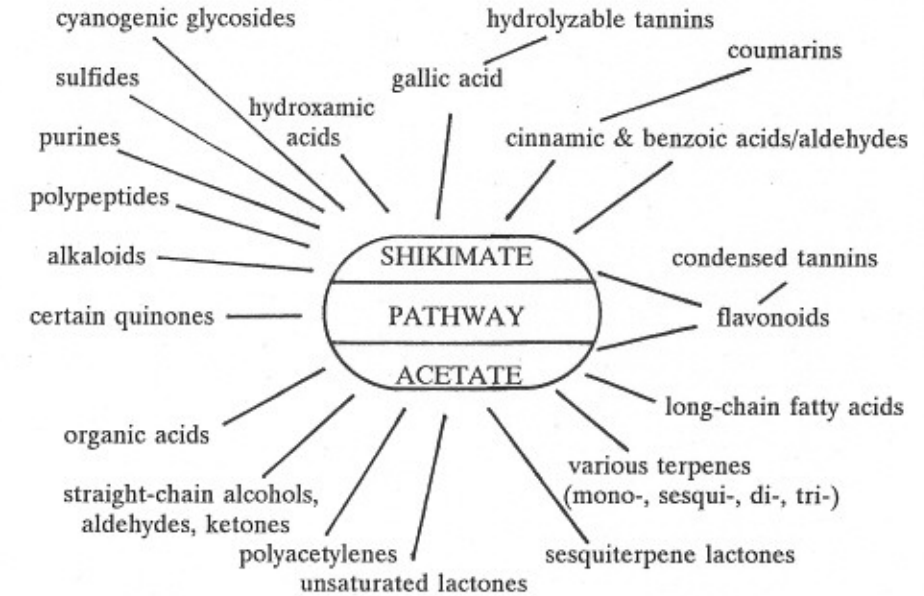


Figure 2. Some of the diversity of allelochemicals implicated in allelopathy. The sketch does not list all classes of allelochemicals and it is not intended to show amino acid intermediates or other pathway details.

Whittaker and Feeny (67) classified allelochemicals into five groups: phenylpropanes, acetogenins, terpenoids, steroids, and alkaloids. Based on chemical similarity, Rice (1) designated 14 categories of allelopathic compounds, plus a miscellaneous group. Although some commonality in the primary pathways of their biosynthesis is evident, there is an extensive diversity of structures among the several hundred known allelopathic chemicals and a review of their chemistry is beyond the scope of this overview.

Activity of Compounds. The range for biological activity of different allelochemicals reported in the literature covers several orders of magnitude. Activity of compounds within a particular chemical class can be quite different and the sensitivity among species and in the numerous bioassay systems varies a great deal. Many coumarins, cinnamic and benzoic acids, flavonoids, monoterpenes, and sesquiterpene lactones affect growth of whole-plant seedlings at thresholds of inhibition between 100 to 1000 μM , but certain ones from these groups have lower inhibition thresholds (68,69). Sorgoleone, a *p*-benzoquinone, is more toxic than most of these phenolics and terpenes, inhibiting seedling growth at 10 μM (70). When tested at the chloroplast level, exposure to 0.1 μM sorgoleone inhibited chloroplast photosynthesis (71). Polyacetylenes also are highly toxic, reducing root elongation of barnyard grass (*Echinochloa crus-galli*) and several other seedlings at 10 ppm or less (72). Relatively few structure-

function studies within chemical classes have been done (69,73), and none have established what mechanisms cause differences in toxicity among compounds in a chemical class. Interestingly, often an inhibitory compound will stimulate growth when its concentration is relatively low.

Allelochemicals Within Plants. Other than their activity in allelopathy, certain allelopathic compounds also have structural or physiological functions within the producing plant. Cinnamic acid, ferulic acid, *p*-coumaric acid, and other phenylpropanoids commonly identified in the phenomenon of allelopathy are intermediates of lignification. Salicylic acid, in my experience the most growth inhibitory of the benzoic acid allelochemicals (74), appears to be an endogenous signal in systemic activation of plant defenses after a localized exposure to certain viral and fungal pathogens (75-77). It does not appear to be a signal compound in response to ultraviolet-C radiation (78). An array of chemicals implicated in allelopathy have protective functions against various disease organisms, insect predation, and other herbivores (79-81), and we should not be quick to dismiss them as of no value to the producing plant.

Mode of Action

Bioassays. The primary tool used to establish allelopathic activity for plant residue, plant extracts, substances in plant releases, or compounds that have been isolated from these sources has been a bioassay. This is a critical step for investigations because answers obtained in a study are intimately tied to the sensitivity of the test system employed. The range of bioassays include effects on seed germination, radicle elongation, whole-plant growth, microbial numbers, or some functional process (82-84). In spite of advances in analytical chemistry, these techniques cannot determine biological responses and bioassays will continue at the heart of studies in allelopathy.

Bioassay results are altered by solubility of the allelochemical, the relative amount of the chemical to bioassay tissue, and numerous environmental conditions (85-88). Investigators frequently use several different assays in a screening procedure. We have employed a whole-plant *Lemna* bioassay because it is applicable with a small quantity of putative allelochemical and has sensitivity to effects on a range of physiology process (74,89).

Physiological Effects. A major future challenge is to determine the mechanisms of action of allelochemicals. At present, we know that the coumarins and phenolic compounds derived from cinnamic and benzoic acids interfere to some degree with many vital plant processes, including cell division, mineral uptake, stomatal function, water balance, respiration, photosynthesis, protein and chlorophyll synthesis, and phytohormone activity (68, Einhellig, this book). No clear separation of primary from secondary effects has been possible, but membrane perturbations may be a starting point for the multiple actions of these compounds. Information on the physiological effects and possible mode of action for other groups of allelochemicals on higher plants is even more embryonic.

One of the greatest deficits in our knowledge about allelochemical activity is an explanation for differences in species sensitivity to these compounds. A large seed size or seedling biomass may explain why some species are more tolerant than species with smaller seeds or biomass. However, physiological mechanisms that can explain differences in sensitivity have seldom been investigated.

Activity of allelochemicals against plants is often indirect through inhibition of the growth of microbial symbionts. Suppression of fungal-root colonization hinders water and nutrient absorption, slowing growth and perhaps contributing to delays in reforestation or decline problems in perennial crops (90-92). The sensitivity of *Rhizobium* spp. to allelochemicals leads to poor nodulation and subsequent reduction in nitrogen available to legumes growing in association with allelopathic plants or residue (93,94). There is even a more indirect affect on higher plants as allelochemicals inhibit free-living nitrogen-fixing bacteria and blue-green algae, thus disrupting the nitrogen cycle and having ramification for mineral nutrition. Allelochemicals from higher plants have been reported to alter microbial respiration (92), but for the most part their mode of action is unknown. On the other hand, mechanisms for certain antibiotics are well characterized.

The challenge to explain how allelochemicals act is complicated by the many chemical classes and array of different structures identified as agents in allelopathy. There is no generic allelochemical, and certainly we should anticipate different mechanisms of action among allelopathic chemicals. In many instances, the lack of a sufficient quantity of a substance for study is a hindrance to elucidating its mechanism or mode of action. Further advancements in isolation and purification procedures and synthesis of natural products are critical to pushing the frontiers on compound uptake, transport, and function. Likewise, information on how they alter growth is central to explaining differences in species sensitivity to allelopathy. These mode of action questions are among several keys to exploring the use of allelochemicals or avoiding their detrimental effects in agroecosystems.

Stress Combinations

It is important to recognize that the allelopathic phenomenon is not independent of other stresses. Allelochemical and environmental stress act in concert to affect plant growth. More work is needed on stress interactions, but there is sufficient data to conclude that both the production and impacts of allelochemicals are susceptible to other conditions in the environment (95,96). In this paradigm, stresses such as moisture and temperature conditions not only directly affect plant growth, they may enhance allelochemical production which subsequently impacts the growth of associated plants. A further coupling of allelopathy with environmental stress is apparent as effects of allelochemicals are greater when a plant is also stressed by other environmental conditions.

Quantity of Allelochemicals. Some of the pioneer investigations of effects of abiotic stress on allelochemicals demonstrated that coumarins, such as scopoletin

and scopolin, in tobacco and sunflower increased in response to herbicide, nutrient, temperature, and radiation stresses (97). Similarly, Hanson et al. (98) found barley (*Hordeum vulgare*) alkaloids increased when plants were grown under high temperature. Moisture stress caused an increase of allelopathic monoterpenes in *Pinus taeda* and cyclic hydroxamic acids in corn (*Zea mays*) (99,100). On the other hand, aspen tissue culture plantlets grown under water stress had lower levels of catechol, salicortin, and salicin (101). Hall et al. (102) found nutrient deficiency enhanced the allelopathic activity of sunflower (*Helianthus annuus*) debris and this was attributed to modification in total phenolic compounds. Nutrient and water stresses appear to favor a general increase in secondary plant metabolites (103). There are many reports on the increased production of secondary metabolites, particularly a variety of phenolics, in plants damaged by insect or disease (26,79). While it appears that both abiotic and biotic stresses often stimulate production of certain allelochemicals, research is needed to determine what plants and which secondary compounds exhibit this type of plasticity, the conditions that will induce an accumulation of allelochemicals, and any quantitative or qualitative changes in these compounds found in leachates and exudates due to stress.

Allelochemical Plus Nonallelochemical Stress. Plants are regularly subjected to environmental conditions that are less than optimal, and these collective stresses may interact in additive, synergistic, or antagonistic ways (96). Temperature, moisture, nutrient, herbicide, and disease stresses are common. Einhellig and Schrich (88) found grain sorghum (*Sorghum bicolor*) and soybean (*Glycine max*) were more susceptible to damage from ferulic acid when they were grown at temperatures at the higher end of the plant's range of tolerance. Soybean seedlings grown with a day temperature of 23° C were not affected by 100 μ M ferulic acid in the culture medium, but plants grown at 34° C were significantly inhibited even though the temperature difference by itself had no effect on growth. Similarly, under laboratory conditions almost any degree of water stress seems to lower the ferulic acid-inhibition threshold on germination or seedling growth (96). In some cases the pathogenesis of disease organisms, such as root rot fungi, is increased by allelopathic effects from decomposing plant residue (104-106).

Data from my laboratory indicated that herbicide stress from atrazine and trifluralin works in concert with allelopathy to impair seedling growth (95,96). This type of interaction is a very important area for future investigation in view of weed control strategies designed to reduce herbicide inputs.

When allelochemicals enter the soil, microbial transformations often occur or their biological activity may be altered as they are adsorbed on soil particles. Yet the impacts of these phenomena and other interactions in the soil on allelopathy are not well understood. Recently, Blum et al. (107) reported that the amount of nitrates and other organic carbon sources in the soil modified the allelopathic action of *p*-coumaric acid. Higher levels of nitrate increased the amount of *p*-coumaric acid required to reduce growth of morning-glory (*Ipomoea pedunculata*), but elevated glucose or methionine in the soil reduced the concentration for growth inhibition. This interaction with soil carbon shows a

new dimension in allelopathy-environmental interrelationships and it illustrates the need for data that will help predict the influence of the soil matrix on allelopathy.

Combinations of Allelochemicals

In my opinion almost all cases of allelopathic inhibition in a plant community result from the combined effect of a several compounds. Perhaps the action of juglone in black walnut (*Juglans nigra*) allelopathy may be one of a few rare exceptions (108), but even then I suspect other allelochemicals make a contribution.

Einhellig (96) reported the joint action of 50 μ M each of ten benzoic acid allelochemicals was generally as inhibitory to the growth of velvetleaf (*Abutilon theophrasti*) as 500 μ M of a single compound. As is a common reality when comparing molecular derivatives of a particular chemical class, certain of these phenolic acids were more toxic than others. A review of investigations on phenolic acids, alkaloids, sesquiterpene lactones, monoterpenes, and volatile fatty acids, volatile methyl ketones and alcohols indicates that when several compounds are present together their inhibitory action will either be additive or sometimes synergistic, depending on the relative concentrations of the allelochemicals (96,109).

In the 1980s, the challenge went out to develop more specific proofs of allelopathy by adhering to a specific protocol like Koch's postulates for demonstrating pathogenicity (106,110,111). A cardinal point was to isolate and identify the chemical(s) responsible. Unfortunately, critics of the science of allelopathy have often formulated their questions in terms of the amount, presence, and biological activity of a specific allelochemical. Such questions do not fit with the reality that case histories repeatedly show several compounds implicated as the agents in the allelopathic action of a particular situation, and they do not recognize interactive effects with other stresses. The bias that carried over from Koch's rules also has frustrated work in allelopathy by not enough attention being given to disease and abiotic stresses that complement allelopathy.

Impacts on Ecosystems

Allelopathy influences vegetational associations and patterns, succession, invasion of exotic plant species, nitrogen fixation, seed preservation, the extent of disease and other dynamics of natural plant communities. Although terrestrial ecosystems have been the focus of most of the investigations, allelopathy occurs in aquatic ecosystems as well. Occasionally the role of allelochemicals dominates, but more often it is a subtle, difficult to measure component of community relationships. The case studies chosen to illustrate the capacity of plant chemicals to influence community relationships not only show the direct action of allelochemicals on higher plants, they also illustrate effects on microorganisms that subsequently impact the vegetational community.

Vegetational Patterns. The most visual evidences of allelopathy in natural communities are instances of bare-looking areas, a "halo" zone, around a plant or stand of one type of vegetation. This effect has been intensely scrutinized in the chaparral of southern California and in the sand pine scrub community of Florida's central ridge and costal dunes.

The classic studies on the zonation of vegetation in the chaparral showed *Salvia leucophylla*, *Artemisia californica*, and other aromatic shrubs release a variety of volatile terpenes that solubilize into the leaf cuticle of associated species or adsorb on soil particles from which they may later transfer into root tissue of seedling that will try to establish in proximity to the shrub (53,112). Water-soluble phenolic acids are leached from leaves of these and other shrubs, adding to the complex of inhibitory allelochemicals that will be encountered by the associated herb and grassland vegetation. Annual grasses are sensitive to these allelochemicals and the net result is a border zone of sparse vegetation near the shrubs that may wax and wane to some degree with seasonal precipitation. As pointed out by Halligan (113), the situation is complicated by moisture conditions, mammals, and other factors interacting with the chemical environment to create the vegetational pattern.

In Florida, sharp ecotones often marked by persistent bare zones exist between the sandhill and pine scrub communities, and there is little ground cover under the scrubs. Both allelopathy and fire cycles appear to contribute to vegetational patterns associated with the scrubs (114-117). Grasses are excluded from the immediate vicinity of *Polygonella myriophylla* (118). *Ceratiola ericoides* and several of the other early scrub colonizers also inhibit grasses. A variety of allelochemicals have been implicated in this activity. For *C. ericoides*, these include mono-, di-, and triterpenes and several flavonoids (115-117). Ceratiolin, a novel flavonoid, may be among the more important compounds since it degrades by photochemical action to produce the very toxic hydrocinnamic acid. It appears that allelopathy interacts with other environmental stresses to generate some discreteness to the distribution of the vegetation in the pine scrub community.

Succession. Rice and coworkers at the University of Oklahoma provided the most comprehensive documentation of allelopathy in succession (1). Their studies focused on the sequence of natural succession after fields of low fertility in Central Oklahoma had been abandoned. These "old fields" revegetated with a 2 - 3 year period of robust, annual weeds, followed by an extended period of perhaps a dozen years wherein an annual grass, triple awn grass (*Aristida oligantha*), dominated. This second stage of succession eventually gave way to an abundance of the prairie bunchgrass, little bluestem (*Schizachyrium scoparius*). If left undisturbed long enough, succession reached a stable mixture of the true prairie grasses.

Investigations in the 1960s and 1970s established that the short tenure of the weed stage was a case of autotoxicity. These weeds, *Helianthus annuus*, *Ambrosia psilostachya*, *Sorghum halepense*, *Digitaria sanguinalis* and others, released chemicals which reduced their ability to survive, while the second-stage triple awn grass was more tolerant to this chemical environment (119-122).

Scopoletin, chlorogenic acid, tannic acid, and many of the phenolic derivatives of cinnamic and benzoic acid were identified as causative agents. Improvement in nitrogen availability was slowed during the early successional stages because allelochemicals from the first stage weeds and triple awn grass suppressed nitrogen fixation by blue-green algae and both free-living and nodulating bacteria (93,123). As a low nitrogen-requiring species, triple awn grass was favored. While activity of nitrifying bacteria was somewhat affected by allelochemicals early in succession, further work suggested that plants of the climax community were more allelopathic to nitrification and caused retention of a higher percentage of available nitrogen in the ammonium form (124-126). The kind of plant material added to soil markedly affected the kinds and numbers of microorganisms; soil invertase, amylase and cellulase activity also decreased with progression of old-field succession (127).

The studies that have been cited on succession and patterning of vegetation pioneered valuable techniques in allelopathy. These include (a) extensive use of bioassays for detection of allelochemical activity, (b) use of bioassay species relevant to the field situation, (c) isolation and identification of putative allelochemicals, and (d) a variety of experimental designs to isolate allelopathic from competitive interference. There continues to be considerable allelopathy work on the roles of certain species in community dynamics.

Seed Preservation. The mechanisms of how seeds can remain viable many years in the soil without destruction by decay organisms are still not well understood. However, there is abundant evidence showing allelochemicals in the seed coat and other seed tissue are a deterrent to microbial action and in some cases these compounds help regulate when germination can occur (1,36). Investigations are needed to evaluate the extent to which allelochemicals exit and form a localized sphere of influence around seeds.

Agricultural Ecosystems

Productivity of agricultural fields, including pasture land and agroforestry environments, is routinely influenced by allelopathy. The source of allelochemicals may be either the crop, weeds, or microorganisms of the decomposition processes (62,128). Alternately, any of these groups could be the affected species and allelochemical transformations in the soil always complicate our insights. Even though a variety of scenarios are possible, it is the net effect on crop yield that has been a primary concern. As shown in this book and other literature (6), agricultural allelopathy issues have drawn the attention of scientists from many regions of the world. A few specific examples will be used to illustrate the range of allelopathic impact on the agricultural economy.

Weed Interference. Since weeds are a major cause of yield losses, the aggressive growth habits of some of the most tenacious species have come in for scrutiny. Putnam and Weston (129) listed 90 species that show allelopathic potential and others have been reported since then. The data implicate some of the world's worst weeds in allelopathy, including ragweed parthenium (*Parthenium*

hysterophorus) (130), quackgrass [*Elytrigia repens* (L.) Nevski (*Agropyron repens*)](129,131), Johnsongrass (*Sorghum halepense* (42,119), Canada thistle (*Cirsium arvense*)(132) and giant foxtail (*Setaria faberi*)(133).

The most complete investigations on weeds have tied field-based evidence with a search for allelochemicals. *Parthenium hysterophorus*, a tropical weed endemic to America, has done great damage since arriving as an exotic to the India landscape and other places. Numerous reports of the last two decades document the phytotoxicity of its living and decomposing tissue, leachates, and root exudates (134-137). Effects on the receiving crop plants and other weeds include reductions in chlorophyll, water uptake, nutrient uptake, and legume nodulation. Several sesquiterpene lactones, phenolic acids, and organic acids have been identified as the responsible agents.

Quackgrass is a second example where multiple investigations spread over many years have elucidated toxicity problems. Decomposing residues and foliage and rhizomes of living plants all reduce crop growth. Putnam and Weston (129) found quackgrass residues left on the surface in no-till systems reduced the biomass of eight crop species tested by at least 50%, with alfalfa (*Medicago sativa*) and carrot (*Daucus carota*) reduced more than 90%. Quackgrass inhibited legume nodulation, crops associated with living quackgrass exhibited symptoms of mineral deficiency, and added fertilizer did not solve the problem. These examples show there is a need for awareness of allelochemical toxicity in residue management practices.

Allelopathy of Crops. Some of the major agronomic crops produce allelochemicals which can affect weed growth, result in autotoxicity, or influence growth of the next crop (128). Sunflower (*Helianthus annuus*), *Sorghum* crops, and rye (*Secale cereale*) are perhaps the better documented examples of both living biomass and residue allelopathy, albeit a number of other crops could be cited. Although allelochemical production and activity is apparent in crop plants, it has been postulated that through the processes of domestication and plant breeding for yield parameters the current crop varieties are less capable of producing allelochemicals than ancestral germplasm. This hypothesis has important implications for more sustainable agricultural practices that are being demanded, yet it needs more rigorous testing. Supporting data was obtained on cucumber (*Cucumis sativus*) and oat (*Avena sativa*)(138,139). Some accessions of oats produced three times as much scopoletin as a standard cultivar and the former provided better weed control. However, varietal differences in allelopathic potential were not shown when comparing a number of sunflower cultivars (140,141).

Crops Affect Weeds. It is more than a tantalizing idea that crop plants may provide their own herbicides---some do, but modern agriculture has seldom acted on this reality. Leather (141) reported that sunflower grown without a herbicide had no more weed problems than when a herbicide was employed. Our three years of field data from eastern Nebraska demonstrated that grain sorghum greatly reduced weediness in the next growing season (142). When grain sorghum was strip cropped with corn and soybean, weed biomass where *Sorghum*

had previously grown was reduced by more than 50% compared to the other two crops. Since that data was reported, I have had personal communication from several agronomist indicating they have observed the weed suppressing action of grain sorghum. I project the mechanism of *Sorghum* action is a combination of phenolic allelochemicals, cyanogenic glycosides, and sorgoleone (Einhellig, this book).

Crop Autotoxicity. Grain sorghum and sunflower yields show a marked decline when these crops are replanted year after year, and to a lesser extent this is seen with wheat (*Triticum aestivum*), rice (*Oryza sativa*), corn, and several others (128). Proper crop rotations can avoid this pattern and sometimes stimulatory effects are obtained from the rotation. Production of alfalfa and other perennial legumes diminishes due to autotoxicity, and immediate replanting in the same field is problematic. The alfalfa replant problem has been controversial and certainly unique factors may be involved according to local conditions, but my experience (143,144) fits with the allelopathy scenario proposed by Miller (145).

Agroforestry. Lichens, a variety of understory vegetation, and many weeds contribute to regeneration problems in managed forestry systems. Either direct or indirect allelopathic effects are often part of the complexities in regeneration failure (146,147). Indirect effects on mycorrhizal fungi and organisms of the nitrogen cycle appear to be particularly important (147,148). Economic realities of allelopathy in black walnut (*Juglans nigra*) plantations show a different dimension. When a nurse crop of black alder (*Alnus glutinosa*), a tree species forming a microbial nitrogen-fixing association, was interplanted with walnut to improve fertility, the alder eventually died due to the black walnut toxicity (108,149).

Applications of Allelopathy

Modern agriculture is challenged to reduce environmental damage and health hazards from chemical inputs, minimize soil erosion, and yet maintain a high level of production (150). Strategies capitalizing on allelopathy can help in efforts toward this ideal of a more sustainable agriculture (128,151). The actions of allelochemicals should be a consideration in crop rotations, residue management, tillage practices, and implementation of biological control. Opportunities also exist for alteration of crop genomes to enhance production of herbicide and pesticide constituents, and direct commercial uses of allelochemicals may be feasible.

Field Strategies. After several decades of limited advocacy, crop rotations are again being promoted and these decisions need to recognize allelopathic activity. Although specific effects must be worked out for local regions, the weed suppressing action of *Sorghum* spp. (142), sunflower (141), and other crops can reduce the use of herbicides both in the crop year and subsequent year. Similarly, cover crops and residues of rye, oats, barley, wheat, grain sorghum,

and sudangrass (*Sorghum arundinaceum*) are effective in limiting weed growth (151-157). Scenarios for using these crops for weed control include (a) their direct suppression of weed populations when they are the harvested crop, (b) their use as a ground cover in orchards with subsequent desiccation from freezing or a herbicide, (c) double cropping into the stubble and surface residue left from such a crop, and (d) a crop rotation with no-till planting in the year following an allelopathic crop.

Another approach is to coplant a weed control crop simultaneously with a production crop. However, we found when rye and soybean were seeded together the living rye depressed soybean yield (158). The risk of interference from the weed control crop must be evaluated in any management strategy. Interplanting of two or more harvestable crops is another way to take advantage of natural product-mediated weed and pest control (159). Gliessmann (160) reported that some combinations of interplanted crops, as well as allowing "good weeds" to persist, can enhance yield and reduce the reliance on chemical control measures. Peach growers in southeastern United States have found a reduction in nematode problems when they interplant wheat in their orchards (161).

If allelopathy only provides a partial control of weed populations, some combination of allelopathy management along with herbicides may be desired. The complementary action of natural phytotoxins and herbicides has received very little attention, but there is some indication that their additive action would justify a reduced level of herbicide input (95,96). Since control of weeds and pests is the key issue to any of the management options mentioned, the strategies can be employed without a complete understanding of the interference mechanisms.

Market Products. A few allelochemicals or products that have a functional basis in allelopathy have been marketed and a number of companies are actively pursuing programs focused on these opportunities. These include screening for and isolation of biological active allelochemicals, modification and development of natural products as herbicides, efforts to formulate and market growth-enhancing microorganisms, and ways for expanded use of biological control.

Protectants and Stimulants. DeFreitas and Germida (65,162) found applications of certain pseudomonads promoted winter wheat growth and they indicated antibiosis towards phytopathogens may be part of the mechanism. Chemical signals also may be involved in the initial colonization. Agrochemical companies have recognized the value of seed-applied inoculants and plant growth-promoting rhizobacteria which colonize roots and enhance aspects of plant growth. Quantum 4000 and Kodiak, marketed by Gustafson, Inc., are seed-treatment biological fungicides which contain *Bacillus subtilis*. This beneficial bacteria takes root space from pathogens and it has been suggested that antibiotic production may be involved (64,163). These products have been used on cotton (*Gossypium hirsutum*), peanuts (*Arachis hypogaea*), soybean, and several other beans. Stanley (161) reported ISK Biotech Corporation is developing a strain of *B. subtilis* for protection against brown rot fungus (*Monilinia fructicola*) on peaches and grapes.

Biological Herbicides. The success of two mycoherbicides marketed several years ago, Collego and DeVine (164,165), fostered an expansion of efforts in this direction. These mycoherbicides control northern jointvetch (*Aeschynomene virginica*) and stranglevine (*Morrenia odorata*). DeVine contains a strain of the fungus *Phytophthora palmivora* that kills stranglevine, although it is not known for certain that toxic substances are involved.

A range of viral, bacterial, and fungal pathogens are being tested as biological control agents against specific target weeds. I have no doubt that research will eventually establish that the action of some of these biological herbicides is mediated by chemicals they produce. The use of higher plants, including noncrop plants, to control weedy species has received much less attention, but this avenue needs exploration. Leafy spurge (*Euphorbia esula*), the worst rangeland weed of the United States northern plains, does not encroach into areas with small everlasting (*Antennaria microphylla*), perhaps due to the sensitivity of leafy spurge to hydroquinone and other substances produced by small everlasting (166,167).

Natural Product Herbicides. The thousands of secondary compounds produced by plants and microorganisms provide an amazing diversity in chemical structures which offer opportunities for new herbicides, pesticides, growth stimulants, or growth regulators (168). Isolating and testing compounds for biological activities is an ongoing endeavor of several agrochemical companies. Important insecticides have their basis in natural products, but gaining herbicides from plant and microbial sources has been more difficult. On balance, microbial compounds appear to have greater potential as herbicides than do many of the allelochemicals from higher plants (169-174). Microbial compounds are often more selective and have higher phytotoxicity. Of the many natural-product compounds with herbicidal activity, only two discovered from nonpathogen bacteria are currently marketed; bialaphos, a tripeptide, and glufosinate, a phosphonate amino acid analog.

The chemistry of natural product isolation and identification is complicated, screening bioassays to detect active compounds are problematic, and many barriers challenge the synthesis and production of the more complicated structures. Nevertheless, it is likely that allelochemicals will provide some useful products to aid crop production. The hope is that these compounds will be less toxic to nontarget organisms and, have a shorter residence time in the environment.

Future Directions and Challenges

Certain aspects for the future of allelopathy are a replay of the past; that is (a) in-depth autecological studies on species, (b) evaluation of allelopathy in plant associations and crop production (c) isolation, identification and characterization of allelochemicals, (d) efforts to determine mechanisms of action, (e) learning more about soil transformations and residence times, and (f) continuation of work on practical applications for allelochemicals and the allelopathic phenomenon. However, I anticipate a much stronger focus on the

last point, including all the chemistry, biotechnological manipulations, and field management strategies this will entail. More scrutiny also will be given to allelochemical activity in disease and defense roles, including chemical communications from one plant to another. The role of chemicals as control factors in plant-microbe and host plant-parasite association will be more fully explored. Finally, advances in biological control programs will evolve in concert with a better understanding of the role of allelopathy in these interactions.

In summary, the pervasive involvement of plant-produced chemicals in plant-plant and plant-microorganism interactions provides many challenging frontiers. This science has the potential to contribute greatly to agricultural production and stability. It should be no surprise that many of the chapters in this book are focused on agroecosystem problems and ways to capitalize on allelopathy. These include some specifics on weed interference, tillage practices, rotations, studies on specific agronomy systems, parasitic plant-host plant communications, and a number of perspectives on problems and approaches to biological control. Topics in this book also address findings on a few specific chemicals, how allelochemicals function, stress interactions, and other issues that have only been touched on in this overview chapter. Collectively, they provide valuable insights into allelopathy and the functions of allelochemicals.

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