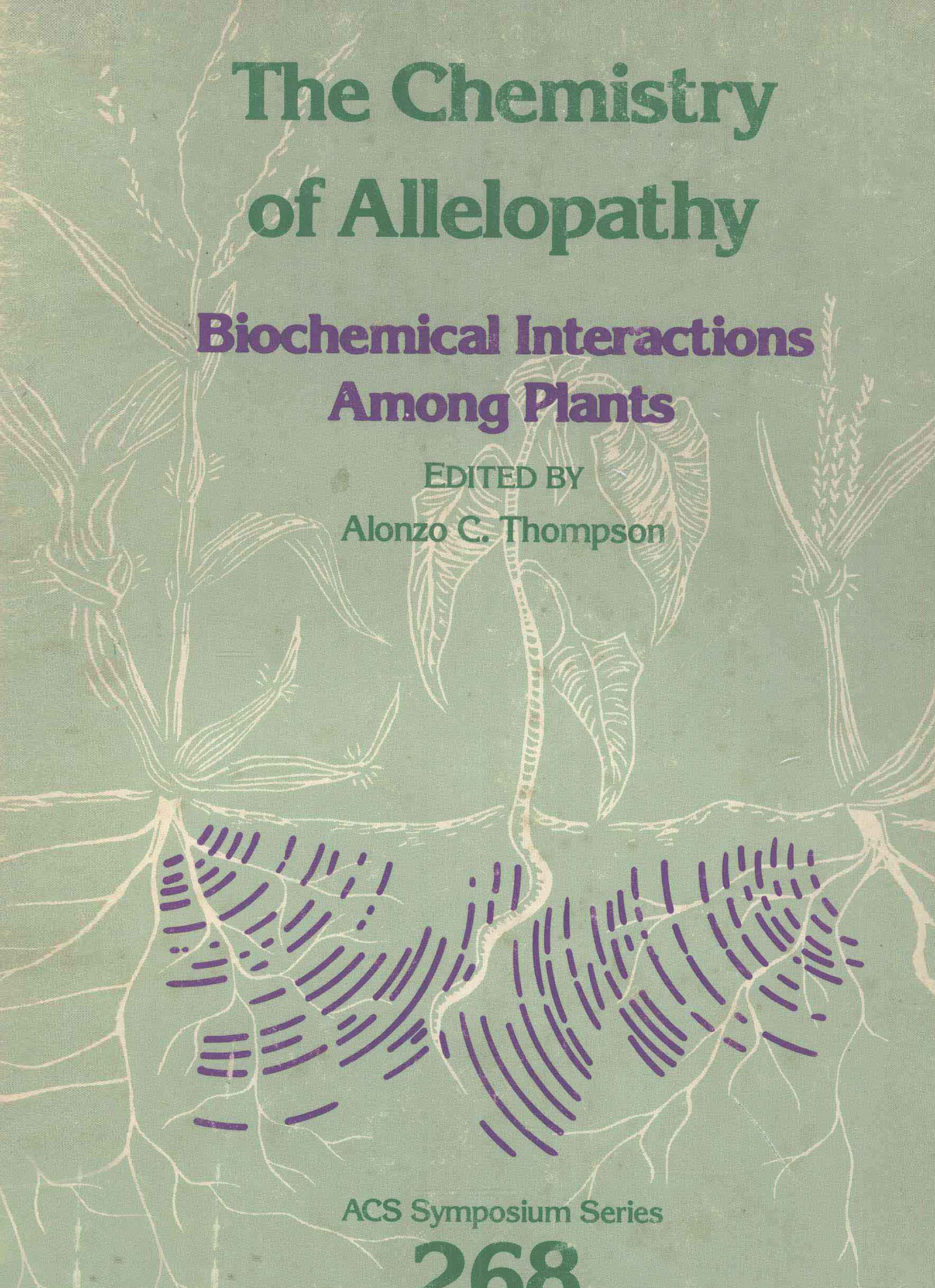
The Chemistry of Allelopathy

Biochemical Interactions Among Plants

EDITED BY

Alonzo C. Thompson



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The Chemistry of Allelopathy

Biochemical Interactions Among Plants

Alonzo C. Thompson, EDITOR
U.S. Department of Agriculture

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FOREWORD

The ACS Symposium Series was founded in 1974 to provide a medium for publishing symposia quickly in book form. The format of the Series parallels that of the continuing Advances in Chemistry Series except that in order to save time the papers are not typeset but are reproduced as they are submitted by the authors in camera-ready form. Papers are reviewed under the supervision of the Editors with the assistance of the Series Advisory Board and are selected to maintain the integrity of the symposia; however, verbatim reproductions of previously published papers are not accepted. Both reviews and reports of research are acceptable since symposia may embrace both types of presentation.

PREFACE

THE CLASSIFICATION OF CHEMICAL SUBSTANCES as allelopathic agents requires bringing together the talents of several scientific disciplines. Biologists have obtained a large mass of evidence that documents the presence of substances produced by one plant that interfere, in some way, with the growth of another plant. However, the relationship is not a straightforward, one-step process. As in most natural cause-and-effect observations, we are dealing with a diverse process, including environmental conditions, acting upon plants to produce a given result. We can often measure the results, but we have difficulty isolating which parts are exerted by the individual components in producing those results. Generally, our studies and understanding tend to be based on research of an individual organism.

Through the years, natural product chemists have isolated, identified, and synthesized from plants many compounds that have been subsequently used by the biochemist to establish biosynthetic pathways. Through this cooperative effort, much has been learned about how plants grow and about the mechanisms that mediate growth. These disciplines, however, are closely related; and the respective scientists have little difficulty in understanding one another. A working relationship must be developed between the biologist and chemist to elucidate the biological–chemical relationships of possible allelopathic substances. This relationship necessitates that each become, to some degree, knowledgeable about the other's work.

Once biological activity has been established (in the laboratory or the field) and once the chemical work has been accomplished, we need to confirm allelopathic activity in the natural environment. To accomplish this end, the effects of soil and microbial flora must be considered. Thus, the disciplines of soil chemistry and microbiology are required. The chapters in this volume deal primarily with the biology and chemistry of phytotoxins isolated from plants; however, we hope that these topics will stimulate soil chemists and microbiologists to contribute to solving the problems associated with the study of allelopathy. Thus, the purpose of this volume is not only to bring before the scientific community a representation of research efforts in the area of allelopathy, but also to promote the relationships among the scientific disciplines required to solve and utilize this natural phenomenon for our benefit.

As editor, I am grateful to the authors for their contributions and to the U.S. Department of Agriculture for its support of this effort.

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June 1984

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1

Allelopathic Research in Agriculture
Past Highlights and Potential

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Allelopathy produces marked impacts in diverse terrestial and aquatic ecosystems including influences on plant succession and patterning, inhibition of nitrogen fixation and nitrification, and inhibition of seed germination and decay. There are two major challenges to agricultural researchers: To minimize the negative impacts of allelopathy on crop growth and yield, and to exploit allelopathic mechanisms as additional pest control or crop growth regulation strategies. Plant products, microbial products, or their synthetic analogs could comprise the next generation of pesticides and growth regulaators. Joint efforts of chemists, plant physiologists, microbiologists, ecologists, and perhaps others, will be required to achieve maximum progress in this endeavor. Allelopathy research offers unlimited opportunities to solve practical agricultural problems and to contribute fundamental knowledge regarding the chemistry and biology of interspecific relationships.

The term allelopathy was coined by Molisch in 1937 (1). Presently, the term generally refers to the detrimental effects of higher plants of one species (the donor) on the germination, growth, or development of plants of another species (the recipient). Allelopathy can be separated from other mechanisms of plant interference because the detrimental effect is exerted through release of chemical inhibitors (allelochemicals) by the donor species. Microbes associated with the higher plants may also play a role in production or release of the inhibitors (2).

Allelopathy is included among a higher-level order of chemical ecology involving interactions among many different organisms. Whittaker and Feeny (3) have defined interspecies

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allelochemic effects and classified allelochemicals on the basis of whether the adaptive advantage is gained by the donor or recipient. Allomones, which give adaptive advantage to the producer include repellants, escape substances, suppressants, venoms, inductants, counteractants, and attractants. Allelopathic chemicals may be classified as suppressants. Some inhibitors from plants may also induce intraspecific effects (autotoxicity).

Impacts in Agroecosystems

The fact that allelopathy can exert detrimental impacts on agriculture was apparently recognized by Democritus and Theophrastus in the fifth and third century BC respectively, by deCandolle in 1832, and more recently by many ecologists and agronomists (4, 5). Allelopathy has been related to problems with weed:crop interference (6), with phytotoxicity in stubble mulch farming (7), with certain types of crop rotations (8), and with orchard replanting (9) or forest regeneration (10). In some alleged allelopathic interactions, it is not clear whether reduced crop growth is a direct result of released toxins, or whether the toxins precondition the crop plant to invasions by plant pathogens. Rice (4) indicated that allelopathy may contribute to the weed seed longevity problem through at least two mechanisms: chemical inhibitors in the seed prevent seed decay induced by microbes or inhibitors function to keep seed dormant, although viable for many years.

There is extensive evidence that allelopathy may contribute to patterning of vegetation in natural ecosystems (11). Distinct zones of inhibition are present under and adjacent to a variety of woody species, and often toxins from their litter are implicated (12). One might speculate that aggressive perennial weed species quickly gain dominance by exploiting allelopathic mechanisms.

Sources of Allelopathic Chemicals

Chemicals with allelopathic potential are present in virtually all plant tissues, including leaves, stems, roots, rhizomes, flowers, fruits, and seeds. Whether these compounds are released from the plant to the environment in quantities sufficient to elicit a response, remains the critical question in field studies of allelopathy. Allelochemics may be released from plant tissues in a variety of ways, including volatilization, root exudation, leaching, and decomposition of the plant residues.

Reports on volatile toxins originate primarily from studies on plants found in more arid regions of the world. Among the genera shown to release volatiles are *Artemisia*, *Eucalyptus*, and *Salvia* (4). When identified, the compounds were found to be mainly mono- and sesquiterpenes. Work of Muller and associates (13) has indicated that vapors of these compounds may be absorbed by surrounding plants, and that the chemicals can be absorbed from condensate in dew, or by plant roots after the compounds reach the soil.

A myriad of compounds are also released by plant roots (14). The compounds are probably actively exuded, leaked, or they may arise from dead cells sloughing off the roots. Much of the evidence for root-mediated allelopathy has come from studies where nutrient solutions cycled by the root systems of one plant are added to media containing the indicator species. A recent study by Tang and Young (15) successfully utilized an adsorptive column (XAD-4) to selectively trap organic, hydrophobic root exudates while allowing nutrient ions and other hydrophillic compounds to pass through. They identified 16 compounds exuded from the roots of Bigalta limpograss (Hemarthia altissima) including a variety of benzoic, cinnamic, and phenolic acids.

A variety of chemicals may be leached from the aerial portions of plants by rainwater or by fog-drip (16) including organic acids, sugars, amino acids, pectic substances, gibberellic acids, terpenoids, alkaloids, and phenolic compounds. Colton and Einhellig (17) suggested that leaf leachates of velvetleaf (Abutilon theophrasti) may be inhibitory to soybean (Glycine max). We have recently discovered specialized hairs on the stems of velvetleaf plants which exude toxic chemicals.

After death of the plant, chemicals may be released directly by leaching of the plant residues. A variety of compounds may impose their toxicities additively or synergistically. Along with direct release of compounds from the tissue, microbes in the rhizosphere can produce toxic compounds by enzymatic degradation of conjugates or polymers present in the plant tissue. Examples of this phenomenon are the action by microbes on the cyanogenic glycosides of Johnsongrass (Sorghum halepense), and Prunus species to produce toxic HCN, and the corresponding benzaldehydes (18).

The toxicity arising from plant residues undoubtedly provides some of the more challenging problems and opportunities for agronomists, horticulturists, and weed scientists. Where stubble-mulch farming has been practiced in the plains states for soil and water conservation, toxins from the stubble have proven toxic to certain rotational crops (7). Now in agriculture there is a movement to employ conservation tillage (including no-tillage) practices which preserve surface plant residues. Not only can these residues have an influence on crop emergence, growth, and productivity, but they can also influence similar aspects of weed growth. Our recent work indicates that management of selected crop residues can greatly reduce weed germination and growth (19).

Natural Products Identified as Allelopathic Agents

Inhibitors from plants and their associated microbes represent a myriad of chemical compounds from the extremely simple gases and aliphatic compounds to complex polycyclic aromatic compounds.

The compounds implicated in allelopathy have been divided into chemical classes by recent reviewers (4, 20). They can be arbitrarily classed as (A) hydrocarbons, (B) organic acids and aldehydes, (C) aromatic acids, (D) simple unsaturated lactones,

(E) coumarins, (F) quinones, (G) flavonoids, (H) tannins, (I) alkaloids, (J) terpenoids and steroids and (K) miscellaneous and unknowns. Although many of these compounds are secondary products of plant metabolism, several are also degradation products which occur in the presence of microbial enzymes.

New chemicals are constantly being isolated from plants and microorganisms daily. Swain (21) recently reported that over 10,000 low-molecular weight products have already been isolated from higher plants and fungi. In addition, he proposed that the total number might approximate 400,000 chemicals. Some of these chemicals or their analogs could provide important new sources of agricultural chemicals for the future. There is considerable interest within the agricultural chemical industry on at least two approaches involving allelochemics for weed control. One involves the development of crop cultivars (perhaps through genetic engineering) which can either themselves suppress associated weeds or provide sources of natural product herbicides or their precursors. Another approach is to produce natural herbicides through batch culture with microorganisms.

Challenges in Allelopathy Research

Although allelopathic interactions have been observed for centuries, the science of allelopathy is in its infancy. Much needs to be accomplished, and it will require joint efforts of scientists from several disciplines. Although by no means a complete list, the following areas need intensive study.

Improved Methods for Collection, Bioassay, Isolation, and Characterization of Compounds. Techniques used to characterize natural products are evolving rapidly as more sophisticated instrumentation is developed. Plant physiologists and chemists should work closely together on this aspect, since rapid and reproducable bioassays are essential at each step. There is no standard technique that will work effectively for every compound. Briefly, isolation of a compound involves extraction or collection in a appropriate solvent or adsorbant. Commonly used extraction solvents for plants are water or aqueous methanol in which either dried or live plant parts are soaked. After extracting the material for varying lengths of time, the exuded material is filtered or centrifuged before bioassay. Soil extraction is more difficult, since certain solvents (e.g. bases) may produce artifacts.

Chemical separations may first be accomplished by partitioning on the basis of polarity into a series of solvents from non-polar hexane to very polar compounds like methanol. Compounds may also be separated by molecular size, charge, or adsorptive characteristics, etc. Various chromatography methods are utilized, including columns, thin layer (TLC) gas-liquid (GLC), and more recently, high pressure liquid (HPLC) systems. HPLC has proven particularly useful for separations of water soluble compounds from relatively crude plant extracts. Previously, the major effort toward compound identification involved chemical tests to detect specific functional groups, whereas characterization is now usually accomplished by using a series of spectroscopic analyses. Initially, ultraviolet spectroscopy (UV) is useful in this regard to detect specific functional groups. More recently, infrared (IR) spectroscopy and nuclear magnetic resonance (NMR) have helped immensely in determining natural products structure by indicating the functional groups and relative positions of atoms. Mass Spectrometry is a relatively recent addition to the analytical arsenal that provides additional clues as to molecular size and composition. It can quickly provide confirmation of complex organic molecular structures. Tandem Mass Spectrometry (MS/MS) or GC-MS are more recent developments which also allow analyses of mixtures of compounds. Effective studies of allelopathy must now include natural products chemists who can provide structure elucidation rapidly.

Factors Affecting Allelochemical Production or Release and their Modes of Action. This area of research should prove fruitful for the plant physiologists and biochemists who are interested in regulation of plant metabolism. Studies to date have been limited to only a few compounds.

Plants appear to vary in their production of allelopathic chemicals depending upon the environment in which they are grown and in particular, in response to stresses that they encounter. One practical difficulty faced by researchers is that greenhouse-grown plants may produce limited quantities of inhibitors. Ultraviolet (UV) light is absent in closed greenhouses, and several investigations have shown that UV light greatly enhances the production of allelopathic chemicals (4). For example, when greenhouse light was supplemented by UV, sunflower (*Helianthus annuas*) produced much more scopolin and chlorogenic acid (22).

Nutrient deficiencies may also influence the production of allelochemics. The compounds studied in great detail have been the phenolic compounds and scopolin-related chemicals. Deficiencies of boron, calcium, magnesium, nitrogen, phosphorus, potassium, and sulfur have all been reported to enhance the concentration of chlorogenic acids and scopolin in a variety of plants (4). In other species, chlorogenic acids have decreased in plants that are deficient in magnesium or potassium.

The type and age of plant tissues are extremely important since compounds are not uniformly distributed in the plant. Among species, there are great differences in ability to produce allelochemics. Within species, differences may exist in the amount of toxin produced by different genotypes. For example, various oat (*Avena sativa*) lines show differences in their ability to exude scopoletin and related compounds (23). Some cucumber (*Cucumis sativus*) accessions greatly inhibited weed germination, while others had no effect, or even stimulated growth (24). The implications of all these findings are that plant types may be either selected or bred that are more allelopathic, or that inhibitor production can be enhanced by exerting the proper stresses on the plants.

Mode of action research has caused similar challenges for investigators working with either natural products or synthetic pesticides. The major difficulty is to separate secondary effects from primary causes. Although effects can be measured in isolated systems, there always remains the critical questions of whether the inhibitor reaches that site in the plant in sufficient concentration to specifically influence that reaction, and whether other processes may be affected more quickly. At present, allelochemicals have been reported to inhibit nutrient uptake by roots, cell division, extension growth, photosynthesis, respiration, protein synthesis, enzyme activity, and to alter membrane premeability (4), but little is known about their action at the molecular level.

Ecological Studies. Plant succession, particularly in old fields and cut-over forests has intrigued ecologists for decades. The appearance and disappearance of species and changes in species dominance over time has been attributed to numerous factors including physical changes in the habitat, seed production and dispersal, competition for resources, or combinations of all these. Rice and co-workers (4) have presented extensive evidence that allelopathy may play an important role in the disappearance of the pioneer weeds (those most rapidly invading old fields). Additional findings in this area could help us manage vegetation more effectively.

Certain reforestation problems have also been linked to allelopathy. There are logged-over sites on the Allegheny Plateau in Northwestern Pennsylvania that have remained essentially treeless for up to eighty years (10). Several herbaceous weed species have been shown to produce toxins that inhibit establishment of the black cherry (*Prunus serotina*) seedlings that normally reinfest these sites. Among the more active are goldenrods (*Solidago*) and *Aster* species. One wonders why this idea could not be exploited for vegetation management on right-of-way lands.

In many ecosystems, plants tend to pattern themselves as pure stands or as individuals spaced in rather specific densities or configurations. Many desert species show obvious zones of inhibition around which few, if any, alien species are able to invade. These patterns often cannot be adequately explained by competition alone, and are probably caused by a combination of factors including allelopathy. The phenomenon happens with herbaceous plants as well as woody shrubs and trees.

Muller reported that black mustard (*Brassica nigra*) can form almost pure stands after invading annual grasslands of coastal southern California (25). This was attributed to inhibitors released from the dead stalks and leaves which do not permit germination and growth of other plants. These observations provide agronomists hope that similar results could be exploited with crops, specifically to achieve almost pure stands of crops (over weeds) by use of an allelopathic mechanism.

Positive and Negative Impacts of Allelopathy for Weed Science. There is considerable evidence which now suggests that some of the more aggressive perennial weed species, including quackgrass (*Agropyron repens*) (26), Canada thistle (*Cirsium arvense*) (27), Johnsongrass (28), and yellow nutsedge (*Cyperus esculentus*) (29) may impose allelopathic influences, particularly through toxins released from their residues. There are also several annual weed species in which allelopathy is implicated. Perhaps best documented is giant foxtail (Setaria faberi) whose residues severely inhibited the growth of corn (Zea mays) (6).

Extracts of several important weed species were found to inhibit the nodulation of legumes by Rhizobium (4). Among those were Western ragweed, large crabgrass, prostrate spurge and annual sunflower. Our recent studies indicate that quackgrass releases compounds that inhibit nodulation and nitrogen fixation on a number of legumes. Adverse effects of weeds on nitrogen fixation appears to be an agricultural problem that deserves much more research attention.

The classic seed burial studies of W. J. Beal and his successors have shown seeds of at least one weed species, Moth Mullein (Verbascum blattaria L.) can remain viable in soil for a peiod of 100 years, whereas three species continued to germinate after 80 years of burial (30). Weed seeds not only resist decay by soil microbes, but they vary in dormancy characteristics. There is considerable evidence that chemical inhibitors are responsible for both phenomena. Unsaturated lactones and phenolic compounds in particular, are potent antimicrobial compounds present in many seeds (4). Fruits and seeds are also known to contain diverse germination inhibitors including phenolic compounds, flavonoids and/or their glycosides and tannins. Unique methods to destroy inhibitors could provide an excellent weed management strategy.

Recently, some weed scientists have attempted to directly exploit allelopathy as a weed management strategy. One approach has been to screen for allelopathic types in germplasm collections of crops, and to transfer this character into cultivars by either conventional breeding or other genetic transfer techniques. Superior weed suppressing types have been reported in cucumber (24), oat (23), sunflower (31), and soybean collections (32). When thoroughly researched, this idea may have potential for crops that are maintained in high density monocultures i.e. turfgrasses, forage grasses, or legumes.

Another approach is the utilization of allelopathic rotational crops or companion plants in annual or perennial cropping systems (19). Living rye (Secale cereale L.) and its residues have been shown to provide nearly complete suppression of a variety of agroecosystem weeds (33). Similarly, residues of sorghums, barley, wheat and oats can provide exceptional suppression of certain weed species (19). Although some progress has been made on identifying the allelochmicals from these plants, much remains to be accomplished.

Allelopathic plants may also provide a strategy for vegetation management in aquatic systems. The diminutive spikerush (Eleocharis coloradoensis) has been reported to displace more vigorous and unwanted aquatic plants i.e. pondweeds (Potamogenton species) and Elodea in canals and drainage ditches. Frank (34) attributed this to allelopathic effects, and more recently the phototoxic compound dihydroactinidiolide (DAD) was isolated and characterized from the spikerush plant (35). This chemical has since been shown to be inhibitory to pondweeds.

An important contribution from allelopathy research may be the discovery of novel chemicals either useful as pesticides or precursers to pesticides. Both higher plants and microorganisms are rich sources of diverse chemistry. Some excellent leads have already been made in this area. For example, a cineole derivative is now being developed as a herbicide by a major chemical company. In addition, several potential herbicide candidates have been isolated from broths of Streptomyces cultures. Biotechology will undoubtedly complement chemical synthesis for production of our future agrichemicals.

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