# Natural Growth Inhibitors (Allelopathy): Literature Review

*Technical Report*

# Natural Growth Inhibitors (Allelopathy): Literature Review

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# REPORT SUMMARY

This report is part of a larger proposed investigation to develop natural growth inhibitors useful for utility rights-of-way vegetation management.

## Background

Empire State Electric Energy Corporation (ESEERCO) and Consolidated Edison company of New York, Inc., contracted with the Brooklyn Botanic Garden to undertake this work. It is part of a larger potential project to develop natural growth inhibitors for overhead transmission rights-of-way vegetation management in New York state.

## Objectives

To prepare annotated bibliographies of the published scientific literature concerning plant growth inhibitors produced naturally by microorganisms, tree pathogens, and allelopathic plants; to update a checklist of allelopathic plants; and, to develop vegetation biographies of six abandoned fields at Mohonk Preserve, New Paltz, New York, for subsequent research.

## Approach

Four different teams of investigators prepared annotated bibliographies concerning the state-of-scientific knowledge about phytotoxins produced by microorganisms and tree pathogens. Individual principal investigators conducted literature searches in scientific literature databases (for example, Agricola, Bio Abstracts, and Chem Abstracts). They identified pertinent articles using their knowledge and expertise for subsequent screening and review. The teams also researched field biographies of six abandoned fields on the Mohonk Preserve.

## Results

This report contains a comprehensive literature search of the research that has been done or is in progress on tree growth inhibitors produced by microorganisms and on tree pathogens and organisms that parasitize or inhabit tree tissue. Also included is an update of the previously conducted literature search concerning plants allelopathic to trees and their potential for controlling vegetation in rights-of-way. A history of six fields on the Mohonk Preserve that have failed to become reforested since abandonment 10 to 25 years ago is presented.

Each report section has its own set of conclusions and recommendations. Annotated bibliographies include 155 articles and summaries by the investigators.

## EPRI Perspective

The development of herbicides from microbially-produced phytotoxins is highly promising. A striking conclusion from the combined literature reviews is that little research is directed to

discovery and development of microbially-produced inhibitors to control trees and other woody plants. Research into this topic is an overlooked opportunity and should be encouraged by organizations and industries having the specialized need for these inhibitors.

Inhibition produced by allelopathic plants, with a few exceptions, effects a broad range of target species. Allelopathic inhibition is more difficult to identify and reproduce because the complex interactions between plants, soils, and other organisms have not been defined completely. More research needs to be conducted under natural and existing conditions where allelopathic interactions are suspected. Such conditions are apparent and available for investigative research within the Mohonk Preserve in New Paltz, New York. Due to utility interest, EPRI is making this ESEERCO study available to Environmental ROW Target members, offering immediate value to funders of this new Target.

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**Keywords**
Allelopathy
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Herbicides

# ABSTRACT

The objectives of this project were: to prepare annotated bibliographies of the published scientific literature concerning plant growth inhibitors produced naturally by microorganisms, tree pathogens, and allelopathic plants; update a checklist of allelopathic plants; and develop vegetation biographies of six abandoned fields at Mohonk Preserve, New Paltz, New York. Literature searches were conducted by the individual principal investigators of scientific literature databases (Agricola, Bio Abstracts, Chem Abstracts, etc.). Pertinent articles were identified using the knowledge and expertise of each investigator and obtained for subsequent screening and review. Annotated bibliographies of articles considered relevant by the investigators were included in this report. Each investigator summarized their annotated bibliography and developed conclusions and recommendations.

It was concluded that the development of herbicides from microbially-produced phytotoxins is highly promising. Microbially-produced herbicides may be generally safe, breakdown naturally, potent, and may exhibit greater selectivity than synthetic herbicides. They are also synthesized from renewable resources rather than non-renewable, petroleum-based raw materials. Reports of compounds isolated from pathogens of trees that are <u>not</u> host-selective could not be found. Consequently, most, if not all, inhibitors derived from tree pathogens should selectively control the growth of target tree species.

Inhibition produced by allelopathic plants, with a few exceptions, effects a broad range of target species. Allelopathic inhibition is more difficult to identify and reproduce because the complex interactions between plants, soils, and other organisms have not been defined completely. More research needs to be conducted under natural and existing conditions where allelopathic interactions are suspected. Such conditions are apparent and available for investigative research within the Mohonk Preserve in New Paltz, New York. Six areas at Mohonk represent a range of old field succession exhibiting total forest regeneration to no forest regeneration. Allelopathic factors may be responsible for the failure of forest regeneration in these areas.

A striking conclusion from the combined literature reviews is that little research is directed to discovery and development of microbially-produced inhibitors to control trees and other woody plants. Research into discovery of microbially-produced herbicides for trees and woody vegetation is an overlooked opportunity, and should be encouraged by organizations and industries having the specialized need for these inhibitors.

# EXECUTIVE SUMMARY

## Section I - Introduction

Empire State Electric Energy Corporation (ESEERCO) and Consolidated Edison Company of New York, Inc., contracted with the Brooklyn Botanic Garden to undertake this project as part of a larger potential investigation to develop natural growth inhibitors useful for utility rights-of-way vegetation management. The first phase of the investigation prepared an annotated bibliography concerning the state-of-science and knowledge about phytotoxins produced by microorganisms and tree pathogens. A previously prepared literature search of allelopathy articles was updated, including a checklist of vegetation allelopathic to trees. Also, field biographies of six abandoned fields on the Mohonk Preserve were researched and documented.

The objective of the study is to produce an information base concerning: growth inhibition caused by microorganisms, plant pathogens, and plants; and collect historical data of sites at Mohonk Preserve for subsequent reforestation failure research.

## Section II - Plant Growth Inhibitors Produced by Microorganisms

An annotated bibliography was compiled consisting of 114 literature citations encompassing:

1. relationships of microbial phytotoxins to pathogenicity of producing organisms
2. isolation of phytotoxins produced by microorganisms
3. determination of plant response to microbial phytotoxins
4. microbial phytotoxin modes of action
5. chemical identification of microbial phytotoxins
6. potential of microbial phytotoxins for development as herbicides for use in agriculture, forestry, and other types of vegetation management

The annotated bibliography reports approximately 200 phytotoxins from over 100 microbial species. The vast majority of these phytotoxins are produced by fungi, especially phytopathogenic species. These toxins can be broadly classified into two major categories:

1. host specific toxins, and
2. non-host specific toxins

Examples of host specific toxins include bipolaroxin, curvulin, ACTG toxins A to F, and phomozin. Well known examples of non-host specific phytotoxins include anisomycin, produced by Streptomyces spp.; bialaphos, produced by S. hygroscopicus and S. viridochromogenes; the herbicidins, produced by S. saganonensis; the herbimycins, produced by S. hygroscopicus; and tentoxin, produced by Alternaria alternata.

Two general approaches for phytotoxin discovery dominated the literature. One was to develop screening programs directed towards testing a large number of microbial strains for the production of phytotoxic compounds. Such programs typically led to discovery of non-host specific toxins. The other approach was to culture and investigate selected pathogenic microorganisms and to determine the involvement of phytotoxins in causing or enhancing their pathogenicity. This latter approach frequently leads to discovery of host specific toxins.

Studies of phytotoxins active against herbaceous plants were far more common than studies with woody plants. The chemical structures of many of the phytotoxins in these studies have been determined. They are unique and diverse, relative to synthetic pesticides.

A few of the phytotoxins described in the literature have already been developed as commercial herbicides. Bialaphos and phosphinothricin are two examples. Bialaphos is effective against both monocot and dicot perennial weeds. Its toxicity depends on its catabolism within the target plant to phosphinothricin, the phytotoxic molecule. Phosphinothricin is the active ingredient in the commercial herbicide Basta produced by Hoechst AG. The commercial herbicide Glufosinate is a synthetic version of phosphinothricin and is also produced by Hoechst AG.

The development of herbicides from microbially produced phytotoxins is a highly promising area for future discovery. Microbially produced herbicides may have a number of advantages over many synthetic ones. Particularly, they may be safer, both from human health and environmental perspectives. The literature reviewed here clearly indicates that microorganisms have the ability to produce a remarkable arsenal of phytotoxic metabolites.

Little effort is currently being directed to discovery and development of microbially produced herbicides to control trees and other woody plants. The discovery of microbially produced herbicides for trees and woody vegetation is an overlooked opportunity. Industries and organizations that require them should support research to study and develop them.

## Section III - Phytotoxins Isolated from Pathogens of Trees

There are few research reports on phytotoxic substances isolated from pathogens of woody plants, specifically trees or shrubs. Those phytotoxins reported appear to be toxic only to the host plant infected by the toxin-producing pathogen, and are therefore considered “host-selective”.

Phytotoxins to trees have been isolated from:

1. Several isolates of the fungus which causes silverleaf disease of cherry.

2. Seiridium cupressi which causes a canker disease of cypress (Cupressus sempervirens).

3. Pseudomonas syringae, a bacterium which causes citrus blight.

4. Alternaria alternata which causes black spot disease in Japanese pear.

5. Phomopsis sp., several of which are implicated in a wilt disease of Japanese red pine.

6. Pestalotia longiseta the causal organism of tea gray blight.

7. Fusarium solani, a fungus commonly associated with citrus roots in Florida.

8. Guignardia laricina, the causal fungus of shoot blight in larch.

9. Two different fungal pathogens of apple.

Several researchers were contacted to substantiate their findings. Most of those contacted have been researching the use of naturally derived toxins against herbaceous weeds (Dr. J. Hull, Michigan State University; Dr. G. Strobel, Montana State University; Dr. G. Templeton, University of Arkansas; Dr. H.G. Cutler, ARS, USDA, Athens, GA; Dr. A.R. Lax, ARS, USDA, New Orleans, LA). These researchers indicated that from their knowledge and experience, toxins isolated from tree pathogens would be host-specific and generally slow acting. No one knew of any research on this specific topic in progress.

No reports of compounds isolated from pathogens of trees that are not host-selective which could act as herbicides/growth regulators for a broad range of trees and shrubs were found. From the literature gathered and personal communication with researchers, it could be concluded that this avenue of research may be non-productive. Phytotoxins isolated from non-pathogenic soil microorganisms are usually more non-selective than those isolated from plant pathogens. Perhaps further research emphasis should be on soil microorganisms as potential producers of non-host-selective toxins which may be effective against woody plants.

## Section IV - Allelopathy Update

Since production of the previous (1986) literature review of allelopathy (Appendix A), there have been approximately 300 articles written that include a reference to allelopathy. Thirty articles concerned the allelopathic effects of trees on herbaceous species or other trees (5 articles). Only 22 of the articles reviewed concerned the allelopathic effects of herbaceous plants on trees.

Four of the 22 articles directly link allelopathy and mycorrhizal fungi. Mycorrhizae are often overlooked in allelopathy research. Their involvement needs to be investigated further.

The articles mentioned are indicative of the nature and state-of-science of allelopathy research. Most of the investigations demonstrate the complexity of factors involved that determine the effect of other organisms on tree growth, like mycorrhizae and moose browsing. This complexity indicates that a more uniform means of evaluating allelopathic interactions is needed.

To “prove” a plant has an allelopathic effect on another, the following conditions should be met:

1. An identified substance must be shown to be released or exuded from a plant under “normal” growth conditions.

2. The suspect chemical must be shown to be translocated to the target plant by natural means through a natural substrate.

3. The suspect must have an observable direct effect on the target plant. Shoot growth is not a direct effect.

Very few of the investigations of allelopathic interactions reported in the scientific literature stand up to this scrutiny of proof. Consequently, care must be taken in accepting many conclusions derived from previous investigations.

There is substantial evidence to indicate that, tree invasion of a right-of-way can be prevented by herbaceous plants. However, the accumulated scientific knowledge about allelopathy is insufficient to predict what set of conditions will produce the desired results in New York. Further research should be pursued with the specific goal of generating the knowledge necessary to effectively use low growing allelopathic shrubs and herbaceous plants to control tree invasion in rights-of-way.

It is apparent from the lack of published research directed at factors inhibiting tree growth, development of regulation protocols based on allelopathic interactions needs the support of the utility industry. More allelopathy research is conducted on herbaceous plants than woody plants because of the ease with which experiments are conducted on herbs and sponsorship by the agricultural community. Without alternate sponsorship, the focus of allelopathy research will skew toward agricultural purposes.

Further research should be pursued with the specific goal of generating the knowledge necessary to effectively use low growing allelopathic shrubs and herbaceous plants to control tree invasion in rights-of-way.

## Section V - Mohonk Preserve Field Biographies

Field biographies were prepared for Mohonk Preserve Buff Farm #1, Buff Farm #2, Home Farm #1, Home Farm #3, Spring Farm #4, and Spring Farm #11. The location, history, maintenance, present condition, dominant species, soils, and a list of plants present for each field is included in the biographies.

The Buff Farm fields are good representatives of abandoned fields in which tree invasion has occurred. The dominant herbaceous vegetation consists of a mix of goldenrods, northern dewberry, purple loosestrife, beardstongue, grasses, mountain mint, and milkweed.

The Home Farm fields are good representatives of abandoned fields that have received maintenance via mowing on a sporadic basis. Tree invasion in these fields is less than in the Buff Farm fields. The dominant herbaceous vegetation includes grasses, goldenrods, asters, northern dewberry, blackberry, yellow mustard, mints, beardstongue, mullein, and rose.

Spring Farm #4 is dominated by grasses and has been invaded less by trees than the Buff or Home Farm fields. Spring Farm #11 is unique because the dominant vegetation is bedstraw. Bedstraw grows aggressively and is considered a weed. Its dense growth and possibly allelopathic factors account for the lack of tree invasion in this abandoned field. The directors of

Mohonk preserve have considered using bedstraw as an alternative to mowing to maintain abandoned fields.

These fields and others at Mohonk preserve would be ideal sites to investigate allelopathic interactions between herbaceous plants and trees. Development of natural methods of controlling the growth of trees would serve both the needs of the utility industry and sites like Mohonk that have been charged with the task of maintaining aesthetic “vistas”.

# CONTENTS

# LIST OF TABLES

# 1
# INTRODUCTION

## 1.1 An Overview of the Document

This report was prepared as part of a larger proposed investigation to develop natural growth inhibitors useful for utility rights-of-way vegetation management. The first activity of the proposed investigation recommended the generation of annotated bibliographies concerning the state-of-science of knowledge about phytotoxins produced by microorganisms, and tree pathogens. A previously prepared literature search of allelopathy articles was also to be updated, including a checklist of vegetation allelopathic to trees. And, field biographies of six abandoned fields on the Mohonk Preserve were to be researched. Four different groups of investigators compiled the various sections, consequently differences in style will be apparent. Each section has its own set of conclusions and recommendations. The annotated bibliographies include 155 articles and summaries by the investigators.

## 1.2 Statement of Purpose

To produce an information base concerning: growth inhibition caused by microorganisms, plant pathogens, and plants; and collect historical data of potential sites for field investigation at Mohonk Preserve for subsequent research.

1. Microorganisms - A comprehensive literature search of the research that has been done or is in progress on tree growth inhibitors produced by microorganisms will be conducted.

2. Tree Pathogens - A comprehensive literature search of the research that has been done or is in progress on tree pathogens and organisms that parasitize or inhabit tissue of trees will be conducted.

3. Allelopathic plants - An update of the previously conducted literature search concerning plants allelopathic to trees and their potential for controlling vegetation in rights-of-way. A check list of allelopathic plants including herbs, shrubs, and small trees will be updated.

4. Mohonk Preserve - There are 50 fields on the Mohonk Preserve in varying states of reforestation. It has been noted that certain fields have failed to become reforested since abandonment 10 to 25 years ago. The history of six of these fields will be examined.

# 2
# PLANT GROWTH INHIBITORS PRODUCED BY MICROORGANISMS

## 2.1 Description of Research

This report summarizes a literature review of compounds produced by microorganisms that exhibit herbicidal or phytotoxic activity. Special emphasis was placed on obtaining information about compounds having effects on trees and other woody species. An annotated bibliography was compiled consisting of 114 literature citations encompassing:

1. relationship of microbial phytotoxins to pathogenicity of producing organisms,
2. isolation of phytotoxins produced by microorganisms,
3. determination of plant response to microbial phytotoxins,
4. microbial phytotoxin modes of action,
5. chemical identification of microbial phytotoxins,
6. potential of microbial phytotoxins for development as herbicides for use in agriculture, forestry, and other types of vegetation management.

The annotated bibliography reports approximately 200 phytotoxins from over 100 microbial species have been isolated (Tables 2-1 and 2-2). The vast majority of these phytotoxins are produced by fungi, especially phytopathogenic species. The genera Alternaria, Fusarium, Drechslera, Penicillium, and Aspergillus, which are important plant pathogens or decomposers of plant products, were the most prolific phytotoxin producers. Among bacteria, the most frequently reported producers of phytotoxins were Pseudomonas species and the actinomycetes, especially Streptomyces species. Approximately one quarter of the phytotoxins included in the bibliography are produced by two or more different species of microorganisms.

## 2.2 Relationship of Microbial Phytotoxins to Pathogenicity of Producing Organisms

The toxins reported in this summary can be broadly classified into two major categories: (1) host specific toxins, and (2) non-host specific toxins. Host specific toxins are those produced by certain plant pathogenic microorganisms. They typically have a narrow spectrum of activity and usually are most toxic to the host plant and closely related species. In some instances, only particular strains of a specific microbial species produced such phytotoxins. Host specific toxins produced by plant pathogenic microorganisms commonly are most selective when applied at low concentrations, but exhibit a wider spectrum of activity when higher concentrations are applied. The role of these compounds for the producer organism is suspected to be an enhancement of pathogenic ability.

Non-host specific toxins, according to Duke (21), are compounds "that are toxic to plant species that the producing microorganism does not infect in nature." Usually such toxins have a much broader spectrum of phytotoxic activity than host specific toxins. Most non-host specific toxins are produced by non-pathogenic microorganisms, many of which are decomposers of dead organic matter in the soil. The roles of non-host specific toxins for the producer organism, and their ecological effects, are presently uncertain.

Examples of host specific toxins include bipolaroxin, curvulin, ACTG toxins A to F, and phomozin. Bipolaroxin is produced by Bipolaris cynodontis, a fungal pathogen of bermudagrass (43). Bipolaroxin selectively causes lesions on bermudagrass at low concentrations, but at high concentrations, it also affects corn, wild oats, and sugarcane. Curvulin is produced by Drechslera indica, a pathogen of common purslane and spiny amaranth (43). At low concentrations curvulin is selective toward these hosts, but at higher concentrations it is more broadly toxic. The ACTG toxins A to F are host specific toxins produced by Alternaria citri, the causal agent of brown spot disease of mandarins (52). Phomozin is produced by Phomopsis helianthi, a fungal pathogen of sunflower (60). In bioassays, phomozin induced lesions on sunflower leaves but not on leaves of melon, soybean, corn, pea, or tobacco.

Well known examples of non-host specific phytotoxins include anisomycin, produced by Streptomyces spp.; bialaphos, produced by S. hygroscopicus and S. viridochromogenes; the herbicidins, produced by S. saganonensis; the herbimycins, produced by S. hygroscopicus; and tentoxin, produced by Alternaria alternata. Anisomycin is toxic to several grassy weed species, but not to rice and several other crops (21, 96). Bialaphos is relatively non-selective and is active against both monocot and dicot plants, including perennials (21, 96). Herbicidins A and B are toxic to several grassy weed species, but not to rice (13, 21). The herbimycins are effective against both monocot and dicot weeds, and are also non-toxic to rice (21, 96). Tentoxin causes chlorosis in a broad range of plants. (21, 23).

## 2.3 Isolation of Phytotoxins Produced by Microorganisms

Two general approaches for phytotoxin discovery dominated the literature. One was to develop screening programs directed towards testing a large number of microbial strains for the production of phytotoxic compounds. Such programs typically lead to discovery of non-host specific toxins. The other approach was to culture and investigate selected pathogenic microorganisms and to determine the involvement of phytotoxins in causing or enhancing their pathogenicity. This latter approach frequently lead to discovery of host specific toxins. Half or more of all the phytotoxin producing organisms in this literature review are plant pathogens.

Studies of phytotoxins active against herbaceous plants were far more common than studies with woody plants. In addition, herbaceous plants rather than woody species were much more commonly used in bioassays for determination of phytotoxicity. Reasons for this include the greater importance of herbaceous species in agriculture and the greater ease and speed of growing herbaceous species under experimental conditions. Among the plants most frequently used in bioassays were agronomic species such as corn, wheat, beans, and rice, and economically important weeds such as johnsongrass, barnyardgrass, and Canada thistle.

## 2.4 Determination of Plant Response to Microbial Phytotoxins

Various types of bioassays were employed to test for phytotoxicity of isolated compounds. The most common included: (1) germination and growth bioassays where seeds of rapidly germinating species such as garden cress or lettuce were treated in petri dishes with the test solutions, and (2) leaf prick bioassays where test solutions were applied to pinhole wounds on excised or attached leaves. Other bioassays included spraying test solutions onto whole plants, application of test solutions to soil in field plots, or very specialized bioassays involving application of test compounds to small quantities of specific plant tissue or callus.

A myriad of symptoms was observed in bioassays with the different phytotoxins, including: necrotic leaf margins, necrotic lesions, general chlorosis, veinal chlorosis, chlorotic halos, “green islands”, stunting, malformations, stem cankers, wilt, leaf roll, shoot curling, vascular browning or plugging, root die back, stomatal closure, inhibition of seedling root or shoot elongation, and inhibition of seed germination. The type of plant damage observed was, of course, related to the type of bioassay chosen, the indicator species used, and the compounds involved.

## 2.5 Microbial Phytotoxin Modes of Action

Most authors did not discuss phytotoxin modes of action, probably because they were not known. Specific modes of action were suggested in some cases, based on various indirect observations. For a few compounds, modes of action are well understood. Among the modes of action discussed were: inhibition of photosynthesis, $CO_2$ fixation, or photosynthetic electron transport; modification of membranes; decreased chlorophyll stability and synthesis; inhibition of protein synthesis; cell wall degradation; and inhibition of enzymes such as glutamine synthetase, peptidyl transferase, and esterase. Bialaphos, for instance, is a tripeptide produced by <u>Streptomyces hygroscopicus</u> and <u>S. viridochromogenes</u>. It inhibits glutamine synthetase resulting in toxic accumulation of ammonia and inhibition of nitrogen assimilation (21, 95, 96). Tentoxin, produced by the fungus <u>Alternaria alternata</u>, is a non-host specific cyclic tetrapeptide that causes chlorosis by inhibiting chlorophyll production (56, 110). The macrocyclic trichothecenes (roridin A, isororidin E, baccharinol B4, verrucarins A and J, and trichoverrin B), produced by certain soil fungi, are believed to inhibit protein synthesis. They are known to bind to the 60s ribosomal subunit and inhibit peptidyl transferase activity.

## 2.6 Chemical Identification of Microbial Phytotoxins

The chemical structures of many of the phytotoxins in these studies have been determined. They are unique and diverse, relative to synthetic pesticides (21). In some cases where a compound evinces promising herbicidal activity but is not amenable to large scale microbial production, it may be possible to artificially synthesize it or related chemical structures. Microbial phytotoxin structures may also be synthetically modified to optimize their activity and usefulness (21, 61).

A few of the phytotoxins described in the literature have already been developed as commercial herbicides. Bialaphos and phosphinothricin are two examples. Bialaphos is effective against both monocot and dicot perennial weeds (21, 96, 97, 98, 111). Its toxicity depends on its catabolism within the target plant to phosphinothricin, the phytotoxic molecule (21). Phosphinothricin is the active ingredient in the commercial herbicide Basta produced by Hoechst AG (25, 95). The commercial herbicide Glufosinate is a synthetic version of phosphinothricin and is also produced by Hoechst AG (21, 25, 111). Phosphinothricin inhibits glutamine synthetase, resulting in toxic accumulation of ammonia and impaired protein synthesis (21, 95, 96, 111).

Information about the phytotoxins included in the annotated bibliography is summarized in Tables 2-1 and 2-2. Table 2-1 lists phytotoxins that: (1) were tested on woody plant species in bioassays, and/or (2) were produced by woody plant pathogens and suspected of contributing to disease symptoms. Table 2-2 lists phytotoxins produced by microorganisms other than pathogens of woody plants, or compounds not tested on woody plant species. In both tables, phytotoxins produced by fungi are listed first, followed by phytotoxins produced by bacteria.

## 2.7 Potential of Microbial Phytotoxins

The annotated bibliography includes several review articles by researchers in the field of natural products chemistry. The consensus of these authors is that further research into the development of herbicides from microbially produced phytotoxins is a highly promising area for future discovery. In the past, Japan has had much greater interest in commercial exploitation of microbial toxins as pesticides than the United States (62). The reviewers are optimistic, however, about the eventual widespread commercialization of microbial herbicides.

Microbially produced herbicides may have a number of advantages over many synthetic ones. They may be generally safer, both from human health and environmental perspectives. Since they are produced by living organisms, they are also rapidly degraded by microorganisms; hence persistence and accumulation of synthetic chemical structures in the environment is avoided. Microbially produced herbicides usually require relatively low concentrations for effective weed control and often exhibit considerable selectivity (21, 61, 62, 96). They are also synthesized from renewable resources rather than non-renewable, petroleum based raw materials. The researchers agree that with continued efforts, highly efficacious commercial herbicides can be developed from microbially produced phytotoxins.

The literature reviewed here clearly indicates that microorganisms have the ability to produce a remarkable arsenal of phytotoxic metabolites. Some are selectively toxic; others would be useful where a non-selective, broad spectrum herbicide is required (61, 111). A number of the phytotoxins are active against woody species as well as herbaceous ones. Rapid and sensitive screening methods for identification of microbial strains producing such phytotoxins have been developed. Well established methods for chemical identification of phytotoxins also presently exist.

## 2.8 Conclusions

A striking conclusion made apparent by this literature review is that little effort currently is being directed to discovery and development of microbially produced herbicides to control trees and other woody plants. Present research is almost entirely directed toward discovery of compounds for use on herbaceous plants. The major reason is that the needs for, and applications of, herbicides for controlling woody species are highly specialized and represent a much smaller market than that for herbaceous weeds in agricultural crops. Hence, fewer dollars are being allocated to such research. The numerous advantages of microbially produced herbicides for controlling woody plants would be similar to those for herbaceous species.

## 2.9 Recommendations

Research into discovery of microbially produced herbicides for trees and woody vegetation is an overlooked opportunity. If microbially produced herbicides for woody species are to be developed, however, funding for such research will have to come from the organizations having the specialized needs for them.

**Table 2-1**
**Phytotoxins Affecting Woody Plant Species**

| Toxin | Producing Organism | Plant Injury Caused | Reference |
|---|---|---|---|
| fusarubin | Fusarium solani | inhibition of seedling root growth | 7, 108 |
| anhydrofusarubin | Fusarium solani | inhibition of seedling root growth | 108 |
| dihydrofusarubin | Fusarium solani | vessel plugging, leaf roll, wilt, veinal chlorosis | 70 |
| marticin | Fusarium solani | (not mentioned) | 108 |
| isomarticin | Fusarium solani | vessel plugging, leaf roll, wilt, veinal chlorosis | 70 |
| javinicin | Fusarium solani | inhibition of seedling root growth | 7, 108 |
| oxysporone | Fusarium oxysporone<br>Pestalotia longiseta | concentric leaf lesions | 68 |
| tentoxin | Alternaria alternata<br>Alternaria citri | chlorosis | 21, 22, 23, 52, 56, 57, 110 |

**Table 2-1**
**Phytotoxins Affecting Woody Plant Species (Continued)**

| Toxin | Producing Organism | Plant Injury Caused | Reference |
|---|---|---|---|
| dihydrotentoxin | Alternaria citri | chlorosis | 52 |
| tenuazonic acid | Alternaria alternata | necrotic lesions | 52, 88, 103 |
| ACTG toxins A to F | Alternaria citri | chlorosis | 52 |
| isocoumarins | Valsa ceratosperma | browning of cambium and phloem | 74 |
| 6α,7β, 9α-trihydroxy-8 (14), 15- isopimaradiene-20, 6- γ-lactone | Phomopsis spp. | browning and degeneration of pine callus | 67 |
| seiridin<br>iso-seiridin | Seiridium cupressi<br>Seiridium cardinale | (not mentioned) | 8 |
| seiricyprolide | Seiridium cupressi | chlorosis and necrosis | 8 |
| isoevernin aldehyde<br>ergosterol peroxide<br>9,11-dihydroergosterol peroxide | Guignardia laricina | inhibition of seedling growth | 80 |
| 4 juglone derivatives | Guignardia laricina | inhibition of germination and seedling growth, leaf browning | 79 |
| monilidiol<br>dechloromonilidiol | Monilina fructicola | necrosis and inhibition of seedling growth | 93, 105 |
| cerato-ulmin | Ceratosystis ulmi | wilt | 91 |
| syringotoxin<br>syringostatins | Pseudomonas syringae | (not mentioned) | 42 |
| syringomycin | Pseudomonas syringae | (not mentioned) | 10, 42 |
| unnamed toxin | strains of fluorescent Pseudomonas | inhibition or stimulation of growth | 58 |
| unnamed toxin | rickettsialike bacterium | scalding and leaf margin necrosis | 58 |

**Table 2-2**
**Phytotoxins Affecting Herbaceous Plant Species**

| Toxin | Producing Organism | Reference |
|---|---|---|
| maculosins<br>alterosins I and II | Alternaria alternata | 49, 103 |
| altertoxin II (=stemphyltoxin II) | Alternaria alternata<br>A. cassiae<br>Stemphylium botryosum | 37, 59 |
| radicinin | Alternaria chrysanthemi<br>A. radicina<br>A. helianthi<br>Cochliobolus lunatus | 86, 87,<br>107 |
| radicinol | Alternaria chrysanthemi<br>Cochliobolus lunatus | 86 |
| 4-deoxyradicinin<br>3-epideoxyradicinol<br>deoxyradicinol<br>radianthin | Alternaria helianthi | 87, 107 |
| curvularin | Alternaria macrospora | 90 |
| α, β-dehydrocurvularin | Alternaria macrospora<br>A. cucumerina<br>Curvularia sp. | 15, 90 |
| alteichin (=alterperylenol)<br>altertoxin II (=dihydroalterperylenol) | Alternaria cassiae<br>Alternaria spp. | 13, 37,<br>89 |
| cyclodepsipeptide destruxin B<br>demethyldestruxin | Alternaria brassicae<br>Metarrhizium anisopliae | 6 |
| homodestruxin B | Alternaria brassicae | 6 |
| stemphyperylenol | Alternaria cassiae<br>Stemphylium botryosum | 37, 92 |
| bostrycin | Nigrospora oryzae<br>Anthrinium phaeospermum<br>Bostryconema alpestre | 12 |
| 4-deoxybostrycin | Alternaria cichhorniae<br>Nigrospora oryzae<br>Anthrinium phaeospermum<br>Bostryconema alpestre | 12 |
| dactylariol seytalone | Stemphylium botryosum | 92 |
| stemphylin (=altersolanol A) | Stemphylium botryosum<br>Alternaria solani | 4 |

**Table 2-2**
**Phytotoxins Affecting Herbaceous Plant Species (Continued)**

| Toxin | Producing Organism | Reference |
|---|---|---|
| solanapyrones A, B, and C | Alternaria solani<br>Ascochyta rabiei | 2, 41 |
| zinnolide | Alternaria solani | 41 |
| pergillin<br>dihydropergillin | Aspergillus ustus | 17 |
| nigerazine A and B<br>hexylitaconic acid | Aspergillus niger | 13, 43 |
| acetylaranotin terrein<br>bisdethiodi (methylthio) acetylaranotin | Aspergillus terreus | 47 |
| secalonic acid (=ergochrome AA) | Aspergillus ochraceus<br>Pyrenochaeta terrestris<br>Parmelia sp. | 102 |
| pyrenocines A and B<br>pyrenochaetic acids A, B, and C | Pyrenochaeta terrestris | 94 |
| recifeiolides | Cephalosporium recifei | 13 |
| cladospolide A and B | Cladosporium cladosporioides | 13, 34, 35 |
| spiciferone A | Cochliobolus spicifer | 69 |
| unnamed phytotoxin | Diaporthe phaseolorum | 54 |
| chaetoglobosin K | Diplodia macrospora | 16 |
| drechslerol-B | Drechslera maydis | 99 |
| tryptophol | Drechslera nodulosum | 49, 104 |
| resorcylides | Drechslera phlei<br>Penicillium sp. | 49 |
| triticones A and B | Drechslera tritici-repentis<br>Curvularia clavata | 49 |
| ophiobolin A<br>6-epi-ophiobolin A | Drechslera maydis<br>D. oryzae<br>D. sorghicola<br>(=Bipolaris sorghicola)<br>D. heveae | 49, 82 |
| 3-anhydroophiobolin A | Helminthosporium spp. | 49 |

**Table 2-2**
**Phytotoxins Affecting Herbaceous Plant Species (Continued)**

| Toxin | Producing Organism | Reference |
|---|---|---|
| 3-anhydro-6-epi-ophiobolin A | Drechslera sorghicola (=Bipolaris sorghicola)<br>D. maydis<br>D. oryzae<br>Helminthosporium spp. | 49 |
| prehelminthosporol | Helminthosporium sativum<br>Bipolaris sp. | 81 |
| dihydroprehelminthosporol | Helminthosporium victoriae<br>Bipolaris sp. | 81 |
| victotoxin | Helminthosporium sativum<br>H. victoriae<br>Bipolaris sp. | 83 |
| prehelminthosporolactone | Bipolaris sp. | 83 |
| HC toxins I, II, III, and IV | Helminthosporium carbonum | 84 |
| gigantenone petasol | Drechslera gigantea | 49 |
| curvulin<br>O-methylcurvulinic acid | Drechslera indica | 49 |
| de-O-methyldiaporthin | Drechslera siccans | 49 |
| bipolaroxin | Bipolaris cynodontis | 49 |
| enniatins | Fusarium tricinctum<br>F. oxysporum<br>F. acuminatum<br>F. sambucinum<br>F. avenaceum<br>F. lateritium | 11 |
| moniliformin | Fusarium moniliforme<br>F. fusariodes | 25 |
| NMA | unidentified Fusarium sp. | 55 |
| unnamed organic acid | Fusarium culmorum | 48 |
| monocerin | Exserohilum turcicum<br>E. monoceras<br>Fusarium larvarum | 88 |

**Table 2-2**
**Phytotoxins Affecting Herbaceous Plant Species (Continued)**

| Toxin | Producing Organism | Reference |
|---|---|---|
| viridiol<br>viridin<br>gliotoxin | Gliocladium virens | 36, 46 |
| irpexil | Irpex pachyodon | 25 |
| phosalacine | Kitasatosporia phosalacinea | 75, 77 |
| phaseolinone | Macrophomina phaseolina | 49 |
| trichodermadienediol A and B<br>roridin L-2<br>roridin A<br>6-hydroxyroridin L-2 | Myrothecium roridum | 9, 18, 45 |
| isororidin E<br>baccharinol B4<br>trichoverrin B | soil fungi | 18 |
| trichodermin<br>diacetoxyscirpenol<br>seirpentriol<br>trichothecin | not mentioned | 18 |
| T-2 toxin | | 18 |
| verrucarins A and J<br>baccharinoids | saprophytic soil fungi | 18, 45 |
| cyclopenin<br>3, 7-dimethyl-8-hydroxy-6-methoxyisochroman | Penicillium corylophilum | 14 |
| citreoviridin | Penicillium charlesii | 13 |
| 3-hydroxybenzyl alcohol | Penicillium urticae | 31, 38 |
| 2-methylhydroquinone | Nectrina erubescens<br>Penicillium urticae<br>Phoma spp. | 31, 38 |
| terrestric acid | Penicillium terrestre<br>Pyricularia oryzae | 73 |
| pyrichalasin H | Pyricularia grisea | 72 |
| pyriculol<br>pyriculariol | Pyricularia oryzae | 93, 106 |
| cavoxin<br>cavoxone | Phoma batae<br>Phoma cava | 24 |

**Table 2-2**
**Phytotoxins Affecting Herbaceous Plant Species (Continued)**

| Toxin | Producing Organism | Reference |
|---|---|---|
| phonemone | Phoma exigua | 49 |
| sirodesmin PL<br>sirodesmin H<br>sirodesmin J<br>sirodesmin K<br>phomalirazine | Phoma lingam | 101 |
| bataenones | Phoma batae | 92 |
| aphidocolin | Phoma batae<br>Aphalospolium aphidicola<br>Nigrospora sphaerica<br>Harziella entomophilla | 40, 92 |
| phomozin | Phomopsis helianthi | 60 |
| (3R-5Z) – (-) -3-hydroxy-5-dodecanoic acid | Pythium ultimum<br>Serratia marcescens | 39 |
| p-hydroxybenzoic acid | Rhizoctonia oryzae | 1 |
| epiepoformin | Scopulariopsis brumptii | 31, 38 |
| 1(H)-pyrrol-3-yl alanine<br>(E)-5-hydroxy-3-methoxy-2-pentenoic acid | fungi | 5 |
| cycloheximide | actinomycetes | 30, 31,<br>63, 96 |
| coaristermycin | actinomycetes | 5 |
| 5-deoxyguanosine<br>balifomycin $C_1$ and $C_2$<br>hygromycin A<br>coformycin<br>arbinoside A<br>2, 5-dihydrophenylalanine | | |
| indoleisopropionic acid | Actinoplanes sp. | 5 |
| coronatine<br>N-coronafacoylvaline | Pseudomonas syringae | 66 |
| δ-amino-levulate | Pseudomonas riboflavina | 85 |
| unnamed phytotoxin | Pseudomonas phaseolicola | 100 |
| herbicidins A, B, C, E, F, and G | Streptomyces saganonensis | 3, 13,<br>21, 29,<br>63, 96,<br>109, 114 |

**Table 2-2**
**Phytotoxins Affecting Herbaceous Plant Species (Continued)**

| Toxin | Producing Organism | Reference |
|---|---|---|
| herbimycin A and B | Streptomyces hygroscopicus | 21, 26, 44, 63, 76, 96 |
| bialaphos | Streptomyces hygroscopicus<br>S. viridochromogenes | 21, 62, 63, 96, 97, 98 |
| phosphinothricin | Streptomyces viridochromogenes | 25, 95, 111 |
| anisomycin toyocamycin | Streptomyces toyocaensis | 21, 63, 96, 112 |
| harman<br>norharman | Streptomyces spp.<br>Nocardia sp. | 113 |
| homoalanosine | Streptomyces hygroscopicus | 21, 26, 44, 76, 96 |
| geldanamycin<br>nigericin | Streptomyces hygroscopicus | 31, 32, 33 |
| phenylacetic acid<br>tabtoxin-δ-lactam | Streptomyces sp. | 5, 21 |
| algacidins A and B | Streptomyces spp. | 51 |
| oxetin | Streptomyces spp. | 21, 78 |
| cyclocarbamide A and B | Streptoverticillium sp. | 13 |

## 2.10 Annotated Bibliography

1. Adachi, T. and Inagaki, K. 1988. Phytotoxin produced by Rhizoctonia oryzae Ryker et Gooch. Agricultural and Biological Chemistry 52: 2625.

   Rhizoctonia oryzae Ryker et Gooch is the fungus causing sheath spot of rice. The authors isolated a phytotoxin from this organism and identified it as p-hydroxybenzoic acid, previously isolated from other microorganisms and higher plants. In bioassays, root growth of lettuce and Chinese cabbage seedlings was inhibited 50% and 40%, respectively, by p-hydroxybenzoic acid at a concentration of 300 ppm.

2. Alam, S.S., Bilton, J.N., Slawin, A.M.Z., Williams, D.J., Sheppard, R.N., and Strange, R. N. 1989. Chickpea blight: production of the phytotoxins solanapyrones A and C by Ascochyta rabiei. Phytochemistry 28: 2627-2630.

   Ascochyta rabiei is the fungus causing blight of chickpea. When cultures of A. rabiei were grown in a liquid medium supplemented with an extract of the host, two phytotoxins were produced. Identification of these revealed that they are the known phytotoxins solanapyrones A and C. These had been isolated in a similar manner from culture filtrates of Alternaria solani (causal agent of early blight of potato) supplemented with host extract. The authors suggest that the host extract contains a toxin inducing substance. In bioassays with cell suspensions of chickpea leaflets, solanapyrone A was about four times as active as solanapyrone C.

3. Arai, M., Haneishi, T., Kitahara, N., Enokita, R., Kawakubo, K. and Kondo, Y. 1976. Herbicidins A and B, two new antibiotics with herbicidal activity. I. Producing organism and biological activities. Journal of Antibiotics 29: 863-869.

   Two antibiotics, herbicidins A and B, were produced by Streptomyces saganonensis. Various types of biological activities are reported. Among the fungi tested, herbicidins A and B inhibited Trichophyton interdigitale and Pellicularia filamentosa. The herbicidins were tested for inhibition of a bacterial pathogen of rice. Both compounds protected rice seedlings from bacterial leaf blight caused by Xanthomonas oryzae. No diseased leaves were observed when these seedlings were sprayed with 100 and 30 ppm of herbicidin A and B, respectively. When sprayed on the stems and leaves of various plants, the herbicidins exhibited selective herbicidal activity, especially against dicots. Rice was especially resistant to herbicidin A. Mice tolerated an intravenous dose of 800 mg/kg of herbicidin A, 200 mg/kg of herbicidin B, and an intraperitoneal dose of 100 mg/kg of herbicidin A or B. Killifishes were incubated in solutions of 100 ppm of each of the herbicidins, and no harmful effect was observed.

4. Assante, B. and Nasini, G. 1987. Identity of the phytotoxin stemphylin from Stemphylium botryosum with altersolanol A. Phytochemistry 26: 703-705.

   The authors report a revision in the structure of the phytotoxin stemphylin, previously isolated by other researchers from the fungus Stemphylium botryosum Wallr. v. lactucum. Based on this more recent structural determination, it was found that stemphylin is identical to the well-known altersolanol A, first isolated from Alternaria solani. In a leaf puncture test for phytotoxicity to lettuce, altersolanol A produced necrotic brown lesions within 16 hours.

5. Ayer, S.W., Isaac, B.G., Krupa, D.M., Crosby, K.E., Letendre, L.J., and Stonard, R.J. 1989. Herbicidal compounds from micro-organisms. Pesticide Science 27: 221-223.

   The authors summarize results from their screening program to identify microorganisms which produce phytotoxic substances with potential for use in the herbicide industry. Known antibiotics not previously reported to be herbicidal are bafilomycin $C_1$ and $C_2$, hygromycin A, coformycin, arabinoside A, and 2, 5-dihydrophenyl alanine, all produced by actinomycetes. Newly isolated herbicidal compounds include phenylacetic acid from a Streptomyces sp., an indoleisopropionic acid from Actinoplanes sp. and tabtoxinine-δ-lactam from a Streptomyces sp. Coaristermycin and 5'-deoxyguanosine are new herbicidal compounds produced by actinomycetes. Fungi have produced the phytotoxins (1H)-pyrrol-3-yl-alanine and (E)-5-hydroxy-3-methoxy-2-pentenoic acid.

6. Ayer, W.A. and Pena-Rodriguez, L.M. 1987. Metabolites produced by Alternaria brassicae, the blackspot pathogen of canola. Part 1, the phytotoxic components. Journal of Natural Products 50: 400-407.

   Three compounds produced by the fungus Alternaria brassicae, the causal organism of black spot disease of canola were identified. Symptoms of the disease on canola include necrotic black spots surrounded by a chlorotic zone on leaves. The phytotoxic compound responsible for symptom expression was identified as the cyclodepsipeptide destruxin B, previously isolated from Metarrhizium anisopliae. Biological activity of this compound was tested on canola leaves using a modified leaf spot bioassay, and its phytotoxic effects were confirmed. The two other compounds isolated and identified from A. brassicae were demethyldestruxin, also previously isolated from M. anisopliae, and homodestruxin B. These were not tested for biological activity due to limited quantities.

*7. Baker, R.A., Tatum, J.H., and Nemec, S. 1981. Toxin production by Fusarium solani from fibrous roots of blight-diseased citrus. Phytopathology 71: 951-954.

   Isolates of Fusarium solani, the fungus believed to be responsible for citrus blight, were evaluated for production of phytotoxins. Culture extracts from several isolates obtained from blight-diseased citrus trees inhibited root growth of radish and rough lemon seedlings. Two naphthazarin toxins were isolated and identified as javinicin and fusarubin. Both are known phytotoxins previously isolated from F. solani. They inhibit anaerobic and oxidative decarboxylation reactions, disrupting normal plant metabolism.

*8. Ballio, A., Evidente, A. Graniti, A., Randazzo, G., and Sparapano, L. 1988. Seiricuprolide, a new phytotoxic macrolide from a strain of Seiridium cupressi infecting cypress. Phytochemistry 27: 3117-3121.

   The fungus Seiridium cupressi causes a canker disease of cypress (Cupressus sempervirens). Three phytotoxins were isolated and identified from a culture of this fungus. Two of these phytotoxins, the butenolides seiridin and iso-seiridin had previously been isolated from S. cardinale, another pathogen of cypress. The third phytotoxin from S. cupressi, not produced by S. cardinale was identified as a new macrolide and called seiricyprolide. Toxicity was tested on twigs of cypress (C. sempervirens C. arizonica, and C. macrocarpa) and cuttings of tomato and mung bean. Seiricuprolide produced diffuse yellowing followed by browning on the cypress within ten days and chlorosis and necrosis on the treated tomato and mung bean cuttings in only four days. The authors suggest seiricuprolide may be a minor toxin product of S. cupressi since it is produced in small quantities and has lower toxicity to plants. It may, however, contribute to the toxic activity of the pathogen producing it.

*9. Bean, G.A., Fernando, T., Jarvis, B.B., and Bruton, B. 1984. The isolation and identification of trichothecene metabolites from a plant pathogenic strain of Myrothecium roridum. Journal of Natural Products 47: 727-729.

   The fungal genus Myrothecium produces trichothecene metabolites that cause phytotoxic, cytotoxic, and cytostatic effects on number of different organisms. M. roridum is pathogenic to various plant species including red clover, alfalfa, tobacco, cotton, coffee, and muskmelon. In this study, the authors isolated various trichothecenes from a pathogenic strain of M. roridum affecting muskmelon. This strain of M. roridum produced primarily the trichoverroids: trichodermadienediols A and B, roridin L-2, and 16-hydroxyroridin L-2, rather than the macrocyclic trichothecenes. No trichothecenes were detected in muskmelon plants naturally infected with M. roridum. It was inconclusive whether trichothecenes produced by M. roridum are involved in pathogenicity.

10. Bidwai, A.P., Zhang, L., Bachmann, R.C., and Takemoto, J.Y. 1987. Mechanism of action of Pseudomonas syringae phytotoxin, syringomycin. Plant Physiology 83: 39-43.

    Pseudomonas syringae pv. syringae produces a peptide phytotoxin called syringomycin. In previous studies of corn shoots by other researchers, it was suggested that syringomycin acted as an uncoupler and thus stimulated mitochondrial ATPase activity. The authors of this report found that in red beet storage tissue, syringomycin stimulates the activity of vanadate-sensitive ATPase, the enzyme believed to use ATP to pump protons across the plasma membrane. Syringomycin increased activity of tonoplast ATPase only slightly. There was no apparent stimulation of the mitochondrial ATPase. The authors suggest further investigation based on these discrepancies.

11. Burmeister, H.R. and Plattner, R.A. 1987. Enniatin production by Fusarium tricinctum and its effect of germinating wheat seeds. Phytopathology 77: 1483-1487.

    The authors report the first isolation of the known phytotoxin senniatins, from Fusarium tricinctum. These compounds, hexadepsipeptides with alternating residues of 2-hydroxy-isovaleric acid and branched N-methyl amino acids have previously been isolated from F. orthoceras (=F. oxysporum), F. acuminatum, F. sambucinum, F. avenaceum, and F. lateritium. Enniatins are not only phytotoxic, but also have antibiotic and insecticidal activity, and are known to modify membranes. Of the 13 isolates of F. tricinctum analyzed in this study, 10 of them produced enniatins. In bioassays with developing wheat seeds, enniatins inhibited root elongation, and to a lesser extent, leaf development.

12. Charudattan, R. and Rao, K.V. 1982. Bostrycin and 4-deoxybostrycin: two nonspecific phytotoxins produced by Alternaria eichhorniae. Applied and Environmental Microbiology 43: 846-849.

    Two phytotoxins were isolated from Alternaria eichhorniae, causal agent of a leaf blight disease in water hyacinth. The toxins were identified as bostrycin, previously isolated from the fungi Nigrospora oryzae, Arthrinium phaeospermum, and Bostryconema alpestre, and 4-deoxybostrycin, previously described as a derivative of bostrycin but not isolated from a natural source. Phytotoxicity of bostrycin and 4-deoxybostrycin at concentrations of 1-1000 ug/ml was tested in leaf bioassays using pepper, papaya, water hyacinth, hydrilla, tomato, milkweed vine, tobacco, bush bean, pickerelweed, wheat, and corn. The toxins were nonspecifically toxic to test plant leaves at higher concentrations, although the leaves were differentially sensitive to the toxins. Both compounds also showed antibacterial activity against Bacillus subtilis.

13. Cutler, H.G. 1988. Perspectives on discovery of microbial phytotoxins with herbicidal activity. Weed Technology 2: 525-532.

This review lists several classes of microbially-produced phytotoxins. Cyclocarbamide A and B, from Streptoverticillium spp. show pre-emergence herbicidal activity. Nigerazine A and B, produced by Aspergillus niger inhibit root growth. Citreoviridin, a metabolite of Penicillium charlesii, and a synthetic derivative of cladosporin, which is produced by Aspergillus repens, A. flavus, and Cladosporium cladosporioides inhibit growth of monocots. Macrocyclic lactones such as recifeiolide, produced by Cephalosporium recifei, and cladospolide A and B, produced by Cladosporium cladosporioides, inhibit seed germination and root growth, respectively. Herbicidins A and B, produced by Streptomyces saganonensis, controlled the growth of several monocot and dicot weeds. Alteichin, a perylenequinone produced by Alternaria eichhorniae, induces necrotic lesions in water hyacinth, thereby reducing photosynthetic efficiency.

14. Cutler, H.G., Ammermann, E., and Springer, J.P.S. 1988. Diverse but specific biological activities of four natural products from three fungi. In H. G. Cutler (ed.), Biologically Active Natural Products: Potential Use in Agriculture, pp. 79-90. ACS Symposium Series 380. Amer. Chem. Soc., Washington, D.C.

An aberrant strain of Penicillium cyclopium produced cyclopenin, which inhibited growth of wheat coleoptiles, produced malformations of bean leaves, and caused necrosis and stem collapse in corn plants. P. corylophilum produced 3, 7-dimethyl- 8-hydroxy-6-methoxyisochroman. This compound exhibited selective herbicidal activity on corn and wheat (monocots), but not on beans and tobacco (dicots) in greenhouse trials.

15. Cutler, H.G., Arrendale, R.F, Cole, P.D. Roberts, R.G., and Springer, J.P. 1987. Synthetic derivatives of the fungal metabolite dehydrocurvularin: biological activity. Proc. 14th Annual Meeting, Plant Growth Regulator Society of America, p. 236-247.

$\alpha$, $\beta$-dehydrocurvularin had previously been isolated by other researchers from a species of the fungus Curvularia; from Alternaria alternata, a pathogen of cucurbits; and from A. macrospora, a pathogen of cotton. In this study, the authors isolated dehydrocurvularin from A. macrospora and synthesized derivatives to compare their relative biological activities. Dehydrocurvularin itself and diacetyldehydrocurvularin were the most active compounds, inhibiting the growth of etiolated wheat coleoptiles and various Gram positive bacteria. Gram negative bacteria were not affected. Di (chloroacetyl) dehydrocurvularin was less toxic to wheat coleoptiles and gram positive bacteria than the parent material, but was active against the Gram negative bacteria Escherichia coli. Dibutanoyl dehydrocurvularin and dihexanoyldehydrocurvularin were also less toxic to wheat coleoptiles than the parent material, and were inactive against all bacteria tested. Di (3, 5-dinitrobenzoyl) dehydrocurvularin and dehydrocurvularinhydroxylimine were biologically inactive. The authors suggest that the more hydrophilic compounds are more biologically active. They speculate that the inactivity of the hydrophilic dehydrocurvularinhydroxylimine (an exception to this generalization) was possibly a result of its high reactivity in biological systems, which in turn causes it to be metabolized before it reaches its active site.

16. Cutler, H.G., Crumley, F.G., Cox, R.H., Cole, R.J., Dorner, J.W., Springer, J.P., Latterell, F.M., Thean, J.E and Rossi, A.E. 1980. Chaetoglobosin K: a new plant growth inhibitor and toxin from Diplodia macrospora. Journal of Agricultural and Food Chemistry 28: 139-142.

    A metabolite of the fungus Diplodia macrospora, the causal organism of ear and stalk rot of corn was isolated and identified as chaetoglobosin K. Its structure is described as a cytochalasin possessing an attached indol-3-yl group. The authors discuss the phytotoxicity of various other cytochalasins and compare their activity with chaetoglobosin K in wheat coleoptile bioassays. Significant inhibition of coleoptiles is reported with 10, 10, 10, 10, and 10 M solutions of chaetoglobosin K. Based on the comparisons with other cytochalasins, chaetoglobosin K seems to be the most active inhibitor of coleoptile growth. The $LD_{50}$ of Chaetoglobosin K today-old chicks was 25 - 62.5 mg/kg.

17. Cutler, H.G., Crumley, F.G., Springer, J.P., and Cox, R.H. 1981. Dihydropergillin: a fungal metabolite with moderate plant growth inhibiting properties from Aspergillus ustus. Journal of Agricultural and Food Chemistry 29: 981-983.

    A metabolite of the fungus Aspergillus ustus was isolated and identified as dihydropergillin. In previous work, the researchers isolated the metabolite “pergillin” from this organism. Both compounds exhibited moderate plant growth inhibiting properties in wheat coleoptile bioassays, however, dihydropergillin was somewhat more active. Structurally, dihydropergillin is the equivalent of pergillin with the addition of two hydrogen atoms to the C-12 – C-13 double bond. The authors conclude that this structural difference accounts for the greater activity of dihydropergillin, and they speculate that other modifications of the molecule might yield compounds useful in agriculture or medicine.

18. Cutler, H.G. and Jarvis, B.B. 1985. Preliminary observations on the effects of macrocyclic trichothecenes on plant growth. Environmental and Experimental Botany 25: 115-128.

    The simple trichothecenes are fungal metabolites shown to be phytotoxins. The authors summarize these phytotoxic effects. Trichodermin was phytotoxic to tobacco, bean, and corn plants; diacetoxyscirpenol inhibited pea, lettuce, and winter tare growth; and seirpentriol, trichothecin, and T-2 toxin were toxic to cress, bean, and pea, respectively. In this study, the authors examined the effect of the macrocyclic trichothecenes: roridin A, isororidin E, baccharinol B4, verrucarin A, verrucarin J, and trichoverrin B in bioassays with etiolated wheat coleoptiles and with intact bean, corn, and tobacco plants. All of these macrocyclic trichothecenes were inhibitory to wheat coleoptile growth, verrucarins A and J and trichoverrin B being the most potent. Based on this bioassay, verrucarin A is one hundred times more inhibitory than abscisic acid. The various effects observed on intact plants treated with these phytotoxins included chlorosis, necrosis, malformation, and stunting. Roridin A showed the greatest toxicity to intact plants. The authors suggest that the phytotoxicity observed in these experiments is a result of protein synthesis inhibition by the trichothecenes. These compounds have previously been shown to bind to the 60s ribosomal subunit and inhibit peptidyltransferase activity.

19. DeFrank, J. and Putnam, A.R. 1985. Screening procedures to identify soil-borne actinomycetes that can produce herbicidal compounds. Weed Science 33: 271-274.

    In this investigation, isolates of soil actinomycetes were tested for herbicidal activity using a new screening procedure. In this procedure, the test organism was streaked in a band on one side of a petri dish containing a nutrient agar. Following incubation, surface sterilized seeds of barnyardgrass and cucumber were partially inserted into the agar in rows and incubated. Plant growth inhibition was assessed visually. Germination and growth was reduced at least 60% by 8 of the 120 isolates screened. These 8 isolates were retested in replicated experiments. The authors conclude that initial screening for herbicidal compounds produced by actinomycetes should be conducted using an agar screening technique.

20. Demain, A.L. 1983. New applications of microbial products. Science 219: 709-714.

    This review explores future prospects for uses of microbial secondary metabolites. Microorganisms have clearly demonstrated their ability to produce chemicals with herbicidal and plant-growth regulating activities. The author suggests that if economic problems regarding production of herbicidal compounds by microorganisms can be solved, this will be a promising option in the future.

21. Duke, S.O. and Lydon, J. 1987. Herbicides from natural compounds. Weed Technology 1: 122-128.

    This article summarizes the usefulness and advantages of natural products from both plants and microbes as herbicides. It also outlines the various developmental strategies involved in producing commercial herbicides from crude natural products. Plants, fungi, and bacteria produce phytotoxic compounds with varied and complex chemistries. Most of these are safe both from human health and environmental perspectives. Many of these exhibit a high degree of target selectivity. Little effort has been made to develop herbicides from host-specific toxins, primarily because most known host specific toxins affect crop species rather than weeds. Several new herbicides have been developed from nonhost-specific toxins. Anisomycin, a product of Streptomyces phytotoxic to barnyardgrass (Echinochloa crus-galli) and crabgrass Digitaria spp.) provided the chemical basis for the synthetic herbicide NK-049, which disrupts chlorophyll synthesis. Bialophos, produced by Streptomyces viridochromogenes, is effective against perennial weeds, both monocot and dicot. In order to be toxic, it must be metabolized in the target plant to phosphinothricin, the phytotoxic part of the molecule. Synthetic phosphinothricin has been developed as the herbicide Glufosinate by Hoeschst AG. Glufosinate acts by inhibiting glutamine synthetase, resulting in toxic buildup of ammonia and impaired protein synthesis in plants. Other glutamine synthetase inhibitors produced by microorganisms include tabtoxinine-β-lactam, L-($N^5$-phosphono) methionine-S-sulfoximinyl -L-alanyl-L-alanine, and oxetin. The herbicidins produced by Streptomyces saganonensis are toxic to some grassy weeds but not to rice. Herbimycins, also good rice herbicides, are toxic to some monocot and dicot weeds. Tentoxin, produced by Alternaria alternata, controls Johnsongrass (Sorghum halepense) in corn and many weeds in soybeans.

Development of commercial herbicides from natural products involves discovering the toxin, identifying it, determining its selectivity and biochemical site of action, possible modification of the molecule to improve its usefulness, and determining the most practical and economical method of production. The authors suggest that the advantages of using natural products as herbicides outweigh the possible disadvantages.

22. Edwards, J.V., Dailey, O.D., Bland, J.M., and Cutler, H.G. 1988. Approaches to structure-function relationships for naturally occurring cyclic peptides. In H.G. Cutler (ed), Biologically Active Natural Products. ACS Symposium Series 380. Amer. Chem. Soc., Washington, D.C., pp. 35-56.

    This paper describes studies involving molecular structural modifications and their effects on herbicidal activity of tentoxin and other microbially produced peptides. The purpose of such work is to enhance the biological activity of naturally-occurring pesticidal molecules, or to use these naturally-occurring molecules as leads for the development of new synthetic herbicides.

23. Edwards, J.V., Lax, A.R., Lillehoj, E.B., and Boudreaux, G.J 1987. Structure-activity relationships of cyclic and acyclic analogues of the phytotoxic peptide tentoxin. Journal of Agricultural and Food Chemistry 35: 451-456.

    The non-host specific cyclic tetrapeptide tentoxin, a metabolite from the fungus Alternaria alternata, induces chlorosis in a broad range of plants. In this study, it was determined that the cyclic nature of tentoxin is a requirement for full biological activity. Acyclic analogues with the dehydrophenylalanine residue N-methylated exhibited low but significant chlorosis activity. To produce maximum loss of chlorophyll in lettuce seedlings, tentoxin must be in a cis-trans-cis-trans conformation.

24. Evidente, A., Randazzo, G., Iacobellis, N.S., and Bottalico, A. 1985. Structure of cavoxin, a new phytotoxin from Phoma cava and cavoxone, its related chroman-4-one. Journal of Natural Products 48: 916-923.

    The authors isolated and identified two compounds, the tetrasubstituted benzoic acid derivative cavoxin and the structurally related cavoxone, produced by the fungus Phoma cava. In a standard bioassay using tomato cuttings, cavoxone showed no biological activity, but cavoxin caused vascular browning and rapid wilting on leaves.

25. Fischer, H.P. and Bellus, D. 1983. Phytotoxicants from microorganisms and related compounds. Pesticide Science 14: 334-346.

    This review discusses phytotoxins produced by microorganisms and their potential for use as new herbicides. Up to the date of this paper, approximately 160 such compounds had been identified. One of the most promising herbicidal prospects was DL-homoalanin-4-yl (methyl) phosphinic acid (= glufosinate). This is a hydrolysis product of N-{4-[hydroxy(methyl) - phosphinoyl] homoalanyl} alanylalanine produced by the bacterium Streptomyces viridochromogenes. This compound is now the active ingredient of a broad-spectrum herbicide developed and sold by Hoechst AG. Many other herbicidal metabolites from microorganisms are also discussed: anisomycin and toyocamycin produced by Streptomyces toyocaensis, which cause inhibition of grasses and certain other plants; moniliformin produced by the fungi Fusarium moniliforme and F. fusariodes, which inhibit or damage tomato, tobacco, soybeans, corn, wheat, and barley; irpexil produced by the fungus Irpex pachyodon, which causes phytotoxicity symptoms similar to the widely used herbicide glyphosate (= Round-up).

26. Furusaki, A., Matsumoto, T., Nakagawa, A., and Omura, S. 1980. Herbimycin A: an ansamycin antibiotic; x-ray crystal structure. Journal of Antibiotics 33: 781-782.

The herbimycins are herbicidal antibiotics produced by Streptomyces hygroscopicus. Its molecular formula is $C_{30} H_{42} N_2 O_9$. This paper describes the determination of its molecular structure, and illustrates the structural formula.

27. Fushimi, S., Nishikawa, S., Mito, N., Ikemoto, M., Sasaki, M., and Seto, H. 1989. Studies on a new herbicidal antibiotic, homoalanosine. Journal of Antibiotics 42: 1370-1378.

Homoalanosine, a compound isolated from Streptomyces galilaeus was shown to exhibit both herbicidal and antimicrobial activity. The chemical of homoalanosine was determined to be L-2-amino-4-nitrosohydroxyaminobutyric acid. Antimicrobial activity was exhibited against some gram-positive bacteria on synthetic media. Herbicidal activity was shown in field experiments against various common weeds, including black nightshade (Solanum nigrum), barnyardgrass (Echinochloa crus-galli), wild oats (Avena fatua), and especially against common cocklebur (Xanthium strumarium), velvetleaf (Abutilon theophrasti), and ladysthumb (Polygonum persicaria). Homoalanosine, however, was also somewhat toxic to corn. In a rice paddy field experiment, homoalanosine exhibited herbicidal activity against various weeds including barnyardgrass (Echinochloa oryzicola), needle spikerush (Eleocharis acicularis), and arrow head (Sagittaria pygmaea) but not to rice. Appearance of herbicidal activity was very slow (13-18 days after treatment). Since homoalanosine damaged buds and roots rather that treated leaves, it was considered to be translocated in the plant symplastically. Since such movement is necessary for herbicides to control perennial weeds, development of a commercial herbicide from homoalanosine seems promising.

*28. Gardner, J.M., Chandler, J.L., and Feldman, A.W. 1984. Growth promotion and inhibition by antibiotic-producing fluorescent Pseudomonads on citrus roots. Plant and Soil 77: 103-113.

In this investigation, the authors studied the growth effects of root colonizing fluorescent Pseudomonads on rough lemon and sweet orange seedlings. Broth cultures of 43 strains of fluorescent Pseudomonads were applied to the growth medium of the citrus seedlings. After ten months, both inhibition and stimulation of growth were observed, as measured by seedling weight. Approximately half of the bacterial strains were inhibitory and half were stimulatory. In another test, 251 randomly selected strains were evaluated in an in vitro test for antibiotic production. Ninety-four percent had antifungal activity against Geotrichum candidum and 81% had antibacterial activity against Erwinia stewartii.

29. Haneishi, T., Terahara, A., Kayamori, H., Yabe, J., and Arai, M. 1976. Herbicidins A and B, two new antibiotics with herbicidal activity. II. Fermentation, isolation and physico-chemical characterization. Journal of Antibiotics 29: 870-875.

Streptomyces saganonensis produces two compounds, herbicidins A and B, with antimicrobial and herbicidal activity. Herbicidin A is a white powder soluble in water, methanol, ethanol, acetone, and ethyl acetate, but insoluble in chloroform and benzene. Its molecular formula was calculated to be $C_{23} H_{29} O_{11} N_5$-1/2 $H_2O$. Herbicidin B is a white crystal soluble in water, methanol, ethanol, and acetone, but insoluble in ethyl acetate, benzene, and chloroform. Its molecular formula was calculated to be $C_{18} H_{23} O_9 N_5$-1/2 $H_2O$. Both compounds behaved as basic substances.

30. Heisey, R.M., DeFrank, J., and Putnam, A.R. 1985. A survey of soil microorganisms for herbicidal activity. In A. C. Thompson (ed.), The Chemistry of Allelopathy, Biochemical Interactions Among Plants. ACS Symposium Series 268. Amer. Chem. Soc., Washington, D. C., pp. 337-349.

In this investigation, 347 isolates of soil microorganisms, particularly actinomycetes, were screened for production of herbicidal compounds. Ten to twelve percent of these isolates severely inhibited growth of indicator seedlings (cucumber, barnyardgrass, and garden cress). Cycloheximide, a phytotoxic antibiotic with little herbicidal value, was produced by many of the most inhibitory isolates. Several others, however, produced highly toxic broth lacking detectable amounts of cycloheximide. The authors conclude that certain soil microorganisms have potential for production of unique natural product herbicides.

31. Heisey, R.M., Mishra, S.K., Putnam, A.R., Miller, J.R., Whitenack, C.J Keller, J.E., and Huang, J. 1988. Production of herbicidal and insecticidal metabolites by soil microorganisms. In H.C. Cutler (ed.), Biologically Active Natural Products: Potential Use in Agriculture. ACS Symposium Series 380. Amer. Chem. Soc., Washington, D.C., pp. 65-78.

In this study, approximately 1500 isolates of various soil microorganisms were screened for production of herbicidal and insecticidal compounds. In primary screens using seeds of garden cress and barnyardgrass, about 4-12% caused strong inhibition of seed germination or seedling growth. Isolates showing promising herbicidal activity in primary screens were evaluated in secondary screens where solutions of microbial broth were sprayed onto seedlings of barnyardgrass, large crabgrass, green foxtail, proso millet, redroot pigweed, purslane, and velvetleaf. In these screens, 1-2% of the initial total showed strong herbicidal activity.

Among the compounds found to be responsible for phytotoxicity was cycloheximide, well known for its biological activity but having little potential for use as a herbicide in the U.S.

Geldanamycin and nigericin were isolated from a strain of Streptomyces hygroscopicus and evaluated as pre- and postemergence herbicides. Geldanamycin showed greater preemergence activity than nigericin, but had little or no effect postemergence. Nigericin, however, showed striking postemergence herbicidal activity on gardencress and velvetleaf.

3-hydroxybenzyl alcohol, previously isolated from Penicillium urticae, 2-methylhydroquinone, previously isolated from P. urticae, Nectrina erubescens, and Phoma spp., and (+)-epiepoformin, previously isolated from an unidentified fungus were isolated from the culture broth of Scopulariopsis brumptii. Epiepoformin showed strong herbicidal activity against redroot pigweed and mustard, 3-hydroxybenzyl alcohol moderately inhibited redroot pigweed, and 2-methylhydroquinone showed only weak herbicidal activity. The authors conclude that soil microorganisms produce numerous pesticidal metabolites, and believe that these results support the validity of a microbial approach to discovery of new pesticides.

32. Heisey, R.M., and Putnam, A.R. 1986. Herbicidal effects of geldanamycin and nigericin, antibiotics from Streptomyces hygroscopicus. Journal of Natural Products 49: 859-865.

    A wild strain of Stremptomyces hygroscopicus produced two known compounds, geldanamycin and nigericin, not previously recognized as phytotoxins. Both compounds were tested in bioassays for inhibition of garden cress radicle elongation. Both compounds caused 50% reduction in radicle growth at a concentration of 1-2 ppm, and nearly complete inhibitions at 3-4 ppm. Geldanamycin caused radicles to turn brown and disintegrate, whereas nigericin did not cause visible necrosis. Geldanamycin is structurally similar to the herbimycins, previously isolated from S. hygroscopicus, and reported to have herbicidal activity.

33. Heisey, R.M. and Putnam, A.R. 1990. Herbicidal activity of the antibiotics geldanamycin and nigericin. Journal of Plant Growth Regulation 9: 19-25.

    Geldanamycin and nigericin are phytotoxic antibiotics produced by a strain of Streptomyces hygroscopicus. They were tested for herbicidal activity and selectivity on a range of weed and crop plants. In petri dish assays, geldanamycin inhibited radicle growth of all ten plant species tested, whereas nigericin inhibited seven out of ten. When tested on seeds and seedlings in field soil, geldanamycin exhibited preemergent herbicidal activity on certain plant species at applications as low as 0.6 kg/ha, but had no postemergence herbicidal effect. Nigericin has pre- and post emergence herbicidal activity on certain species.

34. Hirota, A., Sakai, H., and Isogai, A. 1985. New plant growth regulators, cladospolide A and B, macrolides produced by Cladosporium cladosporioides. Agricultural and Biological Chemistry 49: 731-735.

    Two compounds with plant growth regulatory activity were isolated from the fungus Cladosporium cladosporioides and identified as cladospolide A and cladospolide B. At 100 ppm, cladospolide A inhibited root elongation of lettuce and rice seedlings by 60 and 30%, respectively. Cladospolide B, on the other hand, promoted root elongation of both lettuce and rice seedlings. Cladospolide A and B were reduced in the laboratory to dihydrocladospolide A and B. Since the dihydrocladospolides were biologically inactive, it is suggested that the double bond is essential for activity. It is further suggested that cladospolide A and B are isomers of each other. The difference in their activities may be related to geometrical and stereochemical factors.

35. Hirota, A., Sakai, H., Isogai, A., Kitano, Y., Ashida, T., Hirota, H., and Takahashi, T. 1985. Absolute stereochemistry of cladospolide A, a phytotoxic macrolide from Cladosporium cladosporioides. Agricultural and Biological Chemistry 49: 903-904.

    The authors of this paper report the absolute configuration of cladospolide A, a phytotoxin produced by Cladosporium cladosporioides. The planar structure of the phytotoxin had previously been described as (E) -4, 5-dihydroxy-2-dodecen-11-olide. The stereochemistry of the three asymmetric carbons was determined by x-ray analysis to be as follows: the configuration at C-4, 5, and 11 is R, S, and R.

36. Howell, C.R. and Stipanovic, R.D. 1984. Phytotoxicity to crop plants and herbicidal effects on weeds of viridiol produced by Gliocladium virens. Phytopathology 74: 1346-1349.

    A phytotoxin was isolated from a strain of Gliocladium virens and identified as the previously known viridiol. This fungus also produces the biologically active compounds gliovirin, gliotoxin, and viridin. Viridin and gliotoxin have previously been shown to inhibit root growth of wheat, white mustard, and red clover seedlings. Viridiol has not been effective as a herbicide under field conditions due to its instability. In this study, a dry granular preparation of the fungal culture grown on rice was incorporated into the soil above planted cotton seed. This preparation inhibited germination of pigweed without toxicity to the cotton. The authors suggest that viridiol is produced by the fungus in culture in sufficient quantity to inhibit pigweed emergence. Since the granular preparation caused radicle stunting and necrosis in all plant species tested, the authors consider it a broad spectrum phytotoxin. They suggest screening for an alternative culture substrate, since rice is not economically feasible.

37. Hradil, C.M., Hallock, Y.F., Clardy, J., Kenfield, D.S., and Strobel, G. 1989. Phytotoxins from Alternaria cassiae. Phytochemistry 28: 73-75.

    Four previously known phytotoxins, stemphyperylenol, stemphyltoxin II, alterperylenol, and altertoxin I, were isolated from the phytopathogenic fungus Alternaria cassiae. A review of the literature about these compounds reveals cases where several different names are assigned to a single structure.

    Stemphyperylenol had previously been isolated from Stemphylium botryosum, a fungal pathogen causing leaf spot of lettuce. Stemphyltoxin II, previously isolated from S. botryosum had also been isolated from A. alternata and named altertoxin II. Alterperylenol had previously been isolated from an Alternaria species. Other researchers had independently named the structure alteichin. In yet another study, alterperylenol and alteichin were erroneously reported to have the same structure as altertoxin II. Altertoxin I had previously been isolated from several Alternaria species. It was named dihydroalterperylenol by Okuno and co-workers.

    In this study, these four compounds from A. cassiae are tested for phytotoxicity to sicklepod, corn, crabgrass, timothy, and soybean. Stemphyperylenol was selectively toxic to crabgrass; altertoxin I was selectively toxic to corn; alterperylenol was somewhat toxic to corn and soybean; and stemphyltoxin II was somewhat toxic to corn.

38. Huang, J., Putnam, A.R., Werner, G.M., Mishra, S.K., and Whitenack, C. 1989. Herbicidal metabolites from a soil-dwelling fungus (Scopulariopsis brumptii). Weed Science 37: 123-128.

    Scopulariopsis brumptii (MSU 42018), isolated from the soil of a potted asparagus plant, produces three herbicidal metabolites: 3-hydroxybenzyl alcohol, 2-methylhydroquinone, and (+)-epiepoformin. The most active compound was (+)-epiepoformin, which provided 99% control of redroot pigweed (Amaranthus retroflexus), 88% control of white mustard (Sinapis alba), and 65% control of green foxtail (Setaria viridis) when sprayed postemergence at 4.5 kg/ha. The other compounds, although phytotoxic to certain species, were considerably less active.

39. Ichihara, A., Hashimoto, M., and Sakamura, S. 1985. (3R, 5Z) – (-) -3-hydroxy-5-dodecenoic acid, a phytotoxic metabolite of Pythium ultimum. Agricultural and Biological Chemistry 49: 2207-2209.

    A phytotoxin was isolated from Pythium ultimum, a fungal pathogen of sugar beet involved in black root disease. The purified phytotoxin, a yellow oil, was identified as (3R, 5Z) – (-) -3-hydroxy-5-dodecenoic acid. 3-hydroxy-5-dodecenoic acid had previously been isolated from Serratia marcescens, but its stereochemistry was not mentioned. Phytotoxicity was tested using seedlings of lettuce, sugar beet, and rice. At 250 ppm, both the root and shoot of sugar beet were darkened; at 100 ppm, only the root was darkened; and 50 ppm appeared to promote growth. The toxin inhibited lettuce shoot and root growth 97.3% and 98.1%, respectively, at 250 ppm. Lower inhibition was observed at lower concentrations. Shoot and root growth of rice were inhibited 31% and 52%, respectively, at 250 ppm. At lower concentrations, less inhibition occurred.

40. Ichihara, A., Oikawa, H., Hayashi, K., Hashimoto, M., Sakamura, S., and Sakai, R. 1984. 3-deoxyaphidicolin and aphidicolin analogues as phytotoxins from Phoma batae. Agricultural and Biological Chemistry 48: 1687-1689.

    The fungus Phoma batae, causal organism of leaf spot disease of sugar beet produced four phytotoxic compounds. Among these was the known antiviral tetrahydroxy diterpene, aphidicolin, previously isolated from Aphalospolium aphidicola, Nigrospora sphaerica, and Harziella entomophilla. Three aphidicolin derivatives were also isolated: aphidicolin-17-mono-acetate, 3-deoxyaphidicolin, and aphidicolin-3, 18-orthoacetate. These inhibited the root growth of both rice and lettuce seedlings. Aphidicolin-17-monoacetate and 3-deoxyaphidicolin also inhibited in vitro DNA synthesis of sea urchin embryos and Hela cells.

41. Ichihara, A., Tazaki, H., and Sakamura, S. 1985. The structure of zinnolide, a new phytotoxin from Alternaria solani. Agricultural and Biological Chemistry 49: 2811-2812.

    A new phytotoxic compound, zinnolide, was isolated from Alternaria solani, causal fungus of early blight of tomato and potato. This fungus also produces three other phytotoxins: solanapyrones A, B, and C. Zinnolide is a colorless solid with a molecular formula of $C_{15} H_{18} O_5$. The structure of zinnolide is closely related to zinniol, isolated from the phytopathogenic fungus A. zinniae. Phytotoxicity of zinnolide was weak compared to that of the solanapyrones. At 100 ppm, zinnolide inhibited hypocotyl and root growth of lettuce 34.5% and 22.0%, respectively.

*42. Isogai, A., Fukuchi, N., Yamashita, S., Suyama, K., and Suzuki, A. 1989. Syringostatins, novel phytotoxins produced by Pseudomonas syringae pv. syringae. Agricultural and Biological Chemistry 53: 3117-3119.

Several phytotoxic compounds referred to as syringostatins were isolated from the bacterium Pseudomonas syringae pv. syringae, the causal organism of bacterial blight of lilac (Syringa vulgaris). This bacterium is pathogenic to a wide range of plant species, causing a variety of symptoms including spotting of leaves and fruits, blossom blight, and stem cankers. It has been previously reported that the phytotoxins syringomycin and syringotoxin are produced by other strains of P. syringae. After partial characterization of the syringostatins, however, the authors conclude that the syringostatins are similar to syringomycin and syringotoxin, but have clearly different amino acid compositions. Syringostatins are reported to have phytotoxic and antifungal activity.

43. Isogai, A., Washizu, M., Kondo, K., Murakoshi, S., and Suzuki, A. 1984. Isolation and identification of (+)-hexylitaconic acid as a plant growth regulator. Agricultural and Biological Chemistry 48: 2607-2609.

Aspergillus niger (K-88 strain) produces (+)-hexylitaconic acid. At concentrations between 2 and 20 ppm (+)-hexylitaconic acid stimulates root growth of lettuce and rice seedlings. At concentrations exceeding 100 ppm, however, (+)-hexylitaconic acid, and its dihydro and methyl ester derivatives all inhibited root growth of lettuce seedlings.

44. Iwai, Y., Nakagawa, A., Sadakane, N., and Omura, S. 1980. Herbimycin B, a new benzoquinonoid ansamycin with anti-TMV and herbicidal activities. Journal of Antibiotics 33: 1114-1119.

The authors report the isolation of a second herbicidal compound, herbimycin B, from a strain of Streptomyces hygroscopicus, that also produces herbimycin A. The chemical and biological properties of herbimycin B indicated it is an analog of herbimycin A. Herbimycin B showed herbicidal activity against both monocot and dicot plant species, however, its activity was weaker than that of herbimycin A.

45. Jarvis, B.B., Midiwo, J.O., Tuthill, D., and Bean, G.A. 1981. Interaction between the antibiotic trichothecenes and the higher plant Baccharis megapotamica. Science 214: 460-461.

In this study, the authors report that the Brazilian shrub Baccharis megapotamica absorbs, translocates, and chemically alters the baccharinoids, trichothecene antibiotics presumably produced by a soil fungus. These compounds, previously isolated from cultures of saprophytic soil fungi and from B. megapotamica are closely related to the macrocyclic trichothecenes known as the roridins and the verrucarins. The baccharinoids found in B. megapotamica were present in concentrations that would normally be phytotoxic. When B. megapotamica was fed roridin A and verrucarin A, the plant had converted these to their 8-hydroxyl derivatives and did not die. Tomato pepper, and artichoke seedlings fed roridin A and verrucarin A showed severe damage and were killed within three days. The authors suggest that the baccharinoids isolated from B. megapotamica are a result of chemical modification of roridin A by B. megapotamica.

46. Jones, R.W., Lanini, W.T., and Hancock, J.G. 1988. Plant Growth response to the phytotoxin viridiol produced by the fungus Gliocladium virens. Weed Science 36: 683-687.

    Several compounds with biological activity are produced by the fungus Gliocladium virens. Among these are the antifungal and antibacterial compounds gliotoxin and gliovirin, and the phytotoxin viridiol. Viridiol causes necrosis on radicles of germinating seed. When cultured on rice grains, the fungus produces levels of viridiol sufficient to prevent weed seed emergence if the rice mixture is incorporated into seed beds. This mycoherbicide mixture was believed to be an attractive method of weed control for several reasons. G. virens is not plant pathogenic, therefore, it cannot infect non-target plants. Also, once the nutrient substrate is depleted, G. virens would exist in the soil as a saprophyte, in which stage it has been reported to suppress some soilborne phytopathogens. Use of the nutrient substrate, rice, however, makes this weed control method uneconomical.

    In this study, the authors cultured G. virens on peatmoss with added sucrose and ammonium nitrate. It was believed this culture medium would result in viridiol production sufficient to control seedling emergence if added to soil. The mycoherbicide mixture was tested on 15 different crop species and 17 different weed species to determine their sensitivity to viridiol. A wide spectrum of activity was observed. Weeds were generally more sensitive than crops, and damage to crops could be avoided by placement of the mycoherbicide mixture away form the crop's root zone. For most weeds, emergence was reduced more than 90%. Those seedlings that did emerge exhibited depressed growth. Viridiol was most effective against annual Composite species and least effective on monocots. The authors conclude that this type of weed control may be useful, particularly in situations where use of chemical herbicides is unfavorable and where localized application is possible.

47. Kamata, S., Sakai, H., and Hirota, A. 1983. Isolation of acetylaranotin, bisdethiodi (methylthio)-acetylaranotin, and terrein as plant growth inhibitors from a strain of Aspergillus terreus. Agricultural and Biological Chemistry 47: 2637-2638.

    Three phytotoxins were isolated from Aspergillus terreus and identified as acetylaranotin, bisdethiodi (methylthio)-acetylaranotin, and terrein. Acetylaranotin was previously known to have antiviral properties. In bioassays using lettuce and rice seedlings, bisdethiodi (methylthio)-acetylaranotin at a concentration of 100 ppm reduced root elongation of lettuce seedlings, but had no effect on rice. Acetylaranotin appeared to be the most active compound, reducing root elongation of lettuce 80% at a concentration of only 10 ppm. Rice root length was reduced by 50% and 80% at 50 and 100 ppm, respectively. Terrein reduced lettuce root length 20% at 50 ppm, and rice root length 40% at 100 ppm. The disulfide bridge of acetylaranotin appears to be responsible for greater biological activity.

48. Katouli, M. and Marchant, R. 1981. Effect of phytotoxic metabolites of Fusarium culmorum on growth and physiology of barley plants. Plant and Soil 60: 377-384.

Two phytotoxic organic acids were isolated from Fusarium culmorum. These were not identified, but their physiological effects were evaluated in studies with barley seedlings. The purified organic acids were added to the nutrient growth medium of barley seeds. Reduction in root growth, nutrient deficiency, leaf rolling, wilt, and stomata1 closure were observed. It was suggested that reduced root growth limited the absorbing surface area sufficiently to produce a water deficit, which in turn caused the closure of stomata to prevent water loss.

49. Kenfield, D., Bunkers, G., Strobel, G. A., and Sugawara, F. 1988. Potential new herbicides - phytotoxins from plant pathogens. Weed Technology 2: 519-524.

In this review article, the authors summarize recent research involving phytotoxins in their Montana State University laboratory. The eremophilanes are a group of bicyclic sesquiterpenoids. Among those showing phytotoxicity are: phonemone, produced by the fungus Phoma exigua; phaseolinone, produced by Macrophomina phaseolina; bipolaroxin, produced by Bipolaris cynodontis, a fungal pathogen of bermuda grass; and gigantenone and petasol, both produced by Drechslera gigantea. Phomenone, phaseolinone, gigantenone, and petasol cause necrosis on many dicots. On monocots, however, phomenone, gigantenone, and petasol cause “green islands” (areas of chlorophyll retention in senescing tissue). Bipolaroxin selectively causes lesions on bermuda grass at low concentrations, but at high concentrations, it also affects corn, wild oats, and sugarcane.

Several species of Dreschlera produce a group of sesquiterpenoids, the ophiobolins. Among these are Epi A (6-epiophiobolin A) and Ophio A (ophiobolin A), produced by D. Maydis, etiological agent of southern corn leaf blight; D. sorghicola, a pathogen of johnsongrass; D. oryzae, causal organism of brown spot on rice; and D. heveae, a pathogen of rubber trees. These compounds were toxic to a variety of dicots and grasses. Epi A selectively inhibits CO fixation in corn with Texas male sterile cytoplasm at concentrations three times smaller than in corn with normal cytoplasm. Ophio A is equally toxic to both types of corn. Interestingly, these two compounds differ only in the orientation of the proton on C6.

The curvulins are cyclic polyketides produced by various fungi. Curvulin and O-methylcurvulinic acid are produced by D. indica, a pathogen of common purslane and spiny amaranth. At low concentrations, curvulin is selective towards common purslane and spiny amaranth, but at higher concentrations, it is more broadly toxic. O-methylcurvulinic acid is also generally phytotoxic.

De-O-methyldiaporthin is a novel isocoumarin produced by D. siccans, a fungal pathogen of perennial ryegrass and oats. When applied to abaxial surfaces of leaves, it is a non-specific toxin.

The resorcylides are compounds first isolated from a species of Penicillium and later from D. phlei. The trans isomer is cytotoxic, antimicrobial, inhibits rice root growth, and causes necrosis on corn, large crabgrass, timothy, wild poinsettia, and common sunflower.

Triticones A and B are toxins containing a spirocyclic r-lactam moiety. They are produced by D. tritici-repentis, causal organism of tan spot on wheat, and Curvularia clavata, a pathogen of turfgrass. Weeds such as common lambsquarters, redroot pigweed, leafy spurge, and dandelion are sensitive to triticone A. In wheat, triticone A kills protoplasts and inhibits esterase activity and CO fixation. In isolated chloroplasts of spinach, oats, and wheat, triticone A inhibits photosynthetic electron transport.

Tryptophol is a compound produced by D. nodulosum, a pathogen of goosegrass. At low concentrations, it is selectively toxic to goosegrass, but at high concentrations, it is toxic to many grasses and dicots.

The maculosins are cyclic dipeptides belonging to the chemical class of diketopiperazines. Maculosins were isolated from Alternaria alternata, a pathogen of spotted knapweed. Some are non-toxic, but maculosin 1 selectively produces necrotic lesions on spotted knapweed at a range of concentrations.

The authors infer from these studies that toxins are usually found as groups of related analogs having a range of various biological activities, and that even crop pathogens may produce toxins with potential as herbicidal compounds.

50. Kida, T., Takano, S., Ishikawa, T., and Shibai, H. 1985. A simple bioassay for herbicidal substances of microbial origin by determining de novo starch synthesis in leaf segments. Agricultural and Biological Chemistry 49: 1299-1303.

The authors point out that herbicides inhibiting photosynthesis are particularly attractive due to their selective toxicity between plants and animals. In screening large numbers of microbial culture broths for metabolites with herbicidal activity, the use of whole plants is impractical. The authors developed an in vitro assay sensitive to small concentrations of herbicidal microbial metabolites. It consists of the de novo detection of starch synthesis in excised leaf segments and algal cell oxygen evolution in photosynthesis. By using this assay, the authors expected to find inhibitors of photosynthetic electron transport, inhibitors of carbon dioxide fixation, and inhibitors of starch synthesis.

51. Kihara, T., Kobinata, K., Kusakabi, H., and Isono, K. 1983. New antibiotics algacidins A and B. Journal of Antibiotics 36: 1777-1780.

Streptomyces sp. RK-1339 produced two antibiotics: algacidins A and B. These were toxic to algae and fungi, but showed only weak activity against bacteria. The antibiotics were also toxic to Yoshida sarcoma cells in culture, and mice. The molecular formulas for algacidin A and B were determined by mass spectroscopy and elemental analysis to be $C_{50}H_{87}NO_{14}$ and $C_{50}H_{85}NO_{13}$, respectively.

*52. Kono, Y., Gardner, J.M., and Takeuchi, S. 1986. Nonselective phytotoxins simultaneously produced with host-selective ACTG-toxins by a pathotype of Alternaria citri causing brown spot disease of mandarins. Agricultural and Biological Chemistry 50: 2401-2403.

Alternaria citri, the fungus responsible for brown spot disease of the Dancy tangerine and other mandarins is known to produce the host-selective ACTG-toxins A to F. In this study, the authors report production of other nonspecific toxins by this fungus. They isolated and identified the previously known phytotoxins tentoxin and tenuazonic acid, and the new stereochemically novel dihydrotentoxin. At a concentration of 100 ug/ml, dihydrotentoxin caused the same degree of chlorosis in lettuce seedlings as tentoxin did at 0.4-0.8 ug/ml. Chemically reduced tentoxin, however, showed no activity even at 200 ug/ml. The authors suggest that dihydrotentoxin retains a conformation close to that of tentoxin more easily than reduced tentoxin does, and that this conformation is essential for biological activity.

53. Kremer, R.J. 1986. Bacteria can battle weed growth. American Nurseryman, October 15 issue: 162-163.

The author discusses two main types of rhizosphere microorganisms: those that benefit the host plant and those that are deleterious to it. The deleterious rhizobacteria are likely to damage the host by release of toxins. The main types of deleterious rhizobacteria are listed. These include the Pseudomonas, Erwinia, Enterobacter, Flavobacterium, and Alcaligenes genera. The author cites an investigation where potentially deleterious rhizobacteria were tested for inhibition of velvetleaf, pigweed, jimsonweed, cocklebur, and morning glory seedlings. Significant decreases in weed seedling growth or vigor were observed in these experiments and attributed to the effects of phytotoxins. The author advocates further investigation of these deleterious rhizobacteria and possible commercial development of these for use in agriculture.

54. Lalitha, B., Snow, J.P., and Berggren, G.T. 1989. Phytotoxin production by Diaporthe phaseolorum var. caulivora, the causal organism of stem canker of soybean. Phytopathology 79: 499-504.

A toxin was isolated from Diaporthe phaseolorum var. caulivora which caused reddish brown lesions on stems and reddish discoloration of leaf veins of soybean. These are symptoms typical of stem canker of soybean, caused by D. phaseolorum var. caulivora. The toxin was not identified, but it was purified and determined to have a molecular weight less than 1000. Using a leaf puncture bioassay, at least 4 ug of dried TLC-purified toxin was required to produce reddish veinal discoloration within 36 hours. Twelve plant species were tested for phytotoxicity by immersing the petioles of excised leaves into toxin solutions. Only soybean and lima bean, both hosts of the fungus, reacted to the toxin. Different amounts of the toxin were produced by various isolates of the fungus, and greater toxin production was correlated with greater symptom expression. High doses of toxin produced longer cankers. It is suspected that this toxin is involved in disease development of stem canker of soybean.

55. Lamprecht, S.C., Marasas, W.F.O., Sydenham, E.W., Thiel, P.G., Knox-Davies, P.S., and VanWyk, P.S. 1989. Toxicity to plants and animals of an undescribed, neosolaniol monoacetate-producing Fusarium species from soil. Plant and Soil 114: 75-83.

Several isolates of a fungus were obtained from soil samples and plant debris in South Africa. These closely resembled Fusarium camptoceras, but differed by the presence of a red pigment, characteristic terminal pairs of chlamydospores, and pedicellate macroconidia produced in sporodochia. In previous studies, this undescribed fungus was tested for pathogenicity to annual Medicago spp. (medics). Seedling damp-off, discoloration, necrosis, and root die-back were observed. Since the Fusarium sp. could not be isolated from diseased plants, it was concluded that a phytotoxin was involved. Fusarium spp. are known to be producers of phytotoxic tricothecenes including DAS, T-2 toxin, and NMA.

In this study, isolates of this undescribed Fusarium sp. and reference cultures of known pathogenic Fusarium isolates were tested for toxicity to animals and plants, and presence of NMA (8-acetylneosolaniol, 4, 8, 15-triacetoxy-3-α-hydroxy-12, 13-epoxy trichothec-9-ene). Production of NMA was not detected in the cultures of Fusarium camptoceras tested. Ten of the twelve isolates of the undescribed Fusarium sp. produced NMA, and all of these isolates were toxic to ducklings. Eleven of the undescribed Fusarium sp. isolates caused from 26 to 78% mortality to medicago plants grown in soil containing solutions of the undescribed Fusarium sp. culture. Surviving plants were stunted, discolored, necrotic, and exhibited root die-back. Six of these Fusarium isolates were significantly more toxic than the known pathogen F. graminearum. Mortality of medicago plants and NMA yield were significantly correlated. It was concluded that the phytotoxin NMA is involved in the phytotoxicity of this Fusarium species.

56. Lax, A.R. and Shepherd, H.S. 1988. Tentoxin: a cyclic tetrapeptide having potential herbicidal use. In H. G. Cutler (ed.), Biologically Active Natural Products. ACS Symposium Series 380. Amer. Chem. Soc., Washington, D.C., pp. 24-34.

Tentoxin is a phytotoxic non-host specific cyclic tetrapeptide produced by the fungus Alternaria alternata. It causes chlorosis in plants due to inhibition of chlorophyll production, resulting in reduced vigor and eventual death. Its mode of action, which is centered in the chloroplasts, included inhibition of ATPase activity in chloroplast and thylakoid membranes and selective disruption of protein transport into chloroplasts. A major current drawback to field testing and possible herbicidal use of tentoxin is low production of the toxin by A. alternata. The use of this compound as a herbicide is estimated to be at least several years away.

57. Lax, A.R., Shepherd, H.S., and Edwards, J.V. 1988. Tentoxin, a chlorosis-inducing toxin from Alternaria as a potential herbicide. Weed Technology 2: 540-544.

Tentoxin, a phytotoxic cyclic tetrapeptide produced by the fungus Alternaria alternata, exhibits characteristics desirable in an ideal herbicide: inherent selectivity, potent phytotoxic activity, and a high degree of environmental safety. It produces chlorosis in various species of both monocots and dicots, but does not kill corn or soybeans. It exhibits a high degree of selectivity, and at least in one instance, resistance to tentoxin is maternally inherited. Tentoxin production by traditional fermentations or laboratory synthesis currently gives yields too low for its economical use as a herbicide. Further understanding of tentoxin biosynthesis, however, may provide a more effective means of production.

*58. Lee, R.F., Raju, B.C., Nyland, G., and Goheen, A.C. 1982. Phytotoxin(s) produced in culture by the Pierce's disease bacterium. Phytopathology 72: 886-888.

The rickettsia like bacterium that causes Pierce's disease of grape is the same organism that causes the diseases almond leaf scorch and alfalfa dwarf. The authors isolated a phytotoxic preparation from grapevines infected with Pierce's disease, almond infected with leaf scorch, and alfalfa infected with alfalfa dwarf. In bioassays using grape leaves and rooted cuttings, the phytotoxic preparation caused scalding and necrosis of leaf margins, characteristic symptoms of Pierce's disease. Detached leaves, spurs, and young shoots of almond and plum treated with the toxic preparation developed necrosis of leaf margins, symptoms characteristic of almond leaf scorch and plum leaf scald, respectively. No burning or scorching symptoms were shown by several other woody and herbaceous plants bioassayed with the toxin. The authors suggest that the toxins produced by this bacterium may be important in disease symptom development.

59. Manulis, S., Kashman, Y., Netzer, D., and Barash, I. 1984. Phytotoxins from Stemphylium botryosum: structural determination of stemphyloxin II, production in culture and interaction with iron. Phytochemistry 23: 2193-2198.

Stemphylium botryosum, causal organism of leaf spot and foliage blight disease of tomato produces two closely related phytotoxins, stemphyloxin I and II. Stemphyloxin I is a β-ketoaldehyde trans-decalone. Stemphyloxin II differs by the absence of a saturated ketone and the alteration of the β-ketoaldehyde group. Even though both toxins were isolated from culture filtrates of S. botryosum, it is uncertain whether stemphyloxin II is a true natural compound since stemphyloxin I easily undergoes acid or base catalyzed transformation into stemphyloxin II. In studying the nutritional factors affecting production of stemphyloxin I and II, it was determined that the presence of dicarboxylic acids, such as succinate, fumarate, or malonate increases production of these toxins. The authors suggest that compounds derived from the tricarboxylic acid cycle are closely linked to the biosynthetic precursors of stemphyloxin I and II. It was also found that secretion of stemphyloxin I and II is regulated by the presence of iron, and both compounds act as ferric chelates. It was speculated that this iron-chelating ability is related to phytotoxic activity. Phytotoxicity was tested by various bioassays including symptom development on tomato leaves, inhibition of root elongation, inhibition of protein synthesis, and growth inhibition of duckweed. The phytotoxicity of stemphyloxin I was approximately 100 times greater than that of stemphyloxin II.

60. Mazars, C., Rossignol, M., Auriol, P., and Klaebe, A. 1990. Phomozin, a phytotoxin from Phomopsis helianthi, the causal agent of stem canker of sunflower. Phytochemistry 29: 3441-3444.

Phomopsis helianthi, a fungal pathogen of sunflower causing leaf necrosis and stem cankering, produced the phytotoxin, phomozin. Phomozin is an ester of orsellinic acid and the diol acid, dimethylglyceric acid. It has a molecular formula of $C_{13}H_{16}O_7 H_2O$. In bioassays where phomozin solutions were applied to excised sunflower leaves, phomozin induced extending brown lesions within 24 hours. Phomozin was ineffective on leaves of melon, soybean, corn, pea, and tobacco. Further biological studies are suggested.

61. Misato, T. 1982. Present status and future prospects of agricultural antibiotics. Journal of Pesticide Science 7: 301-305.

The author lists reasons why natural products research is becoming more popular, outlines advantages and disadvantages of these compounds over synthetic pesticides, and discusses future prospects for development of natural products into commercial pesticides.

The need to increase agricultural productivity necessitates the use of pesticides, preferably ones which are safe from human health and environmental perspectives. Antibiotics possess the following advantages: they degrade rapidly in the environment, the quantity needed to protect crops is 10-100 times less that for synthetic pesticides, many are selectively toxic to target organisms, a single set of equipment may be used to produce several varieties of antibiotics in production facilities, and they are produced by microorganisms, a relatively inexhaustible resource. Antibiotics possess the following disadvantages: greater effort is required for accurate microanalysis, plant pathogens may develop resistance to antibiotics produced by related microorganisms, and regulations regarding the use of antibiotics are rigid.

The author is optimistic about the future of antibiotics as pesticidal products, particularly due to their low mammalian toxicity and non-polluting nature. He also expects rapid progress in the fields of biotechnology and genetic manipulation which could facilitate development of antibiotics as commercial pesticides.

62. Misato, T. 1983. Recent status and future aspects of agricultural antibiotics. pp. 241-246 in Takahashi, N., Yoshioka, H., Misato, T., and Matsunaka, S., eds. Pesticide Chemistry: Human Welfare and the Environment, Vol. 2, Natural Products. Pergamon Press. Oxford.

In this article, the author discusses the use of microbially-produced antibiotics in agriculture. While synthetic pesticides have dramatically increased crop yields, they also may be sources of environmental pollution. This has resulted in the exploitation of antibiotics produced by soil microorganisms, particularly in Japan. Recently, use of antibiotics as fungicides, insecticides, and herbicides has become more wide spread. Commonly used pesticides of microbial origin include Blasticidin S, Kasugamycin, polyoxin, and validamycin as fungicides; streptomycin and Bacillus thuringensis for control of bacteria; tetranactin as a miticide; and bialaphos as a herbicide. The author lists advantages and disadvantages of antibiotics for use in agriculture. Their advantages include rapid degradation and non-polluting nature, effectiveness in small quantities, selective toxicity to target organisms, low equipment requirement in production facilities, and synthesis by a renewable resource. Disadvantages include difficulties in microanalysis, possible development of resistance by plant pathogens, and rigidity in regulations regarding antibiotic use.

The author concludes that the future of agricultural antibiotics is bright, and that progress in biotechnology will facilitate their mass production.

63. Misato, T., and Yamaguchi, I. 1984. Pesticides of microbial origin. Outlook on Agriculture 13: Pergamon Press, Great Britain.

The authors discuss the use of microbial products as fungicides, bactericides, herbicides, and insecticides. Cycloheximide, anisomycin, toyokamycin, herbicidin A and B, herbimycin, and bialaphos are listed as microbial products possessing herbicidal activity. Several advantages and disadvantages of using microbially-produced compounds in agriculture are discussed, as in reference numbers 61 and 62, above. The authors propose that such compounds be designated “micro-origin pesticides” as opposed to “agricultural antibiotics” in hopes of emphasizing their non-polluting nature and stimulating further interest in their development and exploitation.

64. Mishra, S.K., Taft, W.H., Putnam, A.R., and Ries, S.K. 1987. Plant growth regulatory metabolites from novel actinomycetes. Journal of Plant Growth Regulation 6: 75-84.

Approximately 800 isolates of actinomycete bacteria were tested for production of compounds that stimulated or inhibited plant growth. In primary screens of microbial culture broth using the alga Chlamydomonas reinhardtii as an indicator, 60 isolates inhibited algal growth by 30% or more. Over half of these isolates were Streptomyces strains. In secondary screening tests of culture broth extracts on higher plants grown in the greenhouse, 9 actinomycete isolates caused growth inhibition. Again, the genus Streptomyces was the most common producer of plant growth inhibitory substances.

65. Mishra, S.K., Whitenack, C.J., and Putnam, A.R. 1988. Herbicidal properties of metabolites from several genera of soil microorganisms. Weed Science 36: 122-126.

Approximately 900 strains of microorganisms isolated from soil samples were tested for production of herbicidal compounds. These microorganisms included 266 Streptomyces isolates, 502 other actinomycete bacteria, 70 fungi, and 40 isolates of other eubacteria. Compounds produced by 72 of the isolates inhibited germination of garden cress seeds in petri dish assays. Three actinomycete genera yielded a high frequency (13-18%) of herbicide-producing isolates: Streptomyces, Nocardiopsis, and Actinoplanes. Other inhibitory bacteria included isolates of Actinomadura, Micromonospora, Micropolyspora, Streptoverticillium, Streptosporangium, and Bacillus. Toxin-producing fungi included isolates of Penicillium, Aspergillus, Scopulariopsis, and Paecilomyces.

66. Mitchell, R.E. 1984. A naturally-occurring structural analogue of the phytotoxin coronatine. Phytochemistry 23: 791-793.

Pseudomonas syringae pv. atropurpurea is a bacterial pathogen of Italian ryegrass. On leaves, its necrotic infection sites are surrounded by chlorotic haloes. The phytotoxin coronatine is produced by cultures of P. syringae pv. atropurpurea and is believed to be responsible for this chlorosis. In this study, the author reports isolation and identification of a second phytotoxin closely related to coronatine, N-coronafacoylvaline. Both compounds are amides of coronafacic acid, and both induced chlorosis in bean leaves using a leaf prick assay. Coronafacic acid, isolated from carboxylic acids produced by P. syringae pv. atropurpurea had no detectable biological activity. A synthetic analogue of coronatine which contains isoleucine in place of valine showed lower biological activity than coronatine.

*67. Morooka, N., Tatsuno, T., Tsunoda, H., Kobayashi, K., and Sakurai, T. 1986. Chemical and toxicological studies of the phytotoxin, 6-α, 7β, 9α-trihydroxy-8 (14), 15-isopimaradiene-20, 6-γ-lactone, produced by a parasitic fungus, Phomopsis sp., in wilting pine trees. Agricultural and Biological Chemistry 50: 2003-2007.

The authors outline previous research involving wilt disease of Japanese red pine (Pinus densiflora). Pine wilt had been thought to be caused by the pine wood nematode, however, recent studies suggested pathogenic fungi might be responsible. More than 30 species of fungi were found in the trunks of wilting pine trees. Inoculation of young red pines with some of these species, including Phomopsis sp., caused typical pine wilt symptoms within four months. Resin canals of infected trees were invaded by the fungus, and surrounding epithelial cells turned brown. Cytotoxic metabolites were believed to be produced by the invading fungus.

A cytotoxic substance produced by Phomopsis sp. was isolated and identified as isopimarane diterpene γ-lactol, 6, 7, 9-trihydroxy-8 (14), 15-isopimaradiene-20, 6-γ-lactone. It inhibited proliferation of red pine tree callus in bioassays. Browning and degeneration of the callus occurred at a concentration of 150 ppm. Browning of epithelial cells in wilted pines is believed to be related to production of this or other cytotoxins produced by Phomopsis or other fungi infecting these trees.

*68. Nagata, T. and Ando, Y. 1989. Oxysporone, a phytotoxin isolated from the tea gray blight fungus Pestalotia longiseta. Agricultural and Biological Chemistry 53: 2811.

A phytotoxic compound was isolated from the fungus Pestalotia langiseta, the causal organism of tea gray blight. The disease is characterized by concentrically zoned lesions on the leaf. The toxin was identified as oxysporone, previously isolated from Fusarium oxysporum. In a leaf-necrosis assay using the tea cultivar "Yabukita", oxysporone caused leaf necrosis at a dose of about 15 ppm.

69. Nakajima, H., Hamasaki, T., and Kimura, Y. 1989. Structure of spiciferone A, a novel γ-pyrone plant growth inhibitor produced by the fungus Cochliobolus spicifer Nelson. Agricultural and Biological Chemistry 53: 2297-2299.

Spiciferone A, a fungal metabolite containing a bicyclic unit composed of a fully substituted γ-pyrone and a cyclohexenone, was isolated from Cochliobolus spicifer. Lettuce seedling germination was inhibited 70 percent by administration of spiciferone A at a concentration of 100 mg/l.

*70. Nemec, S., Baker, R.A., and Tatum, J.H. 1988. Toxicity of dihydrofusarubin and isomarticin from Fusarium solani to citrus seedlings. Soil Biology and Biochemistry 20: 493-499.

At least eleven naphthoquinones are produced by Fusarium solani, a fungus commonly associated with citrus roots in Florida. The phytotoxic effects of two of these naphthoquinones, dihydrofusarubin and isomarticin, were studied using rough lemon (Citrus limon) seedlings. Lemon seedlings were exposed to solutions of these compounds for up to 19 days. Both compounds caused leaf roll, leaf dehydration, wilt, and veinal chlorosis. The development of resinous vessel plugging was also observed. In previous studies, it had been shown that isomarticin disrupted the chloroplast membrane of peas. It is suggested that vessel plugging probably occurs as a result of membrane leakage or by cell wall degradation since naphthoquinones are low molecular weight compounds and cannot mechanically plug vessels.

*71. Nemec, S., Phelps, D., and Baker, R. 1989. Effects of dihydrofusarubin and isomarticin from Fusarium solani on carbohydrate status and metabolism of rough lemon seedlings. Phytopathology 79: 700-705.

Fusarium solani, an opportunistic pathogen of citrus, produces many phytotoxic naphthoquinones. The fungus causes root rot and stem cankers on infected citrus. The authors suggest that the naphthoquinones may be the responsible agents. Other studies indicate six of these naphthoquinones interfere with respiration by inhibiting anaerobic decarboxylation of pyruvate in vitro and decarboxylation of α-ketoglutaric acid. Some of these compounds have inhibited glutamine synthetase, affected semipermeability of leaf tissue, and have disrupted chloroplast membranes. In this study, the authors examine the effects of F. solani and two of the naphthoquinones, isomarticin and dihydrofusarubin, on seedlings or rough lemon (Citrus limon). Seedlings inoculated with the fungus and those with roots suspended in solutions of isomarticin and dihydrofusarubin developed wilt symptoms, however only those in dihydrofusarubin solution developed chlorosis. In inoculated plants, total soluble and reducing sugars and starch were reduced, but in naphthoquinone-treated plants only starch was reduced. Both inoculated plants and naphthoquinone-treated plants exhibited accumulation of minerals in leaves. Respiration rates increased in dihydrofusarubin-treated plants. The authors suggest this increase is due to stimulation of mitochondrial oxidases.

72. Nukina, M. 1987. Pyrichalasin H, a new phytotoxic metabolite belonging to the cytochalasans from Pyricularia grisea (Cooke) Saccardo. Agricultural and Biological Chemistry 51: 2625-2628.

Pyrichalasin H is a newly identified phytotoxin produced by the fungus Pyricularia grisea (Isolate designation: Saccardo IFO 7287). It inhibits rice seedlings at 1 ug/ml and causes a characteristic curling of the shoot. The structure of pyrichalasin H was determined to be (7S, 16S, 18R, 21R) -21-acetoxy-7, 18-dihydroxy-16, 18-dimethyl-10-p-methoxyphenyl-[11] cytochalasa-6 (12), 13 (E), 19 (E)-triene-1-one.

*73. Nukina, M. 1988. Terrestric acid as a phytotoxic metabolite from Pyricularia oryzae Cavara. Agricultural and Biological Chemistry 52: 2357-2358.

Terrestric acid, previously isolated from Penicillium terrestre, was isolated from two strains of the fungus Pyricularia oryzae Cavara, the causal organism of rice blast disease. Phytotoxicity of this compound was tested on rice seedlings. Root and shoot growth were inhibited at 100 ppm and 300 ppm, respectively. A yellowing of the shoot at 50 ppm suggested possible influence of terrestric acid on chlorophyll synthesis.

*74. Okuno, T., Oikawa, S., Goto, T., Sawai, K., Shirahama, H., and Matsumoto, T. 1986. Structures and phytotoxicity of metabolites from Valsa ceratosperma. Agricultural and Biological Chemistry 50: 997-1001.

Five isocoumarins were isolated from the fungus Valsa ceratosperma, the causal organism of apple canker. Three of these were identified as the known compounds (-)-5-methylmellein, (-)-5-carboxymellein, and (-)-5-hydroxymethylmellein. Two isocoumarins, (+)-(3R, 4S)-trans-4-hydroxy-5- methylmellein and (-) – (3R, 4R) -cis-4-hydroxy-5-methylmellein, produced by V. ceratosperma were not previously known. In bioassays for phytotoxicity, all five compounds caused browning of the cambium and phloem tissue of apple shoots at a concentration of 100 ppm. Lettuce seedlings were inhibited by all five compounds at a concentration of 500 ppm,

with (+)-(3R, 4S)-trans-4-hydroxy-5-methylmellein showing the strongest inhibition. The most potent phytotoxin, however, was considered to be 5-carboxylmellein.

75. Omura, S., Hinotozawa, K., Nobutaka, I., and Murata, M. 1984. The structure of phosalacine, a new herbicidal antibiotic containing phosphinothricin. Journal of Antibiotics 37: 939-940.

The chemical structure of phosalacine, a new phosphorous-containing tripeptide with herbicidal activity, is described. Phosalacine was isolated from the culture filtrate of Kitasatosporia phosalacinea sp. nov. KA-338. It was found to be composed of alanine, leucine, and an unusual amino acid, phosphinothricin. Phosphinothricin is a component of phosphinothricylalanylalanine (bialaphos), a known glutamine antimetabolite.

76. Omura, S., Iwai, Y., Takahashi, Y., Sadakane, N., Nakagawa, A., Oiwa, H., Hasagawa, Y., and Ikai, T. 1979. Herbimycin, a new antibiotic produced by a strain of Streptomyces. Journal of Antibiotics 32: 255-261.

An antibiotic compound, herbimycin, was produced by Streptomyces hygroscopicus. Its molecular formula was determined as $C_{30}H_{42}N_2O_9$. It was soluble in various organic solvents, but insoluble in water. Its physicochemical properties suggest that herbimycin belongs to the ansamycin antibiotics. At a concentration of 200 ug/ml, herbimycin showed weak antimicrobial activity against Sarcina lutea, Candida albicans, Saccharomyces sake, Piricularia oryzae, and Aspergillus niger. No antimicrobial activity was observed at 100 ug/ml. Pre-emergence and post-emergence herbicidal activity were tested on various monocots and dicots. Potent herbicidal activity was observed, especially in the pre-emergence system. The $LD_{50}$ of herbimycin to mice was 19 mg/kg by intraperitoneal injection.

77. Omura, S., Murata, M., Hanaki, H., Hinotozawa, K., Oiwa, R., and Tanaka, H. 1984. Phosalacine, a new herbicidal antibiotic containing phosphinothricin. Fermentation, isolation, biological activity, and mechanism of action. Journal of Antibiotics 37: 829-835.

In screening actinomycetes for compounds possessing antitumor or herbicidal activity, Kitasatosporia phosalacinea sp. nov. KA-338 was shown to produce an antibiotic with herbicidal activity. Its structure was determined to be L-phosphinothricyl -L-alanyl-L-leucine, and the antibiotic was named phosalacine. Phosalacine exhibited antimicrobial activity on various gram-positive and gram-negative bacteria and some fungi. Visual assessment of alfalfa seedlings treated with phosalacine revealed herbicidal activity at a concentration as low as 10 ug/ml. No toxicity was observed when phosalacine was administered to mice. It is speculated that after phosalacine becomes incorporated into bacterial or plant cells it is converted to phosphinothricin, which inhibits glutamine synthetase and results in antimicrobial or herbicidal activity. The authors suggest phosalacine may be a non-specific herbicide like phosphinothricylalanylalanine (bialaphos).

78. Omura, S., Murata, M., Imamura, N., Iwai, Y., Tanaka, H., Furusaki, A., and Matsumoto, T. 1984. Oxetin, a new antimetabolite from an actinomycete. Fermentation, isolation, structure, and biological activity. Journal of Antibiotics 37: 1324-1332.

A new antibiotic, oxetin, was isolated from Streptomyces sp. Its chemical structure was determined to be (2R, 3S)-3-amino-2-oxetane carboxylic acid. On minimal media, oxetin inhibited the growth of Bacillus subtilis and Piricularia oryzae. Herbicidal activity was exhibited by oxetin against alfalfa and turnip. Oxetin concentrations of 125 ug/ml exhibited low herbicidal activity, while concentrations of 1000 ug/ml exhibited high activity. No toxicity of oxetin was observed when administered to mice. Oxetin non-competitively inhibited the glutamine synthetases from B. subtilis and spinach leaves. The authors suggest that the herbicidal activity of oxetin is due to glutamine synthetase inhibition.

*79. Otomo, N., Sato, H., and Sakamura, S. 1982. Novel phytotoxins produced by the causal fungus of the shoot blight of larches. Agricultural and Biological Chemistry 46: 861-863.

Four juglone derivatives were isolated form the fungus Guignardia laricina, the organism causing shoot blight of larch trees. These compounds were: 6-ethyl-5-hydroxy-2, 7-dimethoxy -1, 4-naphthoquinone (compound I), previously isolated from Hendersonula toruloidea, 6-(1-ethoxyethyl)-5-hydroxy- 2, 7- di-methoxy-1, 4-naphthoquinone (compound II), 6-(1-hydroxyethyl)-5-hydroxy-2, 7-dimethoxy-1, 4-naphthoquinone (compound III), also previously isolated from H. toruloidea, and 6-ethyl-l-acetonyl-1, 5-dihydroxy-2, 7-dimethoxy-4-naphthoquinone (compound IV). In lettuce seed bioassays, compounds I and IV were inactive at a concentration of 250 ppm. Compounds II and III, however, were very active. Compound II inhibited germination and growth 100 percent at 100 ppm and more than 95 percent at 50 ppm. Compound III inhibited germination and growth 100 percent at 50 ppm and more than 95 percent at 10 ppm. Compound III showed antimicrobial activity against Candida albicans, Staphylococcus aureus, and Bacillus subtilis.

*80. Otomo, N., Sato, H.; and Sakamura, S. 1983. Novel phytotoxins produced by the causal fungus of the shoot blight of larches. Agricultural and Biological Chemistry 47: 1115-1119.

Several phytotoxic compounds were isolated from the fungus Guignardia laricina, the organism causing shoot blight of larch trees. Two of these phytotoxic compounds were the juglone derivatives: 6-(1-ethoxyethyl)-5- hydroxy-2, 7-dimethoxy- 1, 4 -naphthoquinone (compound II), a new compound, and 6-(1-hydroxy-ethyl)-5-hydroxy-2, 7-dimethyoxy-1, 4-naphthoguinone (compound III), previously isolated from Hendersonula toruloidea. Also isolated were two known sterol peroxides: ergosterol peroxide and 9, 11-dihydroergosterol peroxide, and a new tetrasubstituted benzene: isoevernin aldehyde. In lettuce seedling bioassays, the juglone derivatives (compounds II and III) showed the greatest phytotoxicity, completely inhibiting hypocotyl and root growth at 100 ppm and 50 ppm, respectively. The sterol peroxides and isoevernin aldehyde showed toxicity but were less active. In a larch leaf spot test, compound III induced remarkable browning of leaves at a dosage of 0.2 ug/leaf. This compound also showed antimicrobial activity against several bacterial species.

81. Pena-Rodriguez, L.M., Armingeon, N.A., and Chilton, W.S. 1988. Toxins from weed pathogens, I. Phytotoxins from a Bipolaris pathogen of Johnsongrass. Journal of Natural Products 51: 821-828.

Two metabolites from a pathogenic fungus of the genus Bipolaris, prehelminthosporol and dihydroprehelminthosporol, were found to be toxic to sorghum (Sorghum bicolor) and

Johnsongrass (Sorghum halepense) using a leaf spot assay. Prehelminthosporol had previously been isolated from Helminthosporium sativum, (=Bipolaris sorokiniana), which causes seedling and head blight, root rot, and leaf spot of cereals and grasses. Dihydroprehelminthosporol was previously found to be a metabolite of Helminthosporium victoriae, the fungus causing blight of oats. The leaf lesions caused by these compounds in the leaf spot assay were similar to those caused by the fungus in the field. They appeared as a reddish brown area surrounded by a black circle, enclosed in a chlorotic area.

82. Pena-Rodriguez, L.M. and Chilton, W.S. 1989. 3-anhydroophiobolin A and 3-anhydro-6-epi-ophiobolin A, phytotoxic metabolites of the johnson grass pathogen Bipolaris sorghicola. Journal of Natural Products 52: 1170-1172.

Four phytotoxins were isolated from Bipolaris sorghicola and identified as ophiobolin A, 6-epi-ophiobolin A, 3-anhydroophiobolin A, and 3-anhydro-6-epi-ophiobolin A. Ophiobolin A and 6-epi-ophiobolin A had previously been isolated from Drechslera sorghicola (=Bipolaris sorghicola). 3-anhydro-6-epi-ophiobolin A had previously been isolated from D. maydis, D. oryzae, and Helminthosporium sp. Unepimerized 3-anhydroophiobolin A had previously been isolated from Helminthosporium sp. All of these compounds are reported to be inhibitory to photosynthesis. Leaf spot bioassays using sorghum, sicklepod, corn, morning glory, and bentgrass were conducted to test phytotoxicity. Reddish brown necrotic lesions encircled by dark brown borders appeared on treated sorghum, corn, and bentgrass. On sicklepod and morning glory, however, treated leaves exhibited black necrotic lesions. Chlorosis accompanied necrosis at higher concentrations. The anhydro derivatives were generally less phytotoxic than ophiobolin A and 6-epi-ophiobolin A.

83. Pena-Rodriguez, L.M. and Chilton, W.S. 1989. Victoxinine and prehelminthosporolactone, two minor phytotoxic metabolites produced by Bipolaris sp., a pathogen of johnson grass. Journal of Natural Products 52: 899-901.

Four phytotoxins were isolated from a strain of Bipolaris sp. pathogenic to johnson grass. These toxins were the previously known prehelminthosporol and dihydroprehelminthosporol, victoxinine, and prehelminthosporolactone. Victoxinine is a nitrogen-containing terpenoid previously isolated from Helminthosporium victoriae and H. sativum (=B. sorokiniana). Prehelminthosporolactone was known previously only as an oxidation product of prehelminthosporol. The authors, however, believe it is a metabolite of Bipolaris rather than an oxidation product. The four compounds were tested for phytotoxicity in leaf spot bioassays using johnson grass, sorghum, sicklepod, corn, morning glory, and bentgrass. On johnson grass and sorghum, prehelminthosporol, dihydropre-helminthosporol, and prehelminthosporolactone produced reddish brown lesions encircled by a black border, then a chlorotic halo. This “red wound response” was caused by the presence of 3-deoxyanthocyanidins, wound induced antifungal phytoalexins in sorghum. Victoxinine apparently did not elicit this phytoalexin response. In response to victoxinine, water-soaked areas with necrotic boundaries appeared on leaves of sorghum. All four compounds produced light brown areas surrounded by chlorotic zones on corn and bentgrass. At high concentrations, these toxins produced necrotic lesions on sicklepod and morning glory. The most toxic metabolite was dihydroprehelminthosporol.

*84. Rasmussen, J.B., and Scheffer, R.P. 1988. Isolation and biological activities of four selective toxins from Helminthosporium carbonum. Plant Physiology 86: 187-191.

Four phytotoxic compounds were isolated from the fungus Helminthosporium carbonum, the causal organism of a leaf spot disease of maize. Two of these compounds (HC toxin I and HC toxin II) were previously known. HC toxin I is a cyclic tetrapeptide containing two residues of alanine, one residue of proline, and one residue of Aoe, an unusual epoxide-containing amino acid. This toxin was previously identified as cyclo-(2-amino-8-oxo-9, 10-epoxydecanoyl-propyl-alanyl-alanyl). HC toxin II, an analog of HC toxin I, differs structurally from HC toxin I by the substitution of glycine for one of the alanine residues. Using a new purification procedure, the authors isolated two previously unknown analogs of HC toxin I: HC toxin III (a hydroxyproline-containing compound) and HC toxin IV (not fully identified at the time of the writing).

Phytotoxicity was tested in a maize seedling root growth bioassay. ED values for HC toxins I, II, III, and IV were 0.2, 0.4, 2.0, and 20 ug/ml, respectively. Inhibition of root growth in resistant seedlings required concentrations 100 times greater.

85. Rhee, H., Murata, K., and Kimura, A. 1987. Formation of the herbicide, δ-aminolevulinate, from L-alanine and 4, 5-dioxovalerate by Pseudomonas riboflavina. Agricultural and Biological Chemistry 51: 1701-1702.

δ-aminolevulinate has selective herbicidal activity against dicotyledons, but not against monocotyledons. This herbicidal compound can be synthesized from glycine and succinyl CoA through the action of δ-aminolevulinate synthetase, but an alternative pathway has been demonstrated in mammals, plants, and a few bacterial strains. In this pathway, the enzyme L-alanine: 4, 5-dioxovalerate aminotransferase catalyzes the transamination between L-alanine and 4, 5-dioxovalerate.

In this study, bacterial cells were screened for high L-alanine: 4, 5-dioxovalerate aminotransferase activity. Pseudomonas riboflavina showed the highest activity. The conditions for δ-aminolevulinate formation by this bacterium were studied. Increased temperature increased enzyme activity up to 70 C, and optimal pH for the reaction was 8.0.

86. Robeson, D.J., Gray, G.R., and Strobel, G.A. 1982. Production of the phytotoxins radicinin and radicinol by Alternaria chrysanthemi. Phytochemistry 21: 2359-2362.

Two phytotoxins were isolated from the fungus Alternaria chrysanthemi and identified as radicinin and radicinol. A. chrysanthemi causes a leaf spot disease of Shasta daisy. Radicinin, previously isolated from A. radicina (=Stemphylium radicinum) exhibits insecticidal, antifungal, phytotoxic, and antibacterial activity. Radicinol, also previously known, exhibits phytotoxic and antifungal activity. In a bioassay using cuttings of Canada thistle, the crude culture filtrate of A. chrysanthemi caused necrosis within 20 hours. In a time course experiment where levels of radicinin and radicinol were measured in liquid cultures of A. chrysanthemi, no lag phase for radicinin production was observed. Production began immediately and increased rapidly to a maximum concentration of approximately 626 mg/l after 20-24 days. After 20 days, radicinol levels increased while radicinin levels decreased. Radicinin is believed to be converted to radicinol by

A. chrysanthemi in liquid culture. Both compounds have previously been reported to occur together in cultures of Cochliobolus lunatus.

87. Robeson, D.J. and Strobel, G.A. 1982. Deoxyradicinin, a novel phytotoxin from Alternaria helianthi. Phytochemistry 21: 1821-1823.

A phytotoxin was isolated from Alternaria helianthi and identified as 4-deoxyradicinin. A. helianthi is the pathogenic fungus causing seedling blight and leaf spot of sunflower. Radicinin, an analog of deoxyradicinin, is produced by A. chrysanthemi, a fungal pathogen of Shasta daisy similar in morphology and pathogenicity to A. helianthi. In bioassays with Canada thistle and sunflower, necrosis and loss of turgor was observed within 24 hours of treatment with deoxyradicinin. Antifungal activity was demonstrated in the growth suppression of Cladosporium sp.

88. Robeson, D.J. and Strobel, G.A. 1982. Monocerin, a phytotoxin from Exserohilum turcicum (=Drechslera turcica). Agricultural and Biological Chemistry 46: 2681-2683.

The fungi Exserohilum turcicum and Alternaria alternata were isolated from leaf lesions on johnsongrass. Liquid cultures of these yielded two phytotoxins: tenuazonic acid from A. alternata and monocerin from E. turcicum. Tenuazonic acid is a well known phytotoxin. Monocerin had been previously isolated from E. monoceras (=Helminthosporium monoceras) and Fusarium larvarum. Its insecticidal properties have been demonstrated, however, its phytotoxicity had not previously been described. Phytotoxicity of monocerin was tested in leaf dip bioassays using Canada thistle and tomato. On Canada thistle, leaves exhibited a necrotic spot and necrotic flecks within 16 hours of monocerin treatment. Monocerin-treated tomato leaves wilted and became flaccid within 16 hours of treatment. Cut leaves of johnsongrass sprayed with monocerin solutions at concentrations of 0.1-1.0 mg/ml exhibited chlorosis followed by necrosis in 6 to 8 days. Root elongation and shoot growth of pregerminated johnsongrass seeds was almost completely inhibited by monocerin at 1 mg/ml. Pregerminated cucumber seeds were somewhat less sensitive to monocerin.

89. Robeson, D., Strobel, G., Matusumoto, G.K., Fisher, E.L., Chen, M.H., and Clardy, J. 1984. Alteichin: an unusual phytotoxin from Alternaria eichorniae, a fungal pathogen of water hyacinth. Experientia 40: 1248-1250.

A phytotoxin was isolated from cultures of Alternaria eichorniae and identified as alteichin, a doubly hydrated form of 4, 9-dihydroxy perylene-3, 10-quinone. A. eichorniae is pathogenic to water hyacinth, a noxious aquatic weed in tropical and subtropical areas. In puncture wound bioassays, alteichin produced necrotic flecks on leaves of water hyacinth similar to those produced by the pathogen. Necrotic lesions were also produced on tomato, Canada thistle, wheat, sunflower, and barley.

90. Robeson, D.J., Strobel, G.A., and Strange, R.N. 1985. The identification of a major phytotoxic component from Alternaria macrospora as $\alpha,\beta$-dehydrocurvularin. Journal of Natural Products 48: 139-141.

Past research indicated the genus Alternaria produced a diverse range of phytotoxic compounds with various biological activities. A. macrospora causes leaf and twig blight diseases in cotton and also attacks the weed, spurred anoda (Anoda cristata). Two phytotoxic compounds were isolated from A. macrospora and identified as curvularin and α, β-dehydro-curvularin. α, β-dehydrocurvularin had been previously isolated from other fungi, including A. cucumerina, and its biological activity had been noted. In this study, both compounds were bioassayed on cotton leaves and were found to produce lesions. Curvularin and α, β-dehydrocurvularin were also bioassayed using cucumber protoplasts and were found to have $LD_{50}$ values of 21 and 15 ug/ml, respectively.

*91. Russo, P.S., Blum, F.D., Ipsen, J.D., Abul-Hajj, Y.J., and Miller, W.G. 1982. The surface activity of the phytotoxin cerato-ulmin. Canadian Journal of Botany 60: 1414-1422.

Cerato-ulmin is a phytotoxic glycoprotein produced by the fungus Ceratocystis ulmi, the causal organism of Dutch elm disease. Earlier research indicated cerato-ulmin lowered the surface tension of water at very low concentrations (0.03 ppm). In this study, the authors describe the surface activity of cerato-ulmin and suggest a mechanism whereby low levels of the toxin may become concentrated and delivered to intercellular spaces. There, the toxin gains access to the vascular system where it may plug xylem vessels, causing wilt.

92. Sakamura, S., Ichihara, A., and Yoshihara, T. 1988. Toxins of phytopathogenic microorganisms. In H.G. Cutler (ed.), Biologically Active Natural Products. ACS Symposium Series 380. Amer. Chem. Soc., Washington, D.C., pp. 57-64.

Several non-host selective phytotoxins isolated from plant pathogenic fungi are described. Phoma betae, which causes leaf spot and root rot diseases in sugar beets, produces betaenones and aphidicolins. Compounds in both these groups inhibited root elongation of rice seedlings, with betaenone C having greatest inhibitory effect. Stemphylium botryosum causes leaf spot disease in beets and produces the phytotoxins dactylariol, stempyperylenol, and scytalone, which inhibit elongation of lettuce and beet seedlings.

93. Sassa, T., Nukina, M., Sugiyama, T., and Yamashita, K. 1983. Monilidiols, characteristic and bioactive metabolites of benomyl-resistant strains of Monilinia fructicola. Agricultural and Biological Chemistry 47: 2411-2413.

Two new salicylaldehyde-type octaketides were isolated from benomyl-resistant strains of Monilinia fructicola, the fungal pathogen causing brown rot of cherry. These compounds, named monilidiol and dechloromonilidiol, were found to be structurally related to pyriculol and pyriculariol, phytotoxins produced by the rice blast fungus Pyricularia oryzae. In bioassays where the test compound was applied to pinhole injuries in cherry leaves, monilidiol induced dark necrotic spots. It also inhibited the growth of rice seedlings and was active against Staphlococcus aureus. Dechloromonilidiol was less phytotoxic and plant growth inhibitory than monilidiol.

94. Sato, H., Konoma, K., and Sakamura, S. 1981. Three new phytotoxins produced by Pyrenochaeta terrestris: Pyrenochaetic acids A, B, and C. Agricultural and Biological Chemistry 45: 1675-1679.

Several phytotoxins were isolated from Pyrenochaeta terrestris, a fungal pathogen causing onion pink root disease. In a previous study, the authors isolated pyrenocine A and B: 5-crotonoyl-4-methoxy-6-methyl-2-pyrone and 5-(3-hydroxybutyroyl) –4-methoxy -6-methyl-2-pyrone, respectively. In bioassays, these inhibited lettuce seed germination and growth of rice and onion seedlings.

In this study, the new phytotoxins pyrenochaetic acids A, B, and C were isolated and identified as 4-crotonoyl-3-methoxy-5-methylbenzoic acid, 4-(3-hydroxybutyroyl) -3-methoxy-5-methyl-benzoic acid, and 4-butyroyl-3-methoxy-5-methylbenzoic acid, respectively. In bioassays, root growth of onion and rice seedlings was inhibited 100% by 250 ppm and 500 ppm pyrenochaetic acid A, respectively. Root growth of onion and rice seedlings was inhibited 100% and 54%, respectively, by 500 ppm pyrenochaetic acid c. Lettuce seed germination was inhibited equally by all three phytotoxins at high concentrations. At low concentrations, however, root elongation was promoted.

95. Schulz, A., Taggeselle, P., Tripier, D., and Bartsch, K. 1990. Stereospecific production of herbicide phosphinothricin (glufosinate) by transamination: Isolation and characterization of phosphinothricin- specific transaminase from Escherichia coli. Applied and Environmental Microbiology 56: 1-6.

The commercially available broad-spectrum nonselective herbicide Basta (Hoechst AG) contains the active ingredient L-phosphinothricin. This active ingredient is produced as a part of the dialanyl tripeptide bialaphos, isolated from Streptomyces viridochromogenes. L-phosphinothricin inhibits the ammonia-fixing enzyme glutamine synthetase. In this paper the authors describe the isolation of an aminotransferase from Escherichia coli capable of transaminating 2-oxo-4-[(hydroxy) (methyl) phosphinoyl] butyric acid to L-phosphinothricin. This enzyme was most active at pH 8.0 to 9.5 and had an optimum temperature of 55 C.

96. Sekizawa, Y. and Takematsu, T. 1983. How to discover new antibiotics for herbicidal use. pp. 261-268 in Takahashi, N., Yoshioka, H., Misato, T., and Matsunaka, S., eds. Pesticide Chemistry: Human Welfare and the Environment, Vol. 2, Natural Products. Pergamon Press, Oxford.

The authors review studies by various other researchers describing several antibiotics having herbicidal activity, including: cycloheximide, anisomycin and toyocamycin, herbicidins A and B, herbimycin, and bialaphos.

Cycloheximide, {3-[2-(3, 5-dimethyl-2-oxocyclohexyl)-2-hydroxy-ethyl] glutarimide}, controls perennial shrubs and annual weeds when applied as a soil-treatment. In rice paddy experiments, it selectively killed barnyardgrass, needle-upright clubrush, pondweed, and broadleaf weeds.

Anisomycin and toyocamycin, isolated from Streptomyces sp., inhibited shoot growth and to a greater extent root growth of rice, barnyardgrass, crabgrass, lucerne, tomato, and turnip seedlings.

Herbicidins A and B, antibiotics produced by Streptomyces saganonensis, inhibit seed germination and show selective, contact herbicidal activity against dicots.

Herbimycins A and B are described as analogs of ansamycin. They are phytotoxic to most monocots and dicots, especially when applied pre-emergence. Rice, however, is resistant.

The phytotoxic compound bialaphos, {L-2-amino-4-[(hydroxy) (methyl) phosphinoyl]-butyryl-L-alanyl-L-alanine}, (phosphino-thricyl-alanylalanine), was isolated from a strain of Streptomyces. It controls both monocots and dicots, including several agricultural weed pests such as lambsquarters, purple nutsedge, curly dock, and water hyacinth. The mode of action of bialaphos was determined to be inhibition of the enzyme glutamine synthetase, resulting in toxic accumulation of ammonia and inhibition of nitrogen assimilation.

In their concluding remarks, the authors suggest that cooperative research between soil microbiologists and weed scientists may result in discovery of highly adaptable, efficacious, and environmentally safe herbicidal compounds.

97. Seto, H., Sasaki, T., Imai, S., Tsuruoka, T., Ogawa, H., Satoh, A., Imouye, S., Niida, T., and Otake, N. 1983. Studies on the biosynthesis of bialaphos (SF-1293). 2. Isolation of the first natural products with a C-P-H bond and their involvement in C-P-C bond formation. Journal of Antibiotics 36: 96-98.

Bialaphos (phosphinothricylalanylalanine), a herbicidal tripeptide produced by Streptomyces hygroscopicus SF-1293 and S. viridochromogenes is characterized by the presence of a C-P-C bond in the phosphinothricin moiety. The authors discovered the accumulation of two new metabolites containing H-P-C bonds in the fermentation broth of bialaphos. Such bonds had not previously been found in nature. It was shown that the formation of a H-P bond is required for the methylation of phosphorous to take place. The authors believe they are the first to report involvement of H-P metabolites in the formation of a C-P bond. The two metabolites with H-P-C bonds were not biologically active, except that one of them inhibited the growth of the producing organism.

98. Shimotohno, K., Seto, H., Otake, N., Imai, S., and Satoh, A. 1986. Studies on the biosynthesis of bialaphos (SF-1293). 7. The absolute configuration of 2-phosphinomethylmalic acid, a biosynthetic intermediate of bialaphos. Journal of Antibiotics 39: 1356-1359.

Bialaphos, a tripeptide produced by a strain of Streptomyces hygroscopicus, consists of a molecule of phosphinothricin and two molecules of alanine. It has potent herbicidal activity and has attracted much attention for herbicidal development and use. This paper describes the biosynthetic pathway of bialaphos by Streptomyces.

99. Shukla, R.S., Agrawal, P.K., Thakur, R.S., and Husain, A. 1989. Drechslerol-B, a host-selective phytotoxin produced by Drechslera maydis. Phytochemistry 28: 2089-2091.

The authors isolated a phytotoxic compound from the fungus Drechslera maydis, (=Helminthosporium maydis and Cochliobolus heterostrophus), the causal organism of leaf blight disease of Costus speciosus. The compound was identified as

3-hydroxy-eicos-11(z)-enyl eicos-4-(z)-enoate (=drechslerol-B). Biological activity of drechslerol-B was tested by inoculating leaves of young C. speciosus plants with the toxin. Drechslerol-B induced chlorosis in inoculated test plants. It is suggested that drechslerol-B is involved in symptom expression of leaf blight disease of C. speciosus since the toxin was also isolated from tissues infected with D. maydis.

100. Smith, A.G. and Rubery, P.H. 1982. Investigation of the mechanism of action of a chlorosis-inducing toxin produced by Pseudomonas phaseolicola. Plant Physiology 70: 932-938.

The bacterium Pseudomonas phaseolicola, causal organism of haloblight disease of bean, produces a toxin which induced formation of chlorotic halos only in younger, expanding, chlorophyll-synthesizing bean leaves. The toxin, only partially purified, was also known to cause chlorosis in spinach, pea, and barley. It was believed to play a role in inhibition of chlorophyll synthesis rather than in chlorophyll breakdown. In tests with sections of greening barley leaves, chlorophyll, carotene, and xanthophyll synthesis were inhibited by the toxin. Levels of 5-aminolevulinic acid were decreased in toxin-treated leaf sections, possibly accounting for inhibition of chlorophyll synthesis. Based on visual comparisons of toxin-treated and control leaf sections using an electron microscope, it was determined that the toxin did not affect transformation of etioplasts into chloroplasts. It is suggested that the toxin impedes biosynthesis of various lipids, chlorophyll included.

101. Soledade, M., Pedras, C., Seguin-Swartz, G., and Abrams, S. P. 1990. Minor phytotoxins from the blackleg fungus Phoma lingam. Phytochemistry 29: 777-782.

Strains of Phoma lingam, the fungal pathogen causing blackleg of crucifers were screened for production of phytotoxins. Isolates of a highly virulent strain causing leafspots and stem cankers on rapeseed and cabbage produced several phytotoxins including sirodesmin PL, sirodesmin H, phomalirazine, sirodesmin J, and sirodesmin K. Biological activity was tested by puncturing cotyledons or leaves of rapeseed and mustard with needles and placing droplets of test solutions on the wounds. A weakly virulent strain, causing superficial leaf and stem lesions on rapeseed and cabbage and a strain causing disease only on stinkweed produced extracts having no biological activity. The authors studied the effect of acetylation on the biological activity of sirodesmin PL. Based on these results, it was suggested that acetylation of sirodesmin PL at the 14-OH reduces phytotoxicity, but acetylation at the 6-OH does not affect phytotoxicity. It is speculated that the 14-OH is involved in the mode of action.

102. Steffens, J.C. and Robeson, D.J. 1987. Secalonic acid A, a vivotoxin in pink root-infected onion. Phytochemistry 26: 1599-1602.

A phytotoxin was isolated from Pyrenochaeta terrestris, the etiological agent of pink root disease of onion, and identified as secalonic acid A. This fungus was previously reported to produce relatively weak phytotoxins, pyrenocines A, B, and C, and the pyrenochaetic acids. Secalonic acid A, also known as ergochrome AA, was previously isolated from Aspergillus ochraceus, Parmelia Spp., and Pyrenochaeta terrestris. Its non-host specific phytotoxicity was demonstrated in tests against radish and pepper seedlings. In onion seedling bioassays, secalonic acid A was a potent inhibitor of seedling elongation.

103. Stierle, A.C., Cardellina, J.H., and Strobel, G.A. 1989. Phytotoxins from Alternaria alternata, a pathogen of spotted knapweed. Journal of Natural Products 52: 42-47.

The authors isolated and identified several compounds from the fungus Alternaria alternata phytotoxic to spotted knapweed (Centaurea maculosa). Spotted knapweed is a common pest of rangeland in the northwestern United States and in southwestern Canada. The compounds isolated were the diketopiperazine maculosin, tenuazonic acid, and four perylenequinones. Among the perylenequinones, alterlosin I induced small necrotic flecks and alterlosin II induced relatively large necrotic lesions on spotted knapweed at a concentration of 10 M. The other two perylenequinones were not phytotoxic at any concentration tested. Maculosin and tenuazonic acid were the most active phytotoxins, inducing large necrotic lesions, with maculosin showing the most host specificity. After testing these phytotoxins in various combinations, the authors suggest that each toxin may target a specific site of action in the plant.

104. Sugawara, F. and Strobel, G.A. 1987. Tryptophol, a phytotoxin produced by Drechslera nodulosum. Phytochemistry 26: 1349-1351.

Drechslera nodulosum (=Helminthosporium nodulosum), which causes blight and leaf spot diseases in goosegrass, produced the known compound tryptophol. The authors found this compound to be phytotoxic to goosegrass, causing lesions resembling those on infected goosegrass. In addition, tryptophol was detected in leaves of goosegrass infected by D. nodulosum. This implicated tryptophol in disease development. Two bioassays for phytotoxicity were conducted: one in which leaves were placed in tryptophol solution, and one in which a droplet of tryptophol solution was placed over a puncture wound in a leaf blade. Leaves of goosegrass, grain sorghum, barley, crabgrass, foxtail, barnyardgrass, bluegrass, signal grass, lambsquarters, and Canada thistle were tested. At a concentration of 2.6 x 10 M, no selectivity was observed. At 3.1 x 10 M, however, tryptophol was toxic to only some plants, and at 6.2 x 10 M, only goosegrass was affected.

105. Sugiyama, T., Watanabe, M., Sassa, T., and Yamashita, K. 1983. Synthesis of monilidiol and dechloromonilidiol, phytotoxic octaketides of Monilinia fructicola. Agricultural and Biological Chemistry 47: 2411-2413.

The cherry brown rot fungus, Monilinia fructicola produces two phytotoxic, antibacterial compounds: monilidiol and dechloromonilidiol. In this paper, the authors describe the first synthesis of these compounds.

106. Suzuki, M., Sugiyama, T., Watanabe, M., and Yamashita, K. 1986. Synthesis of optically active pyriculol, a phytotoxic metabolite produced by Pyricularia oryzae Cavara. Agricultural and Biological Chemistry 50: 2159-2160.

In this paper, the authors describe the synthesis of optically active pyriculol and determination of its absolute configuration. Pyriculol is a phytotoxic compound isolated from Pyricularia oryzae, the fungus causing rice blast disease. The phytotoxin causes dark necrotic spots on rice leaves. It has a salicylaldehyde skeleton with an unsaturated side chain with two asymmetric centers at the glycol moiety.

107. Tal, B., Robeson, D.J., Burke, B.A., and Aasen, A.J. 1985. Phytotoxins from Alternaria helianthi: radicinin, and the structures of deoxyradicinol and radianthin. Phytochemistry 24: 729-731.

A fungal pathogen of sunflower, Alternaria helianthi, produced several phytotoxic metabolites. These included radicinin, previously isolated from A. chrysanthemi and other organisms; previously known deoxyradicinin and 3-epideoxyradicinol; deoxyradicinol, not previously recognized as a natural product; and the new compound radianthin. When applied to sunflower leaves, droplets of radianthin solution produced dark brown necrotic spots within 24 hours. Studies of relative toxicities of these five compounds were in progress.

108. Tatum, J.H. and Baker, R.A. 1983. Naphthoquinones produced by Fusarium solani isolated from citrus. Phytochemistry 22: 543-547.

Eleven naphthoquinone pigments were isolated from various isolates of the fungus Fusarium solani, causal agent of citrus blight. These were (1) Rel-(3R, 4aR, 10aR)-5, 10-dioxo -3, 4, 4a, 5, 10, 10a-hexahydro-7-methoxy-3-methyl-3, 6, 9-trihydroxy-1-H-naphtho (2, 3-c) pyran; (2) Rel-(3R, 4aR, 10aS) -5, 10-dioxo- 3, 4, 4a, 5, 10, 10a-hexahydro-7-methoxy-3-methyl-3, 6, 9-trihydroxy-1-H-naphtho (2, 3-c) pyran; (3) Rel-(3R, 4aR, 10aR)-5, 10-dioxo-3, 4, 4a, 5, 10, 10a-hexahydro-3, 7- dimethoxy-3-methyl-6, 9-dihydroxy-1-H-naphtho(2, 3-c)pyran; (4) fusarubin; (5) anhydrofusarubin; (6) javanicin; (7) norjavanicin; (8) methyl ether fusarubin; (9) marticin; (10) isomarticin; (11) 5, 8-dihydroxy-6-methoxy-3-methyl-2-aza- 9, 10-anthracene-dione; and (12) ethyl ether fusarubin. Marticin and isomarticin were previously shown to be toxic to tomato and pea. Naphthoquinone (11) had previously been isolated from F. bostrycoides and was called bostrycoidin. All of the compounds except (3) and (8) had been previously reported as metabolites of F. solani.

109. Terahara, A., Haneishi, T., Mamoru, A., Tadashi, H., Harumitsu, K and Chihiro, T. 1982. The revised structure of herbicidins. Journal of Antibiotics 35: 1711-1714.

The herbicidins are a group of antibiotics possessing herbicidal activity. In previous papers, the authors had reported the isolation and biological activities of herbicidins A, B, E, F, and G produced by Streptomyces saganonensis. In this paper, the authors report a revision of the structures of the herbicidins based on new analyses.

110. Wickliff, J.L., Duke, S.O., and Vaughn, K.C. 1982. Involvement of photobleaching and inhibition of protochlorophyll (ide) accumulation in tentoxin effects on greening of mung bean seedlings. Physiologia Plantarum 56: 399-406.

The phytotoxic compound tentoxin, produced by the fungus Alternaria alternata causes chlorosis in greening leaves of tentoxin-sensitive plant species. This chlorosis results from reduced chlorophyll accumulation caused by (1) increased chlorophyll (ide) instability caused by photodestruction, and (2) decreased synthesis of protochlorophyll (ide).

111. Willms, L. 1989. Glufosinate, a new amino acid with unexpected properties. Pesticide Science 27: 219-221.

This summary describes the history of discovery and development of phosphinothricin (=glufosinate), a phosphorous-containing amino acid produced by certain Streptomyces strains. Following discovery of the naturally- occurring compound, phosphinothricin was artificially synthesized and tested for biological activity. It lacked satisfactory antibiotic activity but showed potent herbicidal activity, even at very low doses. Its herbicidal mode of action is inhibition of the enzyme glutamine synthetase, resulting in toxic accumulations of ammonia in plant cells. The resulting deficiency of glutamine also inhibits synthesis of essential proteins and nucleic acids. Glufosinate has several characteristics that make it extremely useful where a non-selective herbicide is required: (1) a short half-life in soil and plants, (2) uptake exclusively by leaves rather than roots of plants, (3) a very high level of herbicidal activity.

112. Yamada, O., Kaise, Y., Futatsuya, F., Ishida, S., Ito, K., Yamamoto, H., and Munakata, K. 1972. Studies on plant growth-regulating activities of anisomycin and toyocamycin. Agricultural and Biological Chemistry 36: 2013-2015.

Two antibiotic compounds were isolated from a strain of Streptomyces sp. and identified as anisomycin and toyocamycin. Herbicidal activity was tested on seeds of rice, barnyardgrass, crabgrass, lucerne, tomato, and turnip. Anisomycin inhibited shoot growth at concentrations greater than 50 ppm and root growth at 12.5 ppm. Toyocamycin inhibited both shoot and root growth in all test plants at 25 ppm.

113. Yomosa, K., Hirota, A., Sakai, H., and Isogai A. 1987. Isolation of harman and norharman from Nocardia sp. and their inhibitory activity against plant seedlings. Agricultural and Biological Chemistry 51: 921-922.

Two phytotoxins were isolated from a strain of Nocardia, a common soil bacterium. These were harman (1-methyl-β-carboline) and norharman (β-carboline) and inhibited root elongation of lettuce and rice seedlings. Although both compounds have previously been isolated from plants, sake, mushroom, Streptomyces, and marine dinoflagellates, their phytotoxic effects have not previously been reported.

114. Yoshikawa, H., Takiguchi, Y., and Terao, M. 1983. Terminal steps in the biosynthesis of herbicidins, nucleoside antibiotics. Journal of Antibiotics. 36: 30-35.

The authors studied the biosynthesis of herbicidins A and B, two phytotoxic antibiotics produced by Streptomyces saganonensis. They suggest herbicidin G is enzymatically converted to herbicidin F, which is then enzymatically converted to herbicidin A, and that herbicidin B is the product of a non-enzymatic, pH dependent conversion of either herbicidin A or F. Herbicidin G may also be converted to herbicidin C non-enzymatically at pH 7.5 or 8.5.

# 3
# PHYTOTOXINS PRODUCED BY PATHOGENS OF TREES

## 3.1 General Characteristics of Phytotoxins Isolated from Trees

There are few research reports on phytotoxic substances isolated from pathogens of woody plants, specifically trees or shrubs. Those phytotoxins reported appear to be toxic only to the host plant infected by the toxin-producing pathogen, and are therefore considered "host-selective". Phytotoxins have been isolated from pathogens of cherry (2, 17), cypress (1), Japanese pear (6, 8), tangerine (8), apple (13, 16), navel orange (5), lilac (7), pine (9), tea (10), citrus (11, 12), and larch (14, 15). There appears to be a correlation between the susceptible host's reaction to a pathogen and the production of toxins by the pathogen (1, 2, 5, 6, 7, 9, 10, 12, 13) although in at least one case there was no strong correlation between the amount of toxin produced in culture and the isolate's pathogenicity (16). Within this there can also be variation among isolates of pathogens in the amount and toxicity of the compounds produced (2, 5, 6).

## 3.2 Description of Research

Several unidentified toxins were isolated from several isolates of the fungus which causes silverleaf disease of cherry (2). Toxins produced by non-cherry sources of the same fungus were also investigated. In this study, cherry was the only plant used in testing the toxin's effects on plant tissue. Severity of symptoms produced by an isolate was correlated with amount of toxin produced by that isolate. In another paper on cherry (17), two phytotoxic and antimicrobial compounds were isolated from the brown rot fungus (Monilinia fructicola). No testing of these compounds against woody plants was reported.

Three phytotoxins were isolated from a fungus (Seiridium cupressi) which causes a canker disease of cypress (Cupressus sempervirens). Two of these toxins were previously known from isolations from a different species of a fungus in the same genus (S. cardinale). The third toxin was new and was given the name seiricuprolide. This third compound showed phytotoxicity towards three species of cypress and to tomato and mung bean. Seiricuprolide was considered a minor toxin which probably contributes to the complete toxic activity of the fungus producing it.

Duke discussed phytotoxins with potential as herbicides, including their chemical structures, organisms which produce them and their effects on growth (3, 4). A distinction was made between how a plant pathologist and a weed scientist might view a "non-host-selective" toxin. To a plant pathologist, these are compounds affecting species other than those naturally infected by the producing pathogen; however for weed science purposes, non-host-selective may still be considered quite selective (e.g. a phytotoxin that kills every major weed of maize but does not affect the crop itself). Tentoxin, stemphyloxin and zinniol are all non-host-selective toxins from pathogens which do not affect all plants, including some important commercial field crops. These are considered good candidates for use as herbicides in certain agronomic crops. Duke also states that phytotoxins isolated from soil organisms which do not cause disease are more likely to be non-selective. In these review articles the "weeds" tested against toxins were herbaceous.

From the bacterium Pseudomonas syringae which causes citrus blight, syringotoxin was isolated (5). Syringotoxin is a wide spectrum biocide and phytotoxin. Navel orange petioles developed citrus blight when treated, and many fungi were shown to be sensitive to syringotoxin and syringomycin (a structurally related compound). Another strain, P. syringae pv. syringae causes a bacterial blight of lilac (Syringa vulgaris). From this strain, several phytotoxic compounds were isolated (7) and called syringostatins. These compounds were shown to be similar to syringomycin and syringotoxin but have different amino acid compositions; they are both phytoxic and antifungal.

Alternaria alternata (fungus) caused black spot disease in Japanese pear and produced host-selective toxins ("AK-toxins I and II") in culture (6). An isolate from strawberry which also causes black spot, produced analogous host-selective toxins ("AF-toxins I, II, and III"). A veinal necrosis bioassay of leaf tissue established the host-selective nature of these compounds. Another study on Alternaria alternata (8) discussed these same host-selective compounds isolated from pathogens of Japanese pear, strawberry, and tangerine. These toxins all share ω-epoxy-8-hydroxy-9-methyldecatrienoic acid structures.

A wilt disease of Japanese red pine (Pinus densiflora) has been studied by many researchers and results are discussed by Morooka et al. (9). The pine wilt nematode was thought to be responsible for the disease but many fungi were also isolated, including Phomopsis sp. This fungus produced wilt symptoms in inoculations of Japanese red pine and the authors (9) isolated a compound from the fungus identified as isopimarane diterpene γ-lactol, 6α, 7β, 9α-trihydroxy-8 (14), 15-isopimaradiene-20, 6-γ-lactone. This compound produced browning and degeneration of callus and inhibition of callus growth in bioassays of red pine callus. Since browning of cells occurs in wilted pines, this toxin or others produced by other fungi were thought to contribute to symptoms of the wilt disease.

The phytotoxic compound oxysporone (previously isolated from the fungus Fusarium oxysporum) was isolated from the fungus Pestalotia longiseta, the causal organism of tea gray blight(10). In this study oxysporone was shown to cause leaf necrosis of one cultivar of tea.

Several phytotoxic compounds have been isolated from Fusarium solani, a fungus commonly associated with citrus roots in Florida (11, 12). Two of these of compounds, isomarticin and dihydrofusarubin, were studied in detail. The authors suggest these two and other naphthoquinones isolated from F. solani are responsible for stem cankers and root rot of infected citrus. The action of these two napthoquinones was shown to be quite varied; chloroplast membranes in peas were disrupted; in rough lemon (Citrus limon) starch was reduced, minerals accumulated in leaves, and respiration increased.

Two studies were done by Otomo et al. (14, 15), on phytotoxins produced by the causal fungus of shoot blight in larch. From this fungus (Guignardia laricina) four juglone derivatives were isolated; also four pigments and three other compounds were isolated. The juglone derivatives were found to be phytotoxic to lettuce seed and to be somewhat antimicrobial. One other compound {6-(1-hydroxy-ethyl) -5-hydroxy-2, 7-dimethoxy-l, 4-naphthoquinone} induced browning of larch leaf tissue in sunlight and also showed antimicrobial activity at low concentrations. No testing against other woody plants was done in either study.

Two different fungal pathogens of apple have been shown to produce phytotoxic compounds. Five isocoumarins were isolated from the fungus which causes apple canker, Valsa ceratosperma (13). All five compounds caused browning of the cambium and phloem tissue of apple shoots at 100 ppm concentration. The most potent phytotoxin was considered to be 5-carboxylmellein. Subbaih et al. (16) reported on phytotoxins produced by the apple pathogen, Botryosphaeria obtusa. Of seventeen apple cultivars tested on detached leaves, two were sensitive to all four toxins isolated, and three cultivars showed resistance against two phytotoxins. There was no strong correlation between the ability of an isolate to cause disease and the amount of toxin produced in culture.

In these reports the phytotoxins are mostly host-selective; however, very few compounds have been tested for their effects on plants other than the host. When compounds have been tested on non-host plants, these plants have been herbaceous. There is a lack of information on the effect these phytotoxins might have on trees other than the host tree.

## 3.3 Summary of Personal Communication with Researchers

We have had personal communication with some of the authors and other professionals involved in research on natural compounds with herbicide potential. Through these discussions our conclusions reached from the literature search have been substantiated. Most of those contacted have been researching the use of naturally derived toxins against herbaceous weeds (Dr. J. Hull, Michigan State University; Dr. G. Strobel, Montana State University; Dr. G. Templeton, University of Arkansas; Dr. H.G. Cutler, ARS, USDA, Athens, GA; Dr. A.R. Lax, ARS, USDA, New Orleans, LA). These researchers indicated that from their knowledge and experience, toxins isolated from tree pathogens would be host-specific and generally slow acting. No one knew of any research on this specific topic in progress. On related topics we found that Dr. C. Michler (Forestry Sciences Lab, North Central, Exp. Station, Wisconsin) is researching tree resistance to herbicides and stresses; Dr. D.L. Hopkins (Agric. Research and Education Center, Florida State) is researching how growth regulators affect bacterial pathogens of citrus; and Dr. S.C. Domir (ARS, USDA, Delaware, OH) is studying chemicals that retard tree growth but with no emphasis on natural compounds, and has not worked with compounds isolated from tree pathogens.

## 3.4 Conclusions

No reports of compounds isolated from pathogens of trees that are not host-selective which could act as herbicides/growth regulators for a broad range of trees and shrubs were found. Since no current research exists in this area, from the literature gathered and personal communication with researchers, it could be concluded that this avenue of research may be non-productive.

According to Duke (1986a) phytotoxins isolated from non-pathogenic soil microorganisms are probably more often non-selective than those isolated from plant pathogens.

## 3.5 Recommendations

Research emphasis should be on soil microorganisms as potential producers of non-host-selective toxins which may be effective against woody plants.

## 3.6 Anotated Bibliograghy

1. Ballio, A., Evidente, A., Graniti, A., Randazzo, G., and Sparapano, L. 1988. Seiricuprolide, a new phytotoxic macrolide from a strain of Seiridium cupressi infecting cypress. Phytochemistry 27: 3117-3121.

   The fungus Seiridium cupressi is known to cause a canker disease of cypress, Cupressus sempervirens in Greece. Several phytotoxins were produced by S. cupressi in culture and two were isolated and identified as seiridin and iso-seiridin. These are identical to the two butenolides previously isolated from cultures of S. cardinale, also pathogenic to cypress. A third phytotoxin was isolated from S. cupressi (not produced by S. cardinale), identified as a new macrolide and named seiricuprolide. Bioassays for phytotoxicity produced diffuse yellowing and then browning of cut twigs of cypress (C. sempervirens, C. arizonica, and C. macrocarpa) within 10 days while chlorosis and necrosis of tomato and mung bean cuttings occurred in 4 days. Seiricuprolide appears to be a minor toxin produced by S. cupressi since it was produced in small amounts in vitro and had lower toxicity in the bioassays. It may contribute to the overall toxicity of the producing pathogen, S. cupressi.

2. Bishop, G.C. 1979. Infection of cherry trees and production of a toxin that causes foliar silvering by different isolates of Chrondrostereum purpureum. Aust. J. Agric. Res. 30: 659-65.

   Susceptibility of pruned sapwood of cherry trees to invasion by basidiospores of Chondrostereum purpureum from several different sources was investigated. Spores from sources other than cherry were just as effective as those from cherry in inducing silver leaf disease in cherry. Toxins produced by isolates were compared. An isolate from broom, Teline monspessulana, which gave no foliar symptoms produced significantly less toxin than other isolates of C. purpureum. Identity of toxin was not established.

3. Duke, Stephen O. 1986. Microbially produced phytotoxins as herbicides - A perspective. In A. Putnam and Chung-Shih Tang (eds). The Science of Allelopathy. John Wiley & Sons, Inc., NY. pp. 287-304.

   This “review” discusses phytotoxic microbial toxins that are being or not being developed as herbicides. Numerous compounds produced by microbes are listed, along with some chemical structures, the organisms which produce them, and their effects on growth. Of interest is tentoxin, a cyclic tetrapeptide, produced by Alternaria alternata. This fungus has a wide host range and tentoxin apparently interferes with up-take of nuclear-coded proteins by developing chloroplasts thus producing chlorosis. Susceptibility to tentoxin is plastome-coded and, thus, maternally inherited.

4. Duke, Stephen O. 1986. Naturally occurring chemical compounds as herbicides. Review of Weed Science 2: 15-44.

   This review covers several biochemical metabolic pathways, classes of compounds formed, and an interpretation of toxins. Non-host selective, or non-specific toxins, are the most chemically, biochemically, and physiologically characterized microbial-produced phytotoxins. Some of these are tentoxin, stemphyloxin, and zinniol but they are not phytotoxic to all plant species; tentoxin and zinniol are produced by pathogenic Alternaria spp. and stemphyloxin is produced by Stemphylium botryosum, a pathogen. Curiously, pathogenic Alternaria spp. isolated from trees, and the toxins they produce e.g. tentoxin, are not tested against trees to determine phytotoxicity; rather the phytotoxin is usually assayed against weeds.

5. Gonzalez, C.F., J.S. DeVay and R.J. Wakeman. 1981. Syringotoxin: A phytotoxin unique to citrus isolates of Pseudomonas syringae. Physiological Plant Pathology 18: 41-50.

   Citrus isolates of Pseudomonas syringae produced syringo-toxin, a wide spectrum biocide and phytotoxin which was unique to the citrus ecotype of P. syringae. Healthy petioles of navel orange trees when treated with syringotoxin developed citrus blast lesions. Identity of syringotoxin was established by biocidal spectrum and amino acid composition from cultures of citrus isolates. Geotrichum candidum was sensitive to syringotoxin and syringomycin, both of which are structurally related i.e. both are peptides which contain serine and an unknown, basic amino acid.

6. Hayashi, N., K. Tenabe, T. Tsuge, S. Nishimura, K. Komoto, and H. Otani. 1990. Determination of host-selective toxin production during spore germination of Alternaria alternata by high-performance liquid chromatography. Phytopathology 80: 1088-91.

   The Japanese pear pathotype of Alternaria alternata, which causes black spot disease, produces host-selective toxins (AK-toxins I and II) in culture; the strawberry pathotype, which also causes black spot disease, produces analogous host-selective toxins (AF-Toxins I, II, and III). Authors state that AK-toxin I and AF-toxin I, respectively, are the major toxins in biological activity. These host selective toxins share a common ester of epoxy-decatrienoic acid. Bioassays against leaf tissue showed host selective activity judged by characteristic veinal necrosis.

7. Isogai, A., Fukuchi, N., Yamashita, S., Suyama, K., and Suzuki, A. 1989. Syringostatins, novel phytotoxins produced by Pseudomonas syringae pv. syringae. Agricultural and Biological Chemistry 53: 3117-3119.

   It was previously reported that many strains of the bacterium Pseudomonas syringae pv. syringae produce the phytotoxic compounds syringomycin or syringotoxin, depending on the host origin. These toxins produce necrosis in plants and are also antimicrobial. About 1980 in Japan the causal organism of bacterial blight of lilac (Syringa vulgaris) was shown to be P. syringae pv. syringae. The authors found that a strain of this bacterium isolated from lilac produced a third type of toxins. These toxins were termed syringostatins and after partial characterization the authors concluded that the syringostatins are similar to syringomycin and syringotoxin, but have clearly different amino acid compositions.

8. Kohmoto, I., Y. Itoh, M. Kodama, H. Otani and S. Natasuka. 1990. Molecular basis that rules the host ranges of pathotypes of Alternaria alternata. Phytopathology 80(10): 1003. (Asbtr.).

   Japanese pear, strawberry and tangerine pathotypes produce potent host-specific toxins. Toxins share ω-epoxy-8-hydroxy-9-methyldecatrienoic acid structures. AK-toxin from the Japanese pear pathotype is toxic to pear, AF-toxin I from the strawberry pathotype is toxic to certain pear and susceptible, strawberry genotypes. The sensitive plant range to each host-specific toxin is coincident with the host range of each pathotype.

9. Morooka, N., Tatsuno, T., Tsunoda, H., Kobayashi, K., and Sakurai, T. 1986. Chemical and toxicological studies of the phytotoxin, 6α, 7β, 9α-trihydroxy-8(14), 15-isopimaradiene-20, 6-γ-lactone, produced by a parasitic fungus, Phomopsis sp., in wilting pine trees. Agricultural and Biological Chemistry 50: 2003-2007.

   Pine wilt had been reported to be caused by the pine wood nematode, however, the authors suggest pathogenic fungi might be responsible since an increase in nematode populations in wilting pines is only possible with excess fungal food. More than 30 species of fungi were found in the trunks of wilting pine trees. Typical pine wilt symptoms appeared within four months from inoculation of young red pines (Pinus densiflora) with certain fungi, including Phomopsis. Fungi invaded the resin canals of inoculated trees and cells surrounding the resin canals turned brown. It was suspected that cytotoxic metabolites were produced by the invading fungus.

   A strain of Phomopsis sp. was isolated from trunks of wilting red pines. From fungal cultures of this strain a cytotoxin was isolated and identified as isopimarane diterpene γ-lactol, 6α, 7β, 9α-trihydroxy-8(14), 15-isopimaradiene-20, 6-γ-lactone. It inhibited proliferation of red pine tree callus in bioassays; browning and degeneration of the callus occurred at a concentration of 150 ppm. The authors believe browning of cells surrounding resin canals in wilted pines to be related to production of this or other cytotoxins produced by Phomopsis or other fungi infecting these trees.

10. Nagata, T. and Ando, Y. 1989. Oxysporone, a phytotoxin isolated from the tea gray blight fungus Pestalotia longiseta. Agricultural and Biological Chemistry 53: 2811.

    Tea gray blight, an important disease of tea plant in Japan, is caused by the fungus Pestalotia longiseta. Lesions on the foliage are concentrically zoned, varying in size from 1 cm to almost the entire leaf in diameter. A phytotoxin was isolated from P. longiseta and identified as oxysporone, the same compound previously isolated from Fusarium oxysporum. In a leaf-necrosis assay using the highly susceptible tea cultivar ‘Yabukita’, oxysporone caused leaf necrosis at a dose of about 15 ppm.

11. Nemec, S., Baker, R.A., and Tatum, J.H. 1988. Toxicity of dihydrofusarubin and isomarticin from Fusarium solani to citrus seedlings. Soil Biology and Biochemistry 20: 493-499.

Fusarium solani is a fungus commonly isolated from roots and trunks of citrus in Florida and shown to cause fibrous and scaffold root rot and cankers on stems of stressed citrus plants. Naphthoquinone pigments with antibiotic activity are commonly produced by this fungus in culture; therefore these pigments were thought to play a part in symptomotolgy of citrus infected with F. solani. Rough lemon (Citrus limon) seedlings were evaluated for their reactions to two naphthoquinones, dihydrofusarubin (DHF) and isomarticin. Seedling roots were immersed in solutions of these compounds, alone and in a mixture, for up to 19 days. Both pigments caused leaf roll, loss of water and electrolytes from leaves, wilt, and veinal chlorosis. Citrus inoculated with F. solani exhibited symptoms similar to, but different from, plants exposed to DHF and isomarticin solutions. Both pigments stimulated resinous vessel plugging in citrus which is the main type of vessel plugging observed in roots inoculated with F. solani. Therefore these pigments may be partially responsible for the vessel plugging seen in infected citrus roots in the field.

12. Nemec, S., Phelps, D., and Baker, R. 1989. Effects of dihydrofusarubin and isomarticin from Fusarium solani on carbohydrate status and metabolism of rough lemon seedlings. Phytopathology 79: 700-705.

    Rough lemon seedlings were inoculated with Fusarium solani, an opportunistic pathogen of citrus, and the symptoms compared to seedlings with roots suspended in solutions of the F. solani - produced naphthoquinones dihydrofusarubin (DHF) and isomarticin. Both inoculation and naphthoquinone treatment produced similar wilt symptoms but only those seedlings treated with DHF developed chlorosis. In inoculated plants, total soluble and reducing sugars and starch were reduced, but in naphthoquinone-treated plants only starch was reduced. Both inoculated plants and naphthoquinone-treated plants exhibited accumulation of minerals in leaves. Respiration rates increased in DHF-treated plants. It is suggested that respiration is stimulated via mitochondrial oxidases.

13. Okuno, T., Oikawa, S., Goto, T., Sawai, K., Shirahama, H., and Matsumoto, T. 1986. Structures and phytotoxicity of metabolites from Valsa ceratosperma. Agricultural and Biological Chemistry 50: 997-1001.

    The neutral extract from the culture filtrate of Valsa ceratosperma (causal fungus of apple canker) was shown to be phytotoxic to detached apple shoots. When purified, five isocoumarins were identified. Three were known compounds: (-)-5-methylmellein, (-)-5-carboxymellein, and (-)-5-hydroxymethylmellein. Two new isocoumarins were identified: (+)-(3R, 4S)-trans-4-hydroxy-5-methylmellein and (-)-(3R, 4R) -cis-4-hydroxy-5-methylmellein. In bioassays for phytotoxicity, all five compounds caused browning of the cambium and phloem tissue of apple shoots at a concentration of 100 ppm. Lettuce seedlings were inhibited by all five compounds at a concentration of 500 ppm, with (+)-(3R, 4S)-trans-4-hydroxy-5-methylmellein showing the strongest inhibition. 5-carboxymellein may be the most potent phytotoxin of the five isocoumarins. These compounds may be important in extending the cankered areas on apple shoots.

14. Otomo, N., H. Sato, and S. Sakamura. 1982. Novel phytotoxins produced by the causal fungus of shoot blight of larches. Agric. Biol. Chem. 46(3): 861-863. (Short Communication)

Guignardia laricina produced four juglone derivatives isolated from fungus mycelium. These were 6-ethyl-5-hydroxy-2, 7-dimethoxy-1, 4-naphthoquinone (I), 6-(1-ethoxy-ethyl)-5-hydroxy-2, 7-dimethoxy-1, 4-naphthoquinone (II), 6-(1-hydroxyethyl)-5-hydroxy-2, 7-dimethoxy-1, 4-naphthoquinone (III) and 6-ethyl-1-acetonyl-1, 5-dihydroxy-2, 7-dimethoxy-4-naphthalenone (IV). Activities were measured in bioassays against lettuce seed and in antimicrobial tests. Compound III had a minimal inhibitory concentration of 1 ppm against Bacillus subtilis. No assays were done against woody seeds or plants.

15. Otomo, N., H. Sato, and S. Sakamura. 1983. Novel phytotoxins produced by the causal fungus of the shoot blight of larches. Agric. Biol. Chem. 47(5): 1115-1119.

This paper reports the isolation of four pigments and three other compounds from culture filtrates of Guignardia laricina. Of these, compound III [6-(1-hydroxy-ethyl)-5-hydroxy-2, 7-dimethoxy-1, 4-naphthoquinone] induced browning of leaf tissue in sunlight, using a leaf spot test. Benzoic acid, p-hydroxybenzoic acid and p-hydroxyphenylacetic acid were active to the same extent as Compound III when 2 ug/leaf were injected into tissue. Compound III also showed remarkable antimicrobial activity at low concentrations e.g. against Candida albicans, Staphylococcus aureus and Bacillus subtilis. No testing was done against other woody plants.

16. Subbaih, P.V., W.S. Chilton, and T.B. Sutton. 1990. Phytotoxins from the apple pathogen Botryosphaeria obtusa. Phytopathology 80(10): 968 (Abstr.).

Four isolates produced abundant mellein, a phytotoxin, in culture. Other toxins produced, in lesser amounts, were tyrosol, 4-hydroxymellein, 5-hydroxymellein, and 4-hydroxybenzaldehyde. Seventeen apple cultivars (cvs) were used in a leaf bioassay to determine phytotoxicity of different toxins. Two cvs showed sensitivity to all toxins and three cvs showed resistance to mellein and 4-hydroxymellein. There was not a strong correlation between isolate pathogenicity and the amount of toxin production in cultures.

17. Sugiyama, T., M. Watanabe, T. Sassa, and K. Yamashita. 1983. Syntheses of monilidiol and dechloromonolidiol, phytotoxic octaketides of Monilinia fructicola. Agric. Biol. Chem. 47(10): 2411-2413.

These two compounds were isolated from culture filtrates of benomyl-resistant strains of the cherry brown rot fungus, Monilinia fructicola. Both compounds exhibited phytotoxic and antibacterial properties. No testing was done against woody plants.

# 4
# ALLELOPATHY UPDATE

## 4.1 Analysis of the Literature Reviewed

Since production of the previous literature review of allelopathy (Appendix A), there have been approximately 300 articles written that include a reference to allelopathy. Allelopathy was the main topic in approximately half of these articles. The other articles make only a general reference to the term. Most (two-thirds) of the relevant articles concern allelopathic interactions between herbaceous plants (weeds versus crops, crops versus crops, or crops versus weeds). Thirty articles concerned the allelopathic effects of trees on herbaceous species or other trees (5 articles). Only 22 of the articles reviewed concerned the allelopathic effects of herbaceous plants on trees.

Four of the 22 articles directly link allelopathy and mycorrhizae (5, 6, 10, 19). Brown (5) described the interactions that occur between pine trees, ground covers, and mycorrhizae as being a "dynamic balance". The failure of some forests to regenerate normally may be due to a loss of this dynamic balance or the balance being tipped in favor of ground cover species.

Cote and Thibault (6) demonstrated that the foliar leachates of raspberry inhibited the growth of ectomycorrhizae associated with black spruce. The subsequent growth of black spruce seedlings was inhibited as well. Stands of raspberry that invade after fire or logging may significantly inhibit the regeneration of black spruce forests.

Goldner, et al., (10) discovered that extracts of a lichen (<u>Cladonia</u> <u>cristatella</u>) were fungicidal to several mycorrhizae. This lichen occurs on abandoned strip mine soils and may be a major factor in the difficulty in reclaiming such areas. Some of the components that were identified in the lichen extracts included; barbitic, usnic, didymic, condidymic, subdidymic, fumarprotocetaric, squamatic, and rhodocladonic acids. These compounds and similar ones need to be investigated further to determine their actual potential to control tree growth.

Perry and Choquette (19) contributed a review article concerning the effects of allelochemicals on ectomycorrhizae for an American Chemical Society symposium. This article is an excellent review of the subject.

Several other articles were published that concerned the effect of herbaceous plants or plant extracts on woody plant growth. Bramble et al. (4) investigated the effects of several existing groundcover types on tree invasion in utility rights-of-way. The method used consisted of identifying vegetation along transects through a rights-of-way, determination of the dominant vegetation type, and estimation of its resistance to tree invasion based on existing tree invasion.

The method overlooks the contribution of several factors that could influence tree invasion such as the existence of mycorrhizae, soil types, and prior vegetation management practices.

Ferguson and Boyd (7) have identified bracken fern (Pteridium aquilinum) as a contributing cause of the failure of conifer regeneration in some areas of Idaho. Bracken fern is a native of New York and could be established as a rights-of-way groundcover using rhizome sections as propagules. Its ability to be established and compete with other plants under conditions of adequate rainfall needs to be investigated.

Sudex, a sorghum sudan grass hybrid was investigated further by Geneve and Weston (8, 25). Although this particular grass hybrid is allelopathic to woody species, it is not hardy in New York. Perhaps, a similar hybrid exists or could be selected for more northern climates.

Gilmore (9) demonstrated that the phenolic acids produced by giant foxtail (Setaria faberii) inhibit root elongation of loblolly pine (Pinus taeda) to a greater extent than shoot elongation. This investigation was performed on pine seedlings over a short period of time. The effect of prolonged treatment of foxtail extracts on pine seedlings needs to be investigated further. A 50% reduction in root growth should eventually result in shoot growth inhibition to a similar extent.

Sunflower (Helianthus sp.) is a well known allelopathic group of plants. Leather (17) has suggested that certain species, particularly H. scaberrimus could be used to control weeds. No particular reference was made to woody plants.

Wyethia mollis, montane chaparral, is an aggressive invader of fields in the western United States. It has been shown to be extremely toxic to pine (18, 26). The mortalilty of Pinus jeffreyii seedlings grown in association with W. mollis is 50%. The subsequent growth of surviving seedlings is reduced by 25 to 33%. Terpenoids and other compounds were indicated to be the potential allelochemicals.

A combination of Sheep laurel Kalmia augustofolia and moose browsing were suggested to be the cause of the failure of balsam fir to regenerate in areas cleared by logging or fire (24). Apparently, moose do not like to browse sheep laurel. The spared sheep laurel grow in dense patches that evidently restricts the growth of balsam fir. Whether allelopathy or competition is involved is not conclusively determined.

## 4.2 Conclusions

The articles mentioned are indicative of the nature and state-of-science of allelopathy research. Several of the investigations can conclusively demonstrate an allelopathic interaction between an herbaceous species and a woody species. A few of the articles establish the probability of allelopathic interactions in a field or forest situation. Most of the investigations demonstrate the complexity of factors involved that determine the effect of other organisms on tree growth, like mycorrhizae and moose. Unfortunately, this complexity is usually not accounted for in most investigation of allelopathy. A more uniform means of evaluating allelopathic interactions is required, and in regard to tree growth a different perspective is needed.

Tree growth and development is different from herbaceous plant growth and development. There are many differences that can confound the extrapolation of results generated through allelopathy investigations using herbaceous plants. Because trees are perennial, their annual growth is independent of seed germination, and seedling growth. Tree growth and development is affected less by adverse conditions associated with seedling growth (competition for light and nutrients). An allelochemical that influences a seedlings ability to survive may not affect a tree. The size of a tree allows a tree to avoid localized allelopathic effects much more easily than seedlings. Trees have evolved associations with mycorrhizal fungi which modify the chemical environment of their root systems. Consequently, the chemistry of allelopathic interactions of trees can be more complex than in herbaceous plants.

Because of these differences and others, investigations of allelopathic factors affecting tree growth need to be designed to account for this increased complexity. Experiments should include confirmation runs using larger than seedling sized tree specimens. Factors like mycorrhizae or moose browsing for example should be considered in the equation.

Plant extracts are often used to model or demonstrate allelopathic interactions between plants. The extracts are often condensed and diluted to various concentrations prior to application. Although water is usually used as the extracting solvent and application base, because the pH and temperature of water can vary greatly, the validity of some the extracts is questionable. Further, allelopathy is caused by the active <u>exudation</u> of chemicals by a plant, not by <u>extraction</u> of chemical from plant tissues. Consequently, conclusions drawn from investigations employing plant extracts should be viewed with skepticism.

To “prove” a plant has an allelopathic effect on another, the following conditions should be met:

1. An identified substance must be shown to be released or exuded from a plant under “normal” growth conditions.

2. The suspect chemical must be shown to be translocated to the target plant by natural means through a natural substrate.

3. The suspect must have an observable direct effect on the target plant. Shoot growth is not a direct effect.

Very few of the investigations of allelopathic interactions reported in the scientific literature stand up to this scrutiny of proof. Consequently, care must be taken in accepting many conclusions, and future experiments need to be designed better. The checklist provided in Table 4-1 should only be used as a guide for determining whether a plant may have the potential to control the growth of trees.

## 4.3 Recommendations

There is substantial evidence to indicate that, tree invasion of a rights-of-way can be prevented by herbaceous plants. The conditions that will produce this effect is dependent on several complex factors which could vary from site to site within a rights-of-way system. The accumulated scientific knowledge is insufficient to predict which set of conditions will produce the desired results in New York. Further research should be pursued with the specific goal of generating the knowledge necessary to effectively use low growing allelopathic shrubs and herbaceous plants to control tree invasion in rights-of-way.

However, it is apparent that such research directed at developing tree growth regulation protocols based on allelopathic interactions needs the support of the utility industry. More allelopathy research is conducted on herbaceous plants than woody plants because of the ease with which experiments are conducted on herbs and sponsorship by the agricultural community. Without alternate sponsorship, the focus of allelopathy research will skew toward agricultural needs.

ESEERCO should attempt to establish a research group under its direct control and supervision. The sole purpose of such a research group would be to develop and improve rights-of-way vegetation management methods. The group should be fully funded and be independent of the control from other institutions. The work required to develop effective natural means of tree growth control is extensive and would be better served by a focused goal-oriented team of experts employed directly by ESEERCO. Such a research group could act on problems presented via ESEERCO more quickly and efficiently than reliance on independent groups or associations with divergent objectives.

The first goal of such a group would be to continue the investigation begun with this literature survey. Specifically, emphasis should be placed on isolating compounds from microorganisms, plant pathogens, and allelopaths that can be demonstrated to inhibit the growth of trees.

**Table 4-1**
**Checklist of Allelopathic Plants**

| Genus Species Name | Common Name | Reference |
|---|---|---|
| Agrostemma githago | | * |
| Agrostis tenuis | | * |
| Amaranthus dubius | | * |
| A. retroflexus | | * |
| Ambrosia psilostachya | | * |
| A. trifida | | * |
| Antennaria microphylla | | * |
| A. neglecta | | * |
| Artemisia absinthium | | * |
| Aster macrophyllus | | * |
| Berteroa incana | | * |
| Boerhavia diffusa | | * |
| Bromus japonicus | | * |
| Calamagrostis epigejos | | * |
| Calluna vulgaris | | * |

**Table 4-1**
**Checklist of Allelopathic Plants (Continued)**

| Genus Species Name | Common Name | Reference |
|---|---|---|
| Camelina alyssum | | * |
| C. sativa | | * |
| Celosia argentea | amaranth | * |
| Cenchrus pauciflorus | | * |
| Centaurea diffusa | | * |
| C. maculosa | | * |
| C. repens | | * |
| Cirsium discolor | | * |
| Citrullus colocynthis | | * |
| C. lanatus | | * |
| Cladonia cristatella | lichen | 10 |
| Cucumis callosus | | * |
| Cyanodon dactylon | | * |
| Daboecia polifolia | | * |
| Digera arvensis | | * |
| Eleusine indica | | * |
| Erica sp. | heath | * |
| Euphorbia corollata | | * |
| E. esula | | * |
| E. supina | | * |
| Galium mollugo | bedstraw | 15, * |
| Hamamelis virginiana | witchhazel | 4 |
| Helianthus annuus | sunflower | * |
| H. scaberrimus | | 17 |
| Hydrocotyle sibthorpiodes | | * |
| Imperata cylindrica | | * |
| Indigofera cordifolia | | * |
| Iva xanthifolia | | * |
| Kalmia augustifolia | Sheep laurel | 24 |
| Lactuca scariola | | * |
| Lepidium virginicum | | * |
| Leptochloa filiformis | | * |
| Lolium multiflorum | | * |

**Table 4-1**
**Checklist of Allelopathic Plants (Continued)**

| Genus Species Name | Common Name | Reference |
|---|---|---|
| Lonicera tatarica | | * |
| Lychnis alba | | * |
| Oxalis latifolia | | * |
| Osmunda claytonia | interrupted fern | 12 |
| Parthenium hysterophorus | | * |
| Plantago purshii | | * |
| Poa pratensis | Kentucky bluegrass | 16 |
| Polygonum sp. | | * |
| Portulaca oleracea | | * |
| Pteridium aquilinum | bracken fern | 7 |
| Quercus ilicifolia | bearoak | 4 |
| Rubus allegheniensis | blackberry | 4 |
| R. idaeus | raspberry | 4 |
| Rumex crispus | | * |
| Salsoli kali | | * |
| Salvadora oleoides | | * |
| Schinus molle | | * |
| Setaria faberii | giant foxtail | 9 |
| S. viridis | | * |
| Solanum dulcamara | | * |
| S. surattense | | * |
| Solidago sp. | goldenrod | 12 |
| S. gigantea | | * |
| Tagetes patula | | * |
| Trichodesma amplexicaule | | * |
| Wyethia mollis | montane chaparral | 18, 26 |
| Vaccinium augustifolium | blueberry | 4 |
| Vaccinium vacillans | blueberry | 4 |
| Xanthium pennsylvanicum | | * |

* referenced in Appendix A, Table A-2.

## 4.4 Annotated Bibliography

1. ANON. 1987. Weed scientists study benefits of Lantana. Am. Nurseryman 166 (2): 10-12.

   This short article describes, briefly, the research efforts of Dr. Megh Singh at the Lake Alfred facility of IFAS. It quotes Dr. Singh as suggesting that the use of the allelopath Lantana (the species is not identified) could save 40% of the costs of using synthetic herbicides in citrus groves.

2. Basu, P.K., Kapoor, K.S., Nath, S., Banerjee, S.K. 1987. Allelopathic influence: an assessment on the response of agricultural crops growing near Eucalyptus tereticornis. Indian Journal of Forestry 10 (4) 267-271.

   The investigators demonstrated a reduced yield of potatoes grown in plots adjacent to a road planted with E. tereticornis. A 1-m irrigation canal separated the potato plots from the line of eucalypts. Potato yield was 48 kg 3.8 m from E. tereticornis; 75 kg 11.8 m from E. tereticornis; and 144 kg 19.8 m from E. tereticornis. Soil pH, % organic C and N, CEC available P, and exchangeable Ca, Mg, Na, and K were measured. Only soil pH differed slightly (5.1 near the eucalypt to 5.5 furthest away). The authors suggest that allelopathic substances from eucalypt litter caused the crop response and the reduction in soil pH. The article is included because it details the measurable inhibition of growth at several distance from the allelopathic agent.

3. Boes, T.K. 1986. Allelopathy: chemical interactions between plants. Am. Nurseryman 163 (2): 67-72.

   This recent article describes what is known about black walnut allelopathy. The effect of black walnut trees on understory vegetation is often used as an example of allelopathy. The chemical involved is called juglone.

4. Bramble, W.C., Byrnes, W.R., Hutnik, R.J. 1990. Resistance of plant cover types to tree seedling invasion on an electric transmission right-of-way. J. Arboriculture 16 (5): 130-135.

   Grass and herb type covers were considered resistant to tree invasion as well as shrub type covers dominated by blueberry (Vaccinium augustifolium, and V. vacillans), and bear oak (Quercus ilicifolia). Shrub type covers dominated by blackberry (Rubus allegheniensis) and witchhazel (Hamamelis virginiana) were deemed to be of low resistance to tree invasion. The conclusions are drawn from data derived from transects of existing ROW and do not consider many factors shown to influence vegetation patterning. For example no data is shown for differences in soil types associated with the types of covers described.

5. Brown, R.T. 1985. Dynamic balance in pine forests–ground cover–mycorrhizae–tree. Proceedings of the 6th North American Conference on Mycorrhizae, June 25-29, 1984, Bend Oregon, edited by R. Molina, p. 277.

   Mycorrhizae effect the successful1 establishment and subsequent health of forests as described in this abstract concerning pine forests. Allelopathic interactions between herbaceous and arboreal plants may be mediated at the level of mycorrhizal interactions.

6. Cote, J.F., Thibault, J.R. 1988. Allelopathic potential of rasberry foliar leachates on growth of ectomycorrhizal fungi associated with black spruce. Am. J. Bot. 75 (7): 966-970.

   Artificial regeneration of black spruce (Picea mariana) forests in Canada is seriously hindered in areas associated with the growth of rasberry (Rubus idaeus). Foliar leachates (50 g air dried leaves in 1000 ml, diluted to 0.1 - 2.5 g/l) were found to inhibit the growth of ectomuccorrhizal fungi associated with black spruce. The authors suggest that this may be one of the reasons for regenration failure.

7. Ferguson, D.E., Boyd, R.J. 1988. Bracken fern inhibition of conifer regeneration in northern Idaho. USDA For. Ser. Res. Paper 388: 1-11.

   Bracken fern (Pteridium aquilinum), according to the USDA forest service, interferes with the reestablishment of conifiers in logged areas. The plant has been previously identified to be allelopathic. Unlike most ferns, this fern grows well in full sunlight with adequate moisture.

8. Geneve, R.L., Weston, L.A. 1988. Growth reduction of eastern redbud (Cercis canadensis L.) seedlings caused by interaction with a sorghum-sudangrass hybrid (Sudex). J.Env.Hort. 6 (1): 24-26.

   Dried leaves of Sudex were applied to the surface of pots and soil surrounding seedlings of redbud as a mulch orginally to reduce the growth of competing weeds. The authors demonstrated that Sudex litter also inhibited the growth of the redbud seedlings.

9. Gilmore, A.R. 1985. Allelpathic effects of giant foxtail on germination and radicle elongation of loblolly pine seed. J.Ch.Ecol. 11 (5): 583-592.

   The germination of Pinus taeda was reduced only 17% by water extracts of Setaria faberii while radicle elongation was reduced 50%. Allelopathic substances identified include vanillic, syringic, o-hydroxyphenylacetic, p-coumaric, ferulic, gentisic acids and scopoletin. The author points out that allelopathic domination of another species is more dependent on growth inhibition than on germination inhibition. The observation suggests that determining allelopathic potential on the basis of seed germination could be erroneous.

10. Goldner, W.R., Hoffman, F.M., Medve, R.J. 1986. Allelopathic effects of Cladonia cristatella on ectomycorrhizal fungi common to bituminous strip-mine spoils. Can. J. Bot. 64 (8): 1586-1590.

    A lichen, C. cristatella, is common on abandoned strip mine lands that have proved difficult to reclaim. Extracts of the lichen were shown to kill ectomycorrhizal fungi; Pisolithus tinctorius, Suillus luteus, Thelephora terrestris, and Cenoioccum graniforme. The extracts were shown to contain; barbatic, usnic, didymic, condidymic, subdidymic, fumarprotocetraric, squamatic, rhodocladonic acid. This is an interesting article because it suggests that reforestation failure could be due to the failure of mycorrhizal growth. An effective tree growth inhibitor could be a fungicide.

11. Gordon, A.M., Williams, P.A. 1988. Intercropping valuable hardwood tree species and agricultural crops. Agrologist 17 (3): 12-14.

The authors suggest that certain hardwood trees could be intercropped with agricultural crops. They allude briefly to the problem of allelopathy.

12. Hansen, P.J., Dixon, R.K. 1985. Allelopathic inhibition of northern red oak by interupted fern and goldenrod. Fifth Central Hardwood Forest Conference: proceedings of a meeting held at the University of Illinois, 4/15-4/17 edited by J.O. Dawson and K.A. Majerus p. 269-274.

    Extracts of interrupted fern (Osmunda claytoniana) and golden rod (Solidago sp.) were shown to inhibit the growth of northern red oak (Quercus borealis). The chemicals involved were not completely identified; however, phenolics and terpenoid compounds were.

13. Harrington, M.G. 1987. Phytotoxic potential of gambel oak on ponderosa pine seed germination and initial growth. USDA For.Ser.Res.Pap.RM 277: 1-7.

    Details experiments demonstrating that extracts of gambel oak leaves inhibit the germination of ponderosa pine seeds and seedlings.

14. Horsley, S.B. 1987. Allelopathic interference with regeneration of the Allegheny hardwood forest. ACS Symposium Series 330: 205-213.

    This is a review article of past work by Dr. Horsley.

15. Huth, P.C., Smiley, D. 1986. Bedstraw in Ulster County: Past, Present, and Future. Mohonk Preserve, Inc. Research Report, 3 pp.

    This brief report describes the history of Gallium mollugo, bedstraw in the Hudson valley of New York. Bedstraw has been considered a nuisance weed in New York. It grows aggressively dominating the growth of the plants in fields where it gets introduced. The authors suggest that growth of bedstraw growth areas where open fields are to be maintained for aethetic purposes could be desirable.

16. Kolb, T.E. 1988. Allelopathic effects of Kentucky bluegrass on northern red oak and yellow-poplar. J.Arboriculture 14 (11): 281-283.

    Leachates of Poa pratensis, Kentucky bluegrass, was shown to slightly reduce the growth of Quercus rubra and Liriodendron tulipifera. The method used did not distinguish specific allelochemicals.

17. Leather, G.R. 1987. Weed control using allelopathic sunflowers and herbicides. Plant and Soil 98 (1): 17-23.

    The author suggests that sunflowers could be used to control weeds: Amaranthus retroflexus, redroot pigweed; Chenopodium album, common lambsquaters; Cirsium arvense, Canadian thistle; and Setaria faberi, giant foxtail. No specific allelchemical is mentioned. Helianthus species have been known to be allelopahtic previously. Helianthus scaberrimus was observed to grow in “fairy ring” like patterns (Cooper, W.S., Stoesz, A.D. 1931. The subterranean organs of Helianthus scaberrimus. Bull. Torrey Bot. Club 58: 67-72).

18. Parker, V.T., Yoder-Williams, M.P. 1989. Reduction of survivial and growth of young Pinus jeffreyi by an herbaceous perennial, Wyethia mollis. Am. Midl. Nat. 121 (1): 105-111.

    The mortality of P. jeffreyi growing in association with W. mollis was 50%. The growth of surviving pine seedlings was reduced 25-33%. Terpenoid compounds from the montane chaparral were identified as potential allelochemicals.

19. Perry, D.A., Choquette, C. 1987. Allelopathic effects on mycorrhizae. Influence on structure and dynamics of forest ecosystems. ACS Symposium Series 330: 185-194.

    This is a review article on the affects of allelochemicals on ectomycorrhizal fungi and the subsequent interaction between these organisms and forests.

20. Ponder, F., Jr. 1989. The importance of below ground interactions for hardwood growth. USDA For.Ser.Gen.Tech.Rep. 132: 129-133.

    This is a general article that comments on the various factors that influence the growth of trees including allelopathy.

21. Putnam, A.R. 1988. Allelochemicals from plants as herbicides. Weed Technology 2 (4): 510-518.

    Dr. Putnam, one of the foremost authorities on allelopathy has reviewed in this article the potential of using allelopathic agents as natural herbicides. The content is general and has been written for the weed control industry.

22. Putnam, A.R., Tang, C-S. 1986. The Science of Allelopathy. John Wiley and Sons, New York, 317 pp.

    This is a must read review of the science of allelopathy. Several chapters are devoted to specific groups of allelochemicals, methodology used to investigate, allelopathy, field observations, and the potential practical uses of allelopathy. Tang has compiled an especially good chapter on continuous trapping methods for the isolation and collection of allelochemicals. The method described should be the standard used by allelopathy investigators.

23. Soni, S.R., Mohnot, K. 1988. Chlorophyll synthsis in jowar seedlings as affected by allelopathic complex of the leaves of Celosia argentea. Comp. Physiol. & Ecol. 13 (3): 152-154.

    A member of the amaranth family, C. argentea has been suggested to be an allelopathic weed in stands of jowar in India. Extracts of this weed inhibit chlorophyll synthesis. The chemical nature of the extract is not identified.

24. Thompson, I.D., Mallik, A.U. 1989. Moose browsing and allelopathic effects of Kalmia angustifolia on balsam fir regeneration in central Newfoundland. Can. J. For. Res. 19 (4): 524-526.

Sheep-laurel, Kalmia augustifolia a small shrub that grows to 1 meter, and moose browsing have combined to severely inhibit the regrowth of balsam fir (Abies balsamea) forests. Moose apparently prefer balsam fir seedlings over laurel. The resulting laurel growth establishes stands that preclude development of other balsam fir seedlings. Although the proof is not conclusive, the authors suggest that allelopathy is involved.

25. Weston, L.A., Geneve, R.L., 1987. 1987. Allelopathic potential of a sorghum-sudangrass hybrid cover crop on herbaceous and woody plants. HortScience 22 (5): 1120.

    The authors suggest that Sudex could be used as a cover crop in nurseries to reduce weed growth.

26. Yoder-Williams, M.P., Parker, V.T. 1987. Allelopathic interference in the seedbed of Pinus jeffreyi in the Sierra Nevada, California. Can.J. of For. Res. 17 (8): 991-994.

    The growth of montane chapparel, Wyethia mollis, is suggested to be the cause of lack of regrowth of Pinus jeffreyi stands. The montane chapparel has increased its habitat range due to overgrazing and canopy fires.

# 5
# MOHONK PRESERVE FIELD BIOGRAPHIES

Mohonk Preserve, New York's largest private preserve, was created through the foresight and generosity of the Smiley family, founders of the well known Mohonk Mountain House resort. For over 120 years, the Smiley family has been involved with Shawangunk Mountain (Mohonk) land use and stewardship. With great attention to details, meticulous records were kept and archived of farming activities and utilization of the land by the Smiley family. This detailed history of land use was available when several of the large Mohonk farms were transferred to the Mohonk Preserve in the early 1970s to provide permanent space for the use and benefit of the public. Today, the Mohonk Preserve with its well-documented history of land use, offers researchers a unique opportunity to investigate successional changes on disturbed land.

As part of the Preserve's own research effort, studies to provide information about land management are encouraged. The Preserve has some sixty former Mohonk farm fields (representing about 10% of the land area) that it intends to keep open as part of its designation as a National Historic Landmark and for the protection of its wildlife and habitat diversity. There is a conscious effort by the Preserve's stewards to reduce soil compaction and mechanical disturbance during maintenance of these lands.

For a number of years, Daniel Smiley and Preserve research staff noted with interest that several of the former fields were not reverting back to forest as is the tendency of most abandoned fields, even though there was little or no control of invasion by woody plants. Knowing what land use had taken place on these fields, no clear answers were apparent as to why this was not happening on these fields. There was a strong likelihood of the answer lying in the relationship of soil and plant associations. Six fields (Buff farm 1 and 2; Home Farm 1 and 3; Spring Farm 4 and 11) on Preserve land were deemed good examples from which land use factors complicating most analyses of this type could be excluded. These fields represented a spectrum of failed responses to reforestation and included a situation where one field failed to regenerate yet regeneration took place on a neighboring field.

The following are biographies and plant check lists compiled for the six fields. The relationships indicated in the biographies between soils and plant species is complex and needs further investigation at the chemical and microbiological level to elucidate the factors that determine reforestation rates in these fields. The biographies provide a background around which future studies can be planned.

Date: 7 January 1991

Field Name or No.: Buff No. 1

Location and Acreage: Northwest of Coxingkill and East of Cedar Hill. Approximately 9 acres.

History and Maintenance: Deeded to Mohonk in 1920, called “Buff Farm.” Used as a Mohonk farm for growing potatoes until the late 1940s, when agriculturally abandoned. Became part of Mohonk Preserve in 1970. Since that time has been left in its natural state — no clipping, mowing or other vegetation control.

Present Condition: An open field with thick, meter-tall, herbaceous vegetation and very widely scattered, low woody shrubs and tree seedlings.

Dominant Species:

a. Field

   Goldenrods (several species), Northern Dewberry, Purple Loosestrife, Beardtongue, Bergamot, Graminoids (grasses and sedges, several species), Mountain Mint, Gray-stemmed Dogwood, Milkweed.

b. Hedgerow/Woods

   White Ash, White Pine, Red and Sugar Maple, Elm, Red Oak, Big-toothed Aspen, Red Cedar, and Hickory spp.

Soils (USDA-1979):

Schoharie Silt loam, 3 to 8 percent slopes (SaB)

Remarks:

Of note: no Red Cedar in field. See list of field plants attached. This field has the largest number of plant species and has the highest potential for revealing allelopathic relationships.

List of Plants – Buff Farm Field No.1

| Species | Common Name |
|---|---|
| **Acer rubrum** L. var. **rubrum** | Red Maple |
| **Agrostis** sp. | Bent Grass |
| **Anthoxanthum odoratum** L. | Sweet Vernalgrass |
| **Asclepias syriaca** L. | Common Milkweed |
| **Aster novae-angliae** L. | New England Aster |
| **Aster** sp. | Aster |
| **Carex squarrosa** L. | Squarrose Sedge |
| **C**. spp. | Sedges |

| | |
|---|---|
| **Cirsium arvense** (L.) Scop. | Canada Thistle |
| **C. vulgaris** (Savi) Tenore | Bull-thistle |
| **Clematis virginiana** | Virgin's-bower |
| **Cornus amomum** Mill. ssp. **amomum** | Silky Dogwood |
| **C. florida** L. | Flowering Dogwood |
| **C. foemina** Mill. spp. **racemosa** (Lam) J. Wilson | Gray Dogwood |
| **Corylus americana** Walt. | Hazelnut |
| **Dactylis glomerata** L. | Orchard Grass |
| **Equisetum arvense** L. | Field Horsetail |
| **Eupatorium fistulosum** Barratt ex Hook | Joe-pye-weed |
| **Festuca** sp. | Fescue |
| **Galium mollugo** L. | White bedstraw |
| **Glechoma hederacea** L. | Ground-ivy |
| **Hieracium (caespitosum** Dumort.**)** | King-devil |
| **Hypericum gentianoides** (L.) BSP. | Orange-grass |
| **Juncus effusus** L. | Soft Rush |
| **Juniperus virginiana** L. | Red Cedar |
| **Lonicera (morrowii** Gray**)** | Honeysuckle |
| **Lythrum salicaria** L. | Purple Loosestrife |
| **Monarda fistulosa** L. | Wild Bergamot |
| **Muhlenbergia** sp. | Muhly |
| **Onoclea sensibilis** L. | Sensitive Fern |
| **Pedicularis (canadensis** L.**)** | Wood-betony |
| **Penstemon digitalis** Nutt. | False-foxglove |
| **Phleum pratense** L. | Timothy |
| **Pinus strobus** L. | White Pine |
| **Pycnanthemum** spp. (2) | Mountain Mint |
| **Quercus palustris** Muenchh. | Pin Oak |
| **Rosa (carolina** L.**)** | Pasture Rose |
| **Rubus allegheniensis** Porter ex Bailey | Northern Blackberry |
| **R. flagellaris** Willd. | Northern Dewberry |
| **Salix discolor** Muhl. | Pussy-willow |
| **Sisyrinchium angustifolium** Mill. | Blue-eyed Grass |
| **S. montanum** Greene | Blue-eyed Grass |
| **Solidago** spp. (at least four species) | Goldenrods |
| **Stellaria graminea** L. | Lesser Stitchwort |
| **Ulmus rubra** Muhl. | Slippery Elm |
| **Veronica chamaedrys** L. | Bird's-eye Speedwell |
| **Viburnum lentago** L. | Nanny-berry |
| **Vitis** sp. | Wild Grape |

52 (+) species

Date: 7 January 1991

Field Name or No.: Buff No. 2

Location and Acreage: North of and across drainage ditch from Buff field No. 1. Approximately 3 l/2 acres.

History and Maintenance: Deeded to Mohonk in 1920, called “Buff Farm.” Used as a Mohonk farm for growing potatoes until the late 1940s, when agriculturally abandoned. Became part of Mohonk Preserve in 1970. Since that time has been left in its natural state — no clipping, mowing or other vegetation control.

Present Condition: A semi-open field with thick herbaceous vegetation and some areas of woody invasives to several meters tall. South-easterly corner most open, with little woody growth.

Dominant Species:

a. Field

   Goldenrods (several species), Northern Dewberry, Blackberry, Common Woolgrass, Purple Loosestrife, Graminoids (grasses and sedges, several species), Dogwood spp., Black Alder, Smooth Sumac (large stand).

b. Hedgerow/Woods

   White Ash, White Pine, Red and Sugar Maple, Elm, Red Oak, Big-toothed Aspen, Red Cedar, Hickory spp., and White Oak.

Soils (USDA-1974):

Schoharie Silt loam, 3 to 8 percent slopes (SaB)

Remarks:

A small amount of invasion by Red Cedar. Much more woody invasion in spots. Dense Dewberry cover. Should be studied with adjacent field, Buff No. 1. See list of field plants attached.

List of Plants – Buff Farm Field No. 2

| <u>Species</u> | <u>Common Name</u> |
|---|---|
| **Cornus amomum** Mill. ssp. **amomum** | Silky Dogwood |
| C. **foemina** Mill. ssp. **racemosa** (Lam) J. Wilson | Gray Dogwood |
| **Graminoids** (grasses and sedges of several species) | |
| **Fraxinus americana** L. | White Ash |
| **Ilex verticillata** (L.) Gray | Winterberry |
| **Juniperus virginiana** L. | Red Cedar |
| **Lythrum salicaria** L. | Purple Loosestrife |
| **Populus grandidentata** Michx. | Big-toothed Aspen |
| **Prunus serotina** Ehrh. | Black Cherry |
| **Rhus glabra** L. | Smooth Sumac |
| **Rubus allegheniensis** Porter ex Bailey | Northern Blackberry |
| **R. flagellaris** Willd. | Northern Dewberry |
| **Scirpus cyperinus** (L.) Kunth | Woolgrass |
| **Solidago** spp. | Goldenrods |

14 (+) species

<u>Date</u>: 7 January 1991

<u>Field Name or No.</u>: Home Farm No. 1

<u>Location and Acreage</u>: 1/4 mile south of Mohonk Lake. Approximately 2 acres.

<u>History and Maintenance</u>: In agricultural use at least since 1850. Acquired by Mohonk in original purchase in 1869. Grapes were raised in the 1890s. In 1917, used for production of hay and grain (1917 Annual Report available in Research Center Archives). 1944-45 vegetables grown. 1950s hay cut. 1960s and 70s, occasional mowing. Became part of Mohonk Preserve in 1967. In 1970s woody sprouts treated with 2-4-5T in a basal bark spray. 1983 mowed by brushhog. 1986 firewood sized invasive White Ash and Maple trees harvested along west and northeast sides.

<u>Present Condition</u>: Open grassy and weedy field with roses and blackberries.

<u>Dominant Species</u>:

a. Field

   Grasses (spp.), Goldenrods (spp.), Asters, Northern Dewberry, Blackberry, Pillar Rose.

b. Hedgerow/Woods

   White Ash, Sugar and Red Maple, White Pine, Red Oak.

<u>Soils</u> (USDA-1974):

Nassau-Manilus shaly silt loams, rolling (NMC).

<u>Remarks</u>:

See list of field plants attached.

List of Plants – Home Farm Field No. 1

| <u>Species</u> | <u>Common Name</u> |
|---|---|
| **Acer rubrum** L. var. **rubrum** | Red Maple |
| **A. saccharum** Marsh | Sugar Maple |
| **Agrostis sp.** | Bent Grass |
| **Asclepias syriaca** L. | Common Milkweed |
| **Asparagus officinalis** L. | Asparagus |
| **Aster** spp. | Asters |
| **Bromus inermis** Leyss. | Smooth (Awnless) Brome |
| **Carex** spp. | Sedges |
| **Cirsium vulgare** L. | Bull-thistle |
| **Clinopodium vulgare** L. | Basil |
| **Dactylis glomerata** L. | Orchard Grass |
| **Daucus carota** L. | Queen-Anne's-Lace |
| **Eupatorium rugosum** Houtt. | White Snakeroot |
| **Fraxinus americana** L. | White Ash |
| **Galium mollugo** L. | White Bedstraw or Wild Madder |
| **Iris** sp. (probably germanica) | Garden Iris |
| **Juncus effusus** L. | Soft Rush |
| **Monarda fistulosa** L. | Wild Bergamot |
| **Panicum** sp. | Panic Grass |
| **Phleum pratense** L. | Timothy |
| **Pinus strobus** L. | White Pine |
| **Polygonum sagittatum** L. | Tearthumb |
| **Prunella vulgaris** L. | Self-heal |
| **Quercus rubra** L. var. **borealis** (Michx. f.) Farw. | Northern Red Oak |
| **Rosa** sp. | American Pillar Rose |
| **Rubus allegheniensis** Porter ex Bailey | Northern Blackberry |
| **R. flagellaris** Willd. | Northern Dewberry |
| **R.** sp. | Blackberry |
| **Solidago** spp. | Goldenrods |

29 (+) species

Date: 7 January 1991

Field Name or No.: Home Farm No. 3

Location and Acreage: 1/4 mile south of Mohonk Lake. Approximately 1 acre.

History and Maintenance: In agricultural use at least since 1850. Acquired by Mohonk in original purchase in 1869. In 1917 corn grown. In 1945 used for raising corn and green beans. During the 1950s hay cut. In the 1960s and 70s occasionally mowed. Became part of Mohonk Preserve in 1967. Probable mowing in early 1980s.

Present Condition: An open grassy field with Goldenrods and Northern Dewberry.

Dominant Species:

a. Field

   Grasses (several species including Awnless-brome), Yellow Mustard, Goldenrods, several Mints, Beardstongue, Mullen, Asters.

b. Hedgerow/Woods

White Ash, Sugar Maple, White Pine, Red Oak.

Soils (USDA-1974):

Nassau-Manilus shaly silt loams, rolling (NMC).

Remarks:

See list of field plants attached.

List of Plants – Home Farm Field No. 3

| Species | Common Name |
|---|---|
| **Allium vineale** L. | Field Garlic |
| **Asclepias syriaca** L. | Common Milkweed |
| **Aster** sp. | Aster |
| **Barbarea vulgaris** R. Br. | Yellow Rocket |
| **Berberis vulgaris** L. | Common Barberry |
| **Bromus inermis** Leyss. | Smooth (Awnless) Brome |
| **Cirsium vulgare** (Savi) Tenore | Bull-thistle |
| **Clinopodium vulgare** L. | Basil |
| **Comptonia peregrina** (L.) Coult. | Sweet-fern |
| **Cornus foemina** Mill. ssp. **racemosa** (Lam) J. Wilson | Gray Dogwood |
| **Dactylis glomerata** L. | Orchard Grass |
| **Hamamelis virginiana** L. | Witch-hazel |
| **Leonurus cardiaca** L. | Motherwort |
| **Monarda fistulosa** L. | Wild Bergamot |
| **Penstemon digitalis** Nutt. | Beard-tongue |
| **Phleum pratense** L. | Timothy |
| **Pinus strobus** L. | White Pine |
| **Rhus typhina** L. | Staghorn Sumac |
| **Rosa** sp. | Rose |
| **Rubus allegheniensis** Porter ex Bailey | Northern Blackberry |
| **R. flagellaris** Willd. | Northern Dewberry |
| **R.** sp. | Blackberry |
| **Rumex obtusifolius** L. | Bitter-dock |
| **Solanum carolinense** L. | Horse-nettle |
| **Solidago** spp. | Goldenrods |
| **Verbascum thapsus** L. | Mullein |

26 (+) species

Date: 7 January 1991

Field Name or No.: Spring Farm No. 4

Location and Acreage: West of 27 Knolls Road, near junction with Mohonk Road. Approximately 5 l/2 acres.

History and Maintenance: Described as “farm premises” in a deed of 1865. Acquired by Mohonk in 1919. Under Smiley ownership Spring Farm was operated as a dairy and hay farm. It became part of Mohonk Preserve in 1982. Since 1982 the only maintenance has been the rotary mowing of a cross-field foot path on the north side and the hand clipping of woody invasives along the west side and edges in the late 1980s.

Present Condition: An open, grass-dominated field.

Dominant Species:

a. Field

   Awnless-Brome grass, Orchard Grass, Reed Canary Grass. On southwest end a damp area of Cat-tail, Loosestrife and Willow.

b. Hedgerow/Woods

   White Ash, Red Oak, Sugar Maple.

Soils (USDA-1974):

Morris-Tuller Complex, very bouldery, gently sloping (MTB) (southwest end)

Mardin-Nassau Complex, 3 to 8% slopes (MgB) (main portion)

Lordstown-Arnot-Rock outcrop complex, sloping (LOC) (west side)

Remarks:

See list of field plants attached.

List of Plants – Spring Farm Field No. 4

| Species | Common Name |
|---|---|
| **Asclepias syriaca** L. | Common Milkweed |
| **Bromus inermis** Leyss. | Smooth (Awnless) Brome |
| **Cirsium** sp. | Thistle |
| **Dactylis glomerata** L. | Orchard Grass |
| **Fraxinus americana** L. | White Ash |
| **Galium mollugo** L. | White bedstraw or Wild Madder |
| **Lythrum salicaria** L. | Purple Loosestrife |
| **Muhlenbergia** sp. | Muhly |
| **Phalaris arundinacea** L. | Reed Canary-grass |
| **Pycnanthemum** sp. | Mountain Mint |
| **Quercus rubra** L. var. **borealis** (Michx.) Farw. | Northern Red Oak |
| **Rosa** sp. | Rose |
| **Rubus allegheniensis** Porter ex Bailey | Northern Blackberry |
| **R. flagellaris** Willd. | Northern Dewberry |
| **Salix** spp. | Willows |
| **Solidago** spp. | Goldenrods |
| **Typha latifolia** L. | Common Cat-tail |

17 (+) species

Date: 7 January 1991

Field Name or No.: Spring Farm No. 11

Location and Acreage: East of 27 Knolls Road, opposite Spring Farm house. Approximately 4 acres.

History and Maintenance: Deeded to Mohonk in 1881. Under Smiley ownership Spring Farm was operated as a dairy and hay farm from 1881 to 1949. It then became the location of Mohonk's beef animal operation until 1974. It became part of Mohonk Preserve in 1982. Since 1982 the only maintenance has been the rotary mowing of a cross-field foot path and irregular clipping of widely-scattered woody invasives.

Present Condition: An open field with a thick mat of field grass turf and White Bedstraw with scattered patches of meter-tall Golden-rod, Milkweed, and Wild Onion.

Dominant Species:

a. Field

   Goldenrod (several species), Graminoids (several species), White Bedstraw, Multiflora Rose, and Blackberry.

b. Hedgerow/Woods

   White Ash and Sugar Maple

Soils (USDA-1974):

Bath-Nassau Complex, 8 to 25% slopes (BnC).

Remarks:

See Mohonk Preserve Research Report “Bedstraw in Ulster County Past, Present and Future” July 1986, and list of field plants attached.

List of Plants – Spring Farm Field No. 11

| Species | Common Name |
|---|---|
| **Allium vineale** L. | Field Garlic |
| **Asclepias syriaca** L. | Common Milkweed |
| **Aster novae-angliae** L. | New England Aster |
| **Carex** spp. | Sedges |
| **Centaurea maculosa** Lam. | Bushy Knapweed |
| **Cirsium arvense** (L.) Scop. | Canada Thistle |
| **C. vulgare** (Savi) Tenore | Bull-thistle |
| **Dactylis glomerata** L. | Orchard Grass |
| **Erigeron** sp. | Fleabane |
| **Fraxinus americana** L. | White Ash |
| **Galium mollugo** L. | White Bedstraw or Wild Madder |
| **Hypericum** sp. | St. Johnswort |
| **Juncus effusus** L. | Soft Rush |
| **Linaria vulgaris** Mill. | Butter-and-eggs or Common Toadflax |
| **Lotus corniculata** L. | Bird’s-foot Trefoil |
| **Lythrum salicaria** L. | Purple Loosestrife |
| **Mentha x piperita** L. | Peppermint |
| **Morus** sp. | Mulberry |
| **Onoclea sensibilis** L. | Sensitive Fern |
| **Phleum pratense** L. | Timothy |
| **Polygonum sagittatum** L. | Tearthumb |
| **Prunus serotina** Ehrh. | Black Cherry |
| **Rosa multiflora** Thunb. ex Murr. | Multiflora Rose |
| **Rubus allegheniensis** Porter ex Bailey | Northern Blackberry |
| **Rumex obtusifolius** L. | Bitter-dock |
| **Scirpus cyperinus** (L.) Kunth | Woolgrass |
| **Solanum carolinense** L. | Horse-nettle |
| **Solidago** spp. | Goldenrods |
| **Toxicodendron radicans** L. | Poison Ivy |
| **Trifolium pratense** L. | Red Clover |

30 (+) species

## Conclusions

Six of some 50 fields owned by Mohonk Preserve, Inc. were identified for further study. These six fields were chosen for a common reason: all have been abandoned (or nearly so) for five to 40 years and in all six the re-growth of woody invasives has been much less and slower than expected when compared to neighboring fields.

Biographies were generated for these six fields and presented in sections 5.1A - F. These biographies establish as of January 7, 1991, a. location and acreage, b. history and maintenance, c. present condition, d. dominant species, e. soil type(s) and f. a basic list of plants. Two fields each are located on former Mohonk Farms, named The Buff (No. 1 and 2), Spring Farm (No. 4 and 11), and Home Farm (No. 1 and 3).

Two fields in particular stand out as having the best potential to reveal allelopathic relationships in further study. These are the fields located on the former Buff Farm. Since their abandonment in the late 1940s, they have been left in their natural state with no management or vegetation control. Remarkably, No. 1 is still open with thick meter-tall herbaceous vegetation and only very widely scattered low shrubs and tree seedlings as invasives. Field No. 2 on The Buff Farm is also generally free of woody invasives although there are areas where woody plants to several meters tall have established themselves (red cedar, dogwoods, black alder and smooth sumac). The soils in Buff Fields No. 1 and 2 are of the same type: Schoharie silt loam, 3 to 8 percent slopes.

The two fields on Home Farm (No. 1 and 3) are both grassy with several other herbaceous species in large numbers as well. In field No. 1 woody invasives were controlled in the last ten years by brushhog (1983), and firewood-sized white ash and maple removed along the west and northeast sides in 1986. Field No. 3 needed less maintenance to keep as an open field. The last mowing of this field was probably in the early 1980s. Both fields are of the soil type Nassau-Manilus shaly loams, rolling.

Both fields on Spring Farms (No. 4 and 11) have, since 1982, received little maintenance; only rotary mowing of a cross-field footpath and hand clipping of woody invasives. Field No. 4 is dominated by grass species and in one damp area, by cat-tail, loosestrife, and willow.
Field No. 11 is of interest because of the large amount of white bedstraw and grass which create a thick mat. Breaking through this mat are scattered patches of goldenrod, multiflora rose and blackberry. White bedstraw (Galium mollugo) is an introduced species to this location and its history has been outlined in the Mohonk Preserve, Inc. Research Report of July 1986. This is a particularly invasive species and considered a serious weed in agricultural crop fields but may be a useful groundcover when attempting control of woody species. Whether acting as an allelopathic plant, or mechanical deterrent, or as a competitor for resources, white bedstraw is of interest.

## Recommendations

Concentrating on Buff Field No. 1, detailed soil and groundwater chemical analyses should be made. In addition, it would be of considerable help to map certain of the dominant species in the field and in the surrounding woods. A more thorough listing of plants should be compiled by surveying the field several times during the growing season. If possible an analysis of the impact of deer browse on the woody invasives should be explored. Selected permanent plots should be established to quantify the successional changes that might be occurring and to determine when they begin.

The remaining five fields should be studied in the same manner. There are also nearby fields in which woody re-growth has been extensive. Maintenance records and history are also available for these and one or two may be useful for “control” data. The role of white bedstraw in Spring Farm No. 11 should be studied to determine if this plant is deterring woody growth and if so, how.

# A
# APPENDIX A – ALLELOPATHY A STRATEGY FOR TREE GROWTH CONTROL


## Abstract

The following report is a review of the previously published scientific literature concerning allelopathy pertinent to determining whether the introduction of an allelopathic plant to an area, such as a utility right-of-way, could control the growth of trees. This review analyzes the history of allelopathy research, how allelopathy has been used previously to control weed growth, what plant species are allelopathic to trees, what factors affect allelopathy, what ecological factors might be pertinent, and whether the idea of using allelopathy to control tree growth is feasible.

The knowledge that some plants inhibit the growth of other plants has a very long history. Most research that has been performed concerns interactions where the growth of desirable species was impaired. The most thoroughly researched allelopathic interactions are horticultural replant problems.

Allelopathy has been suggested previously as a tool to control weeds either by selecting cultivars of crops more allelopathic to the weeds commonly associated with them, breeding more allelopathic crops, using natural allelochemicals as herbicides, planting companion or smother crops in rotation with produce crops to control weeds, or introducing an allelopathic species to control the growth of a weed. The latter strategy has been used successfully to control the growth of aquatic weeds in drainage and irrigation canals in the American southwest.

Many species of plants are allelopathic to trees. Many trees are also allelopathic to other plants. In order to control the growth of a tree species, a plant which is more allelopathic to the tree than the tree is to the plant must be introduced. From the abundant number of known allelopathic plants it is probable that several species would be able to control the growth of trees in utility rights-of-way if introduced. Selection of species which have become the dominant vegetation in other areas of the world, such as chapparal or heath, may achieve long lasting results.

Many factors have been shown to influence allelopathic relationships between plants. Generally, any stress, such as drought, disease, cold, heat, or nutrient deficiency, increase the inhibitory effects of one plant on another. It is rather easy to increase the stress experienced by plants compared with attempts to mitigate a stressful situation.

There are a few ecological problems inherent with introducing a new species to an area. The introduced species may become a problem elsewhere, or it may displace rare or endangered species. All the ecological problems can be investigated and mitigated.

There are advantages and disadvantages to using allelopathy to control tree growth. The idea is feasible and should be considered as an alternative to control tree growth in utility rights-of-way, particularly in environmentally sensitive areas.

## Preface

The following literature review was requested by Mr. James J. Curley, Supervising Landscape Architect for Consolidated Edison Company of New York, inc., as part of a project to determine the potential application of allelopathy as an alternate or additional tool for controlling incompatible tree species along overhead transmission line right-of-way. Previous vegetation management schemes for right-of-way have included extensive use of herbicides and cutting to control tree growth. Promotion of native low-growing shrubs has always been an integral part of such vegetation management. The objective of this project is the establishment of self-perpetuating, low-growing shrubs and plants within the right-of-way domain which actively limit the growth of trees. The following review analyzes the literature pertinent to this objective.

A copy of the literature review proposal submitted to and approved by Consolidated Edison is included at the end of this review (Appendix A). Submission of this report constitutes the end of Phase 1 as described in the proposal (Appendix A). Additional information, pertinent to the objectives outlined in Phase 2, will be collected and incorporated into this report after appropriate approval from Consolidated Edison for continuation of the project is granted.

## Introduction

Allelopathy, the influence of one plant on another via the production of growth regulatory chemicals, is regarded by most horticulturists as being a problem largely to be avoided or mitigated against. This follows because the majority of people concerned with plants want their crop to grow, not to restrict that growth. Consequently, most allelopathy research has concerned identification of sources of lower crop yield and mitigation measures to alleviate allelopathic stress, not ways to increase or introduce allelopathic stress. However, if the research is reviewed with the intention of using allelopathy as a beneficial aid to plant or tree control, then there is much information bearing on this subject.

Several reviews of allelopathy have been written including: Rice, 1974; Rice, 1979; Rietveld, 1979; Fisher, 1980; Rabotnov, 1981; Wang, et al., 1982; Maclaren, 1983; Rice, 1983; Rice, 1984. These reviews include various aspects of allelopathy relating to forestry and trees. This literature survey discusses the history of allelopathic research, allelopathy used as a control for weed growth, plants that are allelopathic to trees, factors affecting allelopathy between species, ecological considerations, when using allelopathy to control tree growth, and the potential for allelopathy to control tree growth?

## The History of Allelopathy Research

The term, allelopathy, was coined by Molisch (1937) referring to biochemical interactions between plants including microorganisms. Rice (1974) defines allelopathy as any direct or indirect harmful effect exerted by one plant on another through the production of chemical compounds that escape into the environment. Rice (1984) concedes that the beneficial effects of one plant on another by the production of chemicals is included in the original definition of allelopathy. Allelopathy should not be confused with the term competition, which suggests the removal from the environment of a growth limiting factor such as nitrogen.

Grummer (1955) suggested the use of the term “koline” to refer to a chemical produced by higher plants effective against higher plants. Consequently, allelopathic relationships between plants could be considered to be mediated by kolines. Other allelopathic compounds include antibiotics, phytoncides, and marasmins.

According to Rice (1984), the earliest recorded observations of allelopathy include those of Theophrastus (ca. 300 B.C.) concerning the inhibitory effects of chickpea (Cicer arietinum) on weeds especially caltrop (Tribulus terrestris), and that of Pliny (1 A.D.) concerning several plant species including the claim that “cytisus and the plant called halimon by the Greeks kill trees.” The genus Cytisus exists in taxonomic references today but not halimon. Cytisus scoparius (L.) Link. (common name Scotch broom) is classified a member of the Fabaceae (Gleason and Cronquist, 1963). Halimon is not listed in any recent text but may be synonymous with Halimium listed in Hortus Third (1976) as a member of the Cistaceae.

Other plants which were recognized previously as having harmful effects on other plants include:

basil on rue (Culpeper, 1633)

grape on cabbage (Culpeper, 1633)

clover on clover (Young, 1804)

thistles on oats (DeCandolle, 1832)

euphorbe on flax (DeCandolle, 1832)

rye on wheat (DeCandolle, 1832)

heath on trees (Beobachter, 1845)

black walnut on everything (Stickney and Hoy, 1881)

Much of the allelopathic research conducted since 1900 has focused on various aspects of replant problems, the effect of weeds on crop yields, and companion cropping. Apple, peach, and citrus replant problems are among the best researched examples of replant problems attributable to allelopathy. A strong case can be made for the involvement of microorganisms which metabolize plant-derived compounds producing allelopathy in each of these replant cases.

Borner (1959) demonstrated that phlorizin, phloretin, phloroglucinol, para-hydroxycinnamic acid, and para-hydroxybenzoic acid, which are decomposition products of apple roots, are inhibitory to the growth of apples. Borner (1959) concluded that the relative importance of these compounds were dependent on the physiological activity of the individual compounds, their concentration in the soil, and the ability of microorganisms to destroy them. These observations have been substantiated by Holowczak et al. (1960), Borner (1963a, b), Berestetsky (1970, 1972), and Williams (1960).

Proebsting and Gilmore (1941) demonstrated that decaying peach roots release amygdalin. Amygdalin, when metabolized by microorganisms, produces potassium cyanide which is very toxic to peach seedlings. Their observations have been substantiated and furthered by several investigators (Proebsting, 1950; Patrick, 1955; Ward and Durkee, 1956; Mountain and Boyce, 1958; Mountain and Patrick, 1959; Patrick et al., 1964).

The citrus decline and replant problem was first recognized by Martin (1948) as a soil biotic factor. Subsequent investigations indicate that production of phenolic acids from plant roots is at least partially responsible for the citrus decline (Martin, 1950; Martin et al., 1953; Martin et al., 1956; Martin and Ervin, 1958; Burger, 1981).

Besides replant problems, much allelopathy research has concerned the inhibitory effects of weeds on crops. The list of weeds that have been shown to be allelopathic to crops is extensive (Table A-1). In most of the cases listed, allelopathic potential was tested against several crop species and results were variable with respect to species.

**Table A-1**
**Allelopathic Weed Species**

| Species Name | Reference |
|---|---|
| Agrostemma githago | Gajic, 1966 |
| Agrostis tenuis | Bergmann, 1979 |
| Amaranthus dubius | Altiera and Doll, 1978 |
| Amaranthus retroflexus | Gressel and Holm, 1964: Bhowmik and Doll, 1979, 1982 |
| Ambrosia artemisia | Gressel and Holm, 1964: Rice, 1964, 1965a: Bhowmik and Doll, 1979 |
| Ambrosia psilostachya | Neill and Rice, 1971 |
| Ambrosia trifida | Rasmussen and Einhellig, 1979a |
| Antennaria microphylla | Selleck, 1972 |
| Antennaria neglecta | Selleck, 1972 |
| Artemisia absinthium | Grummer, 1961 |
| Aster macrophyllus | Norby and Kozlowski, 1980 |
| Berteroa incana | Bhowmik and Doll, 1979, 1982 |
| Boerhavia diffusa | Sen, 1976 |
| Bromus japonicus | Rice, 1964 |
| Calamagrostis epigejos | Bergmann, 1979 |
| Calluna vulgaris | Salas and Vieitez, 1972 |
| Camelina alyssum | Grummer and Beyer, 1960 |
| Camelina sativa | Kranz and Jacob, 1977a, b: Lovett and Duffield, 1981 |
| Celosia argentea | Pandya, 1975: Ashraf and Sen, 1978 |
| Cenchrus pauciflorus | Rice, 1964 |
| Centaurea diffusa | Fletcher and Renney, 1963 |
| Centaurea maculosa | Fletcher and Renney, 1963 |
| Centaurea repens | Fletcher and Renney, 1963 |
| Cirsium discolor | Le Tourneau et al., 1956 |
| Citrullis colocynthis | Bhandari and Sen, 1971 |
| Citrullis lanatus | Bhandari and Sen, 1972 |

**Table A-1**
**Allelopathic Weed Species (Continued)**

| Species Name | Reference |
|---|---|
| Cucumis callosus | Sen, 1976 |
| Cynodon dactyldon | Horowitz and Friedman, 1971 |
| Daboecia polifolia | Salas and Vieitez, 1972 |
| Digera arvensis | Sarma, 1974a |
| Eleusine indica | Altiera and Doll, 1978 |
| Erica spp. | Ballester and Vieitez, 1971: Salas and Vieitez, 1972 |
| Euphorbia corollata | Rice, 1964, 1965a, b |
| Euphorbia esula | Le Tourneau et al., 1956: Le Tourneau and Heggeness, 1957: Selleck, 1972: Steenhagen and Zimdahl, 1979 |
| Euphorbia supina | Rice, 1965b: Brown, 1968 |
| Gallium mollugo | Kohlmuenzer, 1965a, b |
| Helianthus annuus | Rice, 1965a: Wilson and Rice, 1968 |
| Hydrocotyle sibthorpiodes | Tsuzuki et al. 1978 |
| Imperata cylindrica | Abdul-Wahab and Al-Naib, 1972: Eussen, 1978: Eussen and Soerjani, 1978: Mendoza, 1977 |
| Indigofera cordifolia | Sen, 1976 |
| Iva xanthifolia | Le Tourneau et al., 1956 |
| Lactuca scariola | Rice, 1964 |
| Lepidium virginicum | Bieber and Hoveland, 1968 |
| Leptochloa filiformis | Altiera and Doll, 1978 |
| Lolium multiflorum | Naqvi 1972: Naqvi and Muller, 1975 |
| Lonicera tatarica | Norby and Kozlowski, 1980 |
| Lychnis alba | Bhowmik and Doll, 1979, 1982 |
| Oxalis latifolia | Seth et al., 1982 |
| Parthenium hysterophorus | Rajan, 1973: Kanchan and Jayachandra, 1979a, b: Dube et al., 1979 |
| Plantago purshii | Rice, 1964 |
| Polygonum aviculare | AlSaaddawi and Rice, 1982a, b |
| Polygonum orientale | Datta and Chatterjee, 1978, 1980a, b |
| Polygonum pennsylvanicum | Le Tourneau et al., 1956: Gressel and Holm, 1964 |
| Polygonum persicaria | Martin and Rademacher, 1960 |
| Portulaca oleracea | Le Tourneau et al., 1956; Gressel and Holm, 1964 |
| Rumex crispus | Einhellig and Rasmussen, 1973 |
| Salsoli kali | Lodhi, 1979b |
| Salvadora oleoides | Mohnot and Soni, 1976 |
| Schinus molle | Anaya and Gomez-Pompa, 1971 |
| Setaria viridis | Rice, 1964: Bhowmik and Doll, 1979 |
| Solanum dulcamara | Norby and Kozlowski, 1980 |
| Solanum surattense | Sharma and Sen, 1971: Mohnot and Soni, 1977 |
| Solidago gigantea | Norby and Kozlowski, 1980 |
| Tagetes patula | Altiera and Doll, 1978 |
| Trichodesma amplexicaule | Sen, 1976 |
| Xanthium pennsylvanicum | Rice, 1964 |

Many crop plants have also shown to be allelopathic to other crops as well as weeds (Table A-2). Allelopathic crops are quite selective in regards to what weeds or other crops they affect, as any gardener will attest. This is true for most allelopathic species but very little research has attempted to define the complete range of plants a particular allelopath affects. In some cases the kolines involved probably affect a broad spectrum of sensitive species.

**Table A-2**
**Allelopathic Crop Species**

| Species Name | Common Name | Reference |
|---|---|---|
| Allium cepa | onion | Evenari, 1949 |
| Allium sativum | garlic | Evenari, 1949 |
| Armoracia lapathifolia | horse radish | Evenari, 1949 |
| Avena spp. | oats | Guenzi and McCalla, 1962: Fay and Duke, 1977 |
| Brassica caulocarpa | mustard | Evenari, 1949 |
| Brassica napus | rape | Martin and Rademacher, 1960 |
| Bromus spp. | brome grass | Guenzi and McCalla, 1962 |
| Citrus aurantium | sour orange | Evenari, 1949 |
| Citrus limonia | mandarin lemon | Evenari, 1949 |
| Citrus maxima | shaddock orange | Evenari, 1949 |
| Fagopyrum sagittatum | buckwheat | Overland, 1966 |
| Festuca elatior | grass | Peters, 1968: Kochhar et al., 1980 |
| Glycine max | soybean | Guenzi and McCalla, 1962 |
| Helianthus annuus | sunflower | Overland, 1966 |
| Hordeum vulgare | barley | Overland, 1966 |
| Manihot esculenta | cassava | Altiera and Doll, 1978 |
| Meliotus alba | sweet clover | McCalla and Duley, 1948: Guenzi and McCalla, 1962: Overland, 1966 |
| Nicotiana tabacum | tobacco | Patrick and Koch, 1958 |
| Oryza sativum | rice | Chou and Lin, 1976 |
| Parthenium argentatum | guayule | Bonner and Galston, 1944 |
| Phaseolus vulgaris | beans | Altiera and Doll, 1978 |
| Phleum pratense | timothy | Patrick and Koch, 1958 |
| Secale cereale | rye | Patrick and Koch, 1958: Overland, 1966 |
| Setaria italica | foxtail millet | Lee et al., 1967 |
| Solanum melongena | eggplant | Lee et al., 1967 |
| Sorghum sudanese | sudan grass | Overland, 1966 |
| Sorghum vulgare | sorghum | Overland, 1966: Guenzi and McCalla, 1962 |
| Triticum aestivum | wheat | Guenzi and McCalla, 1962 |
| Vaccinium macrocarpon | cranberry | Hussain et al., 1983 |
| Zea mays | corn | Guenzi and McCalla, 1962 |

## Allelopathy Used as a Control for Weed Growth

Allelopathy has been considered as a potential tool to control weeds. Several strategies involving allelopathy have been employed. Among them are the enhancement of allelopathic characteristics in crop plants by conventional breeding methods, the production of allelopathic chemicals as herbicides, the use of allelopathic plants in crop rotation with weeds, and the introduction of desirable allelopathic species to compete with weeds.

Putnam and Duke (1974) concluded that allelopathy could be enhanced by selectively breeding for increased allelopathic potential in some crops. A crop allelopathic to weeds would require less herbicide to control weeds. Fay and Duke (1977) screened 3000 accessions of the USDA World Collection of Avena spp. (oats) germplasm for exudation of scopoletin, a potent root growth inhibitor. Four of the accessions exuded triple the amount of scopoletin compared to a standard oat variety (Garry), and were shown to be more allelopathic to crunchweed. These observations suggest that if a species allelopathic to most trees were found, that it may be possible to enhance the inhibitory interaction. However, very little genetic research has been done on allelopathic agents.

The research of Panchuk and Prutenskaya (1977) and that of Grodzinsky and Panchuk (1974) on wheat grass (Agropyron glaucum), an allelopath, hybridized to wheat (cv Lutescence 329), produced plants that were less allelopathic than wheat grass but more allelopathic than wheat. However, the hybrid wheat which resulted was not suitable for agricultural use. Obviously, the genetic control of allelopathy is complex.

Chemicals produced by allelopathic plants have been suggested as potential natural herbicides to reduce weed growth. Owens (1973) compared the herbicidal effectiveness of rhizobitoxin, a marasmin produced by Rhizobium japonicum (Owens et al., 1972), with the phytotoxicity of amitrole and metflurazone. The phytotoxicity of rhizobitoxin was equivalent to that of amitrole but was more selective against some species such as crabgrass versus Kentucky bluegrass. Gajic (1973) demonstrated that agrostemmin, produced from corn cockle, was an effective herbicide against weedy forbs when applied to pastures at a rate of 1.2 g/ha. Rizvi et al. (1980) screened the ethanolic extracts of 50 species against Amaranthus spinosus and found that coffee (Coffea arabica) was the most inhibitory. The most phytotoxic component of the coffee extract was found to be caffeine (Rizvi et al., 1981). Toxins produced by fungal pathogens of Canadian thistle are being tested for control of this weed (Anonymous, 1980).

Several investigators have studied the possibility of incorporating an allelopathic species in rotation with crop species to reduce the amount of weed growth (Altiera and Doll, 1978; Harwood, 1979; Putnam and DeFrank, 1979, 1983; Drost and Doll, 1980; Leather, 1982, 1983; Hall et al., 1982). The allelopathic species in these cases would be used as a mulch when fields are left fallow. This strategy was found to be dependent upon the season in which the allelopathic cover crop was killed, size of crop seeds, maturity of the allelopathic cover crop, environmental stress, and genotype of the allelopathic cover crop.

Another strategy of using allelopathic plants which has been tried is to use an allelopathic species in companion plantings with crop species. Hunter (1971) reported that Mexican marigold (Tagetes minuta) destroys starchy rooted weeds and suggested this species might be used as a companion plant to some crops.

The strategies which have been mentioned so far would not be suitable towards controlling tree growth in utility rights-of-way, but do indicate the interest others have had in utilizing allelopathy to control weeds. Some aspects of these strategies could be incorporated into a program of using allelopathic plants to control tree growth in rights-of-way, such as the enhancement of allelopathy by genetic selection, and the use of naturally occuring allelopathic chemicals as herbicides.

The strategy of using an allelopathic plant to directly control the growth of weeds (the strategy contemplated in this discussion) has been attempted. Irrigation canals are subject to the growth of undesirable weeds, such as pondweed (Potamogeton spp.), which impede the flow of water and reduce water quality. Oborn et al. (1954) reported that pondweed was eliminated from cultures mixed with needle spikerush (Eliocharis acicularis) or with dwarf arrowhead (Sagittaria subulata). This observation was verified in drainage canals, irrigation canals, and reservoirs in California by Yeo and Fisher (1970). Frank and Dechoretz (1980) demonstrated that dwarf spikerush produces leachates toxic to pondweed. These observations confirm that introduction of a species allelopathic to weeds to control their growth is possible.

Using allelopathic plants to control unwanted vegetation on transmission line rights-of way has been considered recently (Welch, 1984) in conjunction with competitive plants and wildlife. This indicates that research towards this goal is forthcoming.

## Plant Species Allelopathic to Trees

The following is an attempt to list by group (i.e. lichens, herbs, shrubs) plant species which have been shown to directly affect the growth of trees.

1. Lichens

Lichens affect tree growth by influencing the growth of mycorrhizal fungi. Mycorrhizal fungi enhance the ability of plants to obtain nutrients. Extracts of Cladonia, Cetraria islandica, and Stereocaulon paschale have been shown to be allelopathic to the growth of numerous species of fungi including mycorrhizal species (Brown and Mikola, 1974).

2. Ferns and allies

Bracken fern (Pteridium aquilinum) has been shown to be allelopathic to many plant species (Gliessman and Muller, 1972). Horsley (1977a) reported that dense bracken fern cover is partly responsible for the lack of reforestation at some previously clear-cut sites in the Allegheny Plateau of northwestern Pennslyvania. Senescent bracken fronds reduced the germination of thimbleberry (Rubus parviflorus) and delayed the germination of salmonberry (Rubus Spectabilis) seeds (Stewart, 1975). Whitehead (1964) determined that soil associated with bracken fern contains unusually high concentrations of phenolic acids including;

p-hydroxybenzoic acid, vanillic acid, p-hydroxycinnamic acid, and ferulic acid. Decomposition of the fern fronds and subsequent leaching of these phenolics introduce the compounds into the soil (Glass and Bohm, 1969). These phenolic acids have been shown to inhibit the growth of several other plants (Glass, 1976). Hay-scented fern (Dennstaedtia punctilobula), New York fern (Thelypteris noveboracensis), and club moss (Lycopodium obscurum) have also been implicated by as woody plant allelopaths (Horsley, 1977b; Horsley and Marquis, 1984).

3. Herbaceous angiosperms

Grass interference on apple (Malus sylvestris) is one of the earliest known examples of a herbaceous angiosperm affecting the growth of a tree species (Pickering, 1917, 1918). Turf grass has also been shown to inhibit the establishment of Cornus florida, and Forsythia intermedia (Fales and Wakefield, 1981).

Orange hawkweed (Hieracium aurantiacum) according to Levy (1970), accounts for 100, 100, and 87% of the total angiosperms in 3 areas described as “bracken-grassland” in northern Wisconsin. The bracken-grasslands prior to intensive logging and fires in the late 1800’s were forested. Dawes and Maravolo (1973) determined that orange hawkweed produces toxins which inhibit the seed germination and growth of balsam fir (Abies balsamea) and white pine (Pinus strobus).

Broomsedge (Andropogon virginicus) inhibits the growth of loblolly pine (Pinus taeda) (Priester and Pennington, 1978). Vanillic, m-coumaric, and m-hydroxyphenylpropionic acids extracted from broomsedge appeared to be the most active inhibitory compounds.

Cow parsnip (Heracleum lacinatum) has been shown to be allelopathic to Salix pentandra but not spruce (Picea abies) (Junttilla, 1975, 1976). Junittila was investigating why other plant species rarely grow next to Heracleum lacinatum in northern Norway. Other species of Heracleum have also been shown to be allelopathic accounting for their rapid establishment in foreign communities (Zhamba, 1972).

Arizona fescue (Festuca arizonica) and mountain muhly (Muhlenbergia montana) have been shown to inhibit the growth and germination of ponderosa pine (Pinus ponderosa) (Rietveld, 1975). This would account for the dense stands of these species following fire or logging in the pine-bunchgrass communities of northern Arizona.

Fescue has been shown to be inhibitory to the growth of sweetgum (Liguidambar styraciflua) (Walters and GIlmore, 1976), and black walnut (Juglans nigra) (Todhunter and Beineke, 1979).

Bahiagrass (Paspalum notatum) is another cover species of grass which has been shown to be allelopathic to a tree species, slash pine (Fisher and Adrian, 1981).

Lupinus polyphyllus has been shown to be allelopathic to Picea excelsa (Lakhtanova, 1970). The allelopathic relationship in this case was stimulatory, Picea excelsa growth was increased by extracts of Lupine.

Horsley (1977a) determined that in addition to bracken fern, wild oat grass (Danthonia compressa), goldenrod (Solidago rugosa), and flat-topped aster (Aster umbellatus) were all allelopathic, contributing to the lack of reforestation in some areas of northwestern Pennsylvania. Additionally, Horsley (1977b) determined that husk grass (Brachyelytrium erectum) was another species allelopathic to woody plants.

Goldenrod (Solidago canadensis and S. graminifolia) and aster (Aster novae-angliae) have been shown to produce phytotoxins and have been implicated in the failure of sugar maple to grow well on abandoned agricultural lands (Fisher et al, 1978). However, Webb and Althen (1979) found no allelopathic interference between quackgrass (Agropyron repens) and sugar maple seedlings, concluding that physical competition between weeds and sugar maple were responsible for the poor growth of sugar maple on abandoned farmland.

Giant foxtail (Setaria sp.) has been shown to be allelopathic to loblolly pine by Gilmore (1980). Originally, Gilmore and Boggess (1963) attributed the poor growth of loblolly pine in southern Illinois to competition with ragweed and foxtail.

Tall goldenrod (Solidago altissima), broomsedge, crownvetch, wild carrot, tall fescue, and timothy have been shown to inhibit the growth of black locust by Larson and Schwarz (1980). Only crownvetch on the other hand was shown to inhibit the growth of black alder (Alnus glutinosa). This demonstrates that it may not be possible to control all tree species with one allelopath.

English ivy (Hedra helix), liriope (Liriope muscari), and dwarf bamboo (Sasa pigmaea) which are used as cover crops have been shown to reduce the growth of cottonwood (populus deltoides), and silver maple (Acer saccharinum) (Shoup and Whitcomb, 1981).

4. Perennial Shrubs

Many low growing shrubs have been shown to be allelopathic to other species including trees. Many of the reports concerning allelopathic shrubs note the inhibition of the growth of annuals only. It is apparent that, in many of these cases, the allelopathic relationship extends to other woody species, particularly when no growth situations are described in the vicinity of certain shrubs.

Heath (Erica scoparia, E. australis, and E. arborea) produces phenolic acids and has been shown to be allelopathic to red clover (Ballester et al., 1977 and 1979). These species have been implicated as the major factors determining the lack of crop plant growth and by inference tree growth in areas of Galicia, Spain where heath type vegetation has become dominant.

Heather (Calluna vulgaris) has been shown to be allelopathic to Betula pendula and Picea abies (Robinson, 1972; Read, 1984). Apparently, heather inhibits the growth of mycorrhizae (Handley, 1963), which are sensitive to substances exuded by plant roots, and decaying plant tissues (Melin, 1963). Persidsky et al. (1965) determined that extracts of prairie soils which do not support the growth of trees inhibit the uptake of oxygen by mycorrhizal roots compared to extracts of forest soils. Decomposing grass roots produce toxins which reduce the establishment of mycorrhizal root associations (Theodorou and Brown, 1971).

Clerodendrum viscosum common in India, Burma, and Ceylon, grows in dense thickets excluding the growth of all other species including trees (Datta and Chakrabarti, 1978).

Several species associated with the "chaparral" areas of the American southwest have been shown to be allelopathic to the growth of other species. Salvia leucophylla, Artemisia californica, A. tridentata, Lepechinia calycina, Heteromeles arbutifolia, Prunus ilicifolia, P. lyonii, and Umbellularia californica have been shown to be extremely allelopathic due to the production of terpenoids (Muller et al., 1964, Muller, 1966). Chamise (Adenostoma fasciculatum) also has been shown to be allelopathic to other species in the California chaparral (McPherson and Muller, 1969). Manzanita (Arctostaphylos glauca, and A. glandulosa) have also been shown to be extremely allelopathic to other species of the chaparral (Chou and Muller, 1972).

Lambkill (Kalmia augustifolia) has been shown to be allelopathic to black spruce (Picea mariana) trees in eastern Canada (Peterson, 1965).

Rhododendron species have been shown to be allelopathic although more research needs to be performed to determine factors which are involved (Chou, 1980). Del Moral and Cates (1971) determined that Rhododendron albiflorum was allelopathic against douglas fir (Psuedotsuga menziesii).

June (1976) observed the paucity of growth under Griselina littoralis and Psuedowintera colorata in some New Zealand forest systems, but did not test for allelopathy adequately.

Rhus copallina, Rhus glabra, Prunus augustifolia and Cornus drummondii were shown by Petranka and McPherson (1979) to be aggressive invaders of prairie communities in central Oklahoma. Toxins associated with the rhizomes, flowers, fruits, and senescent leaves of these plants were allelopathic to several climax prairie species.

Helietta parvifolia has been shown to be allelopathic in its native range in the submontane scrub zone of Nuevo Leon, Mexico (Wiechers and Rovalo-Merino, 1982).

Oleksevich (1970) demonstrated that barberry (Berberis), rose (Rosa), lilac (Syringa), and viburnum were allelopathic inhibiting adjacent plants.

Coffee (Coffea arabica) is a strong allelopath to many plants (Chou and Waller, 1980a, b).

5. Trees

Finally, it should be noted that many trees are allelopathic to other trees as well as understory shrubs which are also allelopathic (Table A-3). One could imagine that plants are locked in combat from the moment of their germination, and chemical warfare determines the outcome of their battles for dominance. Any attempt to use allelopathy to control the growth of trees must take into account that the trees themselves are capable of maintaining their own dominance of an area via allelopathy. Some trees are better at this than others.

The best example of an allelopathic tree is walnut (Juglans nigra). Black walnut is capable of killing apple trees (Schneiderhan, 1927), white pine (Pinus strobus), black locust (Robinia psuedoacacia) (Perry, 1932), birch (Betula papyrifera) (Gabriela, 1975), red pine (P.resinosa) (Fisher, 1978), and probably many other species judging from the lack of vegetation under black walnut. Butternut (Juglans cinerea) has also been shown to be quite allelopathic (Massey, 1925). The roots of Juglans nigra produces the chemical juglone which has been shown to be toxic to numerous herbaceous and woody species (Rietveld, 1983; Fisher, 1978; Funk et al., 1979; MacDaniels and Pinnow, 1976).

**Table A-3**
**Allelopathic Trees**

| Species Name | Common Name | Reference |
|---|---|---|
| Abies alba | | Becker and Drapier, 1984a, b |
| Abies amabilis | cascade fir | Del Moral and Cates, 1971 |
| Abies grandis | giant fir | Del Moral and Cates, 1971 |
| Abies procera | noble fir | Del Moral and Cates, 1971 |
| Acer campestre | hedge maple | Kokino et al., 1973 |
| Acer circinatum | vine maple | Del Moral and Cates, 1971 |
| Acer ginnala | amur maple | Kokino et al., 1973 |
| Acer laetum | none | Kokino et al., 1975 |
| Acer mandschuicum | none | Kokino et al., 1973 |
| Acer negundo | boxelder | Kokino et al., 1973 |
| Acer platanoides | norway maple | Kokino et al., 1973 |
| Acer psuedoplatanus | sycamore maple | Mensah, 1972: Kokino et al., 1973 |
| Acer saccharinum | silver maple | Kokino et al., 1973 |
| Acer saccharum | sugar maple | Tubbs, 1973, 1976 |
| Acer tataricum | tatarian maple | Kokino et al., 1973 |
| Acer turkestanicum | none | Kokino et al., 1973 |
| Aesculus hippocastanum | horse chestnut | Chumakov and Aleikina, 1977: Oleksevich, 1970 |
| Ailanthus altissima | tree-of-heaven | Mergen, 1959 |
| Albizzia julibrissin | mimosa | Chumakov and Aleikina, 1977 |
| Arbutus menziesii | madrona | Del Moral and Cates, 1971 |
| Bauhinia purpurea | butterfly tree | Chou, 1980 |
| Betula verrucosa | birch | Kolenichenko and Andryushchenko, 1978: Popov and Popova, 1982 |
| Bridelia balansae | none | Chou, 1980 |
| Catalpa bignonioides | catalpa | Chumakov and Aleikina, 1977 |
| Celtis occidentalis | hackberry | Lodhi, 1976 |
| Cornus drummondii | dogwood | Petranka and McPherson, 1979 |
| Dicksonia lanata | tree fern | June, 1976 |
| Eucalyptus baxteri | none | Del Moral et al., 1978 |
| Eucalyptus microtheca | flooded box | Al-Mousawi and Al-Naib, 1975 |
| Eucalyptus tereticornis | none | Rao and Reddy, 1984 |
| Ficus gibbosa | none | Chou, 1980 |
| Ficus retusa | indian laurel | Chou, 1980 |

**Table A-3**
**Allelopathic Trees (Continued)**

| Species Name | Common Name | Reference |
|---|---|---|
| Ficus vasculosa | none | Chou, 1980 |
| Fraxinus excelsior | european ash | Kokino et al., |
| Grevillea robusta | silky oak | Webb et al., 1967 |
| Griselinia littoralis | dogwood | June, 1976 |
| Juglans nigra | black walnut | several |
| Juniperus deppeana | juniper | Jameson, 1961 |
| Juniperus monosperma | juniper | Jameson, 1961 |
| Juniperus osteosperma | juniper | Jameson, 1961 |
| Mallotus japonicus | none | Chou, 1980 |
| Nothofagus fusca | red beech | June, 1976 |
| Phyllostchys makinoi | none | Chou, 1980 |
| Picea engelmannii | engelman spruce | Del Moral and Cates, 1971 |
| Picea pungens | blue spruce | Thomas, 1974 |
| Pinus densiflora | japanese red pine | Lee and Monsi, 1963: Kil andYim, 1983 |
| Pinus edulis | pinyon pine | Jameson, 1961 |
| Pinus nigra | austrian pine | Chumakov and Aleikina, 1977 |
| Pinus ponderosa | ponderosa pine | Kovacic et al., 1984 |
| Pinus radiata | monterey pine | Lill and Waid, 1975: Chu-Chou, 1978 |
| Pinus resinosa | red pine | Tobiessen and Werner, 1980 |
| Platanus occidentalis | sycamore | Lodhi, 1976 |
| Podocarpus dacrydioides | kahikatea | Molloy et al., 1978 |
| Populus tremuloides | quaking aspen | Ellison and Houston, 1958: Younger et al., 1980: Younger and Kapuska, 1981 |
| Prunus augustifolia | chickasaw pear | Petranka and McPherson, 1979 |
| Prunus serotina | black cherry | Norby and Kozlowski, 1980: Horsley and Meinwald, 1981 |
| Psidium guajava | common guava | Chou, 1980 |
| Psuedowintera colorata | none | June, 1976 |
| Quercus alba | white oak | Lodhi, 1976 |
| Quercus borealis | northern red oak | Lodhi, 1976 |
| Quercus eugeniaefolia | none | Gliessman, 1978 |
| Quercus falcata | spanish oak | Hook and Stubbs, 1967 |
| Quercus marilandica | black-jack oak | McPherson and Thompson, 1972 |
| Quercus michauxii | swamp chestnut oak | Hook and Stubbs, 1967 |
| Quercus robur | english oak | Kokino et al., 1973 |
| Quercus shumardii | shumardi oak | Hook and Stubbs, 1967 |
| Quercus stellata | post oak | McPherson and Thompson, 1972 |
| Rhododendron albiflorum | rhododendron | Del Moral and Cates, 1971 |
| Rhus copallina | dwarf sumac | Petranka and McPherson, 1979 |
| Rhus glabra | smooth sumac | Petranka and McPherson, 1979 |
| Robinia psuedoacacia | black locust | Waks, 1936 |

**Table A-3**
**Allelopathic Trees (Continued)**

| Species Name | Common Name | Reference |
|---|---|---|
| Rubus idaeus | raspberry | Norby and Kozlowski, 1980 |
| Sinobamboesa kunishii | none | Chou, 1980 |
| Sinocalamus latiflorus | none | Chou, 1980 |
| Sinocalamus oldhami | none | Chou, 1980 |
| Sophora japonica | coral bean | Chumakov and Aleikina, 1977 |
| Sorbus aucuparia | mountain ash | Kuhn et al., 1943 |
| Taxus brevifolia | english yew | Del Moral and Cates, 1971 |
| Thuja plicata | giant arborvitae | Del Moral and Cates, 1971 |
| Tilia cordata | european linden | Baranetsky, 1973: Moroz and Baranesky, 1983 |
| Tsuga canadensis | hemlock | Ward and McCormick, 1982 |

In the case of maple trees, Kokino et al. (1970) found that decaying leaves of several species of Acer released inhibitory chemicals in the first stages of their decomposition but subsequently released chemicals that stimulated the growth of Lepidium sativum, the indicator plant they used to determine allelopathic potential. Non-climax type vegetation, like maples or shrubs, may actually stimulate the growth of other woody species associated with a true climax type vegetation. This hypothesis ought to be investigated sometime in the future.

## Factors Influencing Allelopathic Relationships

1. Soil factors

Soil type influences the degree of allelopathy between plants. Wang et al. (1971) determined that humic acid or some other organic component in soil binds with phenolic acids. Blum and Rice (1969) determined that the top 5 cm of soil under Rhus copallina contained 600 to 800 ppm of tannic acid, a potent koline, and that in areas devoid of Rhus copallina 400 ppm of tannic acid had to be added to the soil before any tannic acid could be recovered using the extraction methods they used. This indicates that the soil content of phenolics such as tannic acid could be much higher than indicated by extraction procedures because of binding to some soil component. However, Blum and Rice (1969) also demonstrated that the addition of 30 ppm tannic acid to soil reduced nodulation of legumes growing in that soil, suggesting that bound phenolic acids are still biologically active. Rice and Pancholy (1973) surmised that biologically active tannins are bound chemically to proteins of humus and developed an improved method of extracting phenolics from soil by autoclaving for 10 minutes at 20 $lbs/in^2$ with 1N NaOH.

The drainage characteristics of soil also influences allelopathy. Sandy soils allow phytotoxins to leach out of the active root zone of some plants. Ahshapanek (1962) found that buffalobur nightshade (Solanum rostratum) inhibited the growth of tomato in loam but had no effect on tomato grown in sand. Muller and Del Moral (1966) determined that volatile terpenes from Salvia adsorbed to colloidal particles in soil and remained active for a prolonged. Del Moral and Muller (1970) determined that Bromus rigidis radicle growth was reduced to 78% when germinated in sand and 42% in loam compared to the control when treated with leachates from Eucalyptus camadulensis. Mateev (1977a, b) determined that drier soils or conditions increased allelopathic activity.

2. Nutrient Factors

Boron deficiency increases the production of scopolin (Watanabe et al., 1961) and that of caffeic and chlorogenic acid (Dear and Aronoff, 1965).

Calcium and magnesium deficiency cause the concentration of scopolin to increase and chlorogenic acid to decrease in tobaccco leaves (Loche and Chouteau, 1963: Armstrong, et al., 1971).

Increases of 5 to 10-fold have been reported by several investigators in regard to phenolic acids in plants subjected to nitrogen deficiency (Chouteau and Loch, 1965; Armstrong et al., 1970; Lehman and Rice, 1972; Del Moral, 1972). This would suggest that nitrogen fertilizers should be avoided in establishing an allelopathic species to control trees.

Phosphorous deficiency increases phenolic acid biosynthesis (Loche and Chouteau, 1963; Koeppe et al., 1976).

Potassium deficiency has been found to decrease chlorogenic acid biosynthesis but increased scopoletin biosynthesis in tobacco leaves (Chouteau and Loche, 1965; Armstrong et al., 1971). Lehman and Rice (1972), on the other hand, found that total chlorogenic acid increased in sunflower plants maintained on a minus-potassium nutrient solution.

Sulfur deficiency has also been shown to increase chlorogenic acid content and scopoletin content of sunflower leaves, stems and roots (Lehman and Rice, 1972).

3. Physical Factors

Light quality affects the amount of phenolic acids produced by allelopaths. Ionizing radiation increases phenolic acid production (Fomenko, 1968; Koeppe et al., 1970). UV irradiation increases phenolic acid biosynthesis (Lott, 1960; Koeppe,1969; Del Moral, 1972; Hadwiger, 1972). Unless supplementary UV lights are used, differences in results produced between greenhouse and field experiments could be expected. The effect of red versus far-red light on phenolic acid biosynthesis has also been investigated although without conclusive results (Jaffe and Isenberg, 1969; Tso et al., 1970).

Long day photoperiods have been shown to favor phenolic acid biosynthesis (Taylor, 1965; Zucker et al., 1965; Burbott and Loomis, 1967; Zucker, 1969).

Water stress has been shown to increase phenolic acid biosynthesis in sunflower (Del Moral, 1972) and alpha-pinene in loblolly pine (Gilmore, 1977). However, Gilmore found that water stress decreased beta-pinene, myrcene, and limonene in loblolly pine. Del Moral also suggested that water stress acted synergistically with respect to UV irradiation enhancement of phenolic acid biosynthesis.

Elevated temperatures (30 C versus 19 C) increased scopoletin exudation in oak seedlings (Martin, 1957) while lowered temperatures (8-9 C versus 32 C) increased chlorogenic acid content of tobacco leaves and stems but not roots (Koeppe, 1970b). The effect of temperature on phenolic acid biosynthesis is complex and has not been adequately researched.

4. Chemical Factors

How long some kolines are active is dependent upon both their chemical structure and microbial decomposition. The influence of microbial decomposition of plant tissues on the production of allelochemics has been mentioned previously with regard to various replant problems. There are numerous reports in the literature that address the duration of phytotoxic effects of various allelopaths and kolines but, as pointed out by Rice, (1984) the accumulation of a toxin may only need to be effective for a short period of time to confer a growth advantage to an allelopathic species.

Growth inhibitors may influence the production of allelopathic agents. Dieterman et al. (1964a) found that 1000 ppm of 2, 4 D (2, 4 dichlorophenoxyacetic acid) applied to tobacco plants increased the scopolin content 31-fold in the leaves, 28-fold in the stems, and 4-fold in the roots.

Similar results were reported using sunflower. Winkler (1967) demonstrated that maleic hydrazide also increased the concentrations of scopolin in tobacco. Einhellig et al. (1970) found that immersing the roots of tobacco or sunflower in 5 x $10^{-4}$M scopoletin resulted in large (15 to 100-fold) increases in the production of phenolic inhibitors. Ethylene exposure has also been shown to enhance the biosynthesis of total phenols (Sarkar and Phan, 1974).

5. Miscellaneous Factors

The effect of age of a plant tissue on its phenolic acid content is complex. Koeppe et al. (1970b) found that in sunflower total chlorogenic acids increased with an increase in ages of leaves to the sixth node but then declined while total isochlorogenic acid decreased with increasing leaf age. Woodhead (1981) determined that the phenolic acid content of sorghum cultivars decreased with age up to 28 days post-germination and then increased at the time of flowering.

The influence of genotype on enhancement of allelopathy was discussed previously. The genetics of a plant most certainly will affect its production of allelopathic agents. Consequently, the cultivar of a species to be used as an allelopathic control ought to be selected carefully.

It should be noted that combinations of various alleopathic agents with each other sometimes exert a degree of inhibition greater than what might be expected by summing their individual effects (Evenari, 1949; Asplund, 1969; Rasmussen and Einhellig, 1977, 1979b; Einhellig and Rasmussen, 1978; Williams and Hoagland, 1982; Einhellig et al., 1982; Rice et al., 1981). This phenomena is known as synergism and suggests that combinations of allelopaths may be more effective than monocultures in controlling weed growth.

## Ecological Considerations

The environmental impact of using allelopathic plants to control tree species should be considered before commitment of this strategy to practice. There are a few potential environmental problems which, if considered early in the planning stages of implementation, can be avoided. Some allelopathic plant species may cause increased erosion problems due to the lack of adequate ground cover. Obviously, the species of plant chosen as an allelopath must be a good ground cover. Another potential problem could be the invasion of forested areas adjacent to utility rights-of-way by the allelopath. Many allelopathic species are opportunistic and will only become established in areas devoid of other vegetation. Such species would be more desirable than a more active allelopath which could literally take over neighboring areas and become more of a nuisance than a benefit. The compounds produced by allelopathic plants which are leached into the soil could be considered a form of environmental pollution by some people although that would erroneously suggest that plants pollute the environment. The phytotoxic agents of allelopathic plants in many cases are known. Most degrade very quickly in soil.

Another aspect that should be considered is that introduction of an allelopathic species in the rights-of-way could displace native endangered species in that immediate area. This may be a mute point since the creation of the rights-of-way would have resulted in a disturbed habitat allowing such species to grow in the first place. Mitigating measures might include transplanting endangered species to nature preserves.

## The Potential for Allelopathy to Control Tree Growth

There are usually two sides to a question and its answer. First, on the positive side concerning the viability of using allelopathy to control tree growth there have been many species identified which inhibit the growth of trees. Second, there are regions in this country, and elsewhere, where areas previously forested have not reforested subsequent to forest fires and clearcutting. Closer inspection of these regions in recent years have revealed that allelopathy is a predominant cause of this condition. Third, allelopathy has the advantage of being environmentally more compatible than herbicides and with potentially longer duration of control. The effect of herbicides on the environment and the social/economic considerations of their use, are being scrutinized more closely every year (Norris et al., 1981). The use of herbicides in utility rights-of-way has been examined in environmental impact statements with the result being more restrictive protocols being proposed (Malefyt, 1985). Eventually, this aspect of the weed control problem may become the key factor in determining weed control strategy. Finally, allelopathy has been used previously with success to control the growth of unwanted plant species in irrigation ditches in California.

On the negative side, there is a definite lack of research in this area although allelopathy itself is well addressed. No one has attempted to check the growth of tree species with other plant species. The innovative research required would be time consuming and expensive. Attempting to establish an allelopathic species in an area could be expensive. Eventually, another species may invade which does not adequately control tree growth or is a species of tree which is currently not a problem. There is also the hazard of introducing species which are problems unto themselves, like kudzu (Pueraria lobata) or water hyacinth (Eichhornia crassipes).

The negative aspects of the question of whether allelopathy could be used to control tree growth are mostly economic in nature or environmental considerations which can be mitigated against with adequate planning and research. The economics of a situation can change overnight if, for example, a utility company were held accountable for an environmental accident involving the use of herbicides or if a safe herbicide which kills only trees were developed and marketed.

The positive aspects of allelopathic control of trees require additional research to prove they are not overstated and do represent realistic expectations. However, in considering the value that could be placed on both the positive attributes versus the negative attributes of allelopathic control, it can be concluded that not only could allelopathy be used to control the growth of trees in utility company rights-of-way but that it may be economically and environmentally more sound than applying herbicides to and manually trimming trees in the rights-of-way.

This literature review has conservatively and realistically determined the current knowledge regarding the potential of using allelopathy to control tree growth. The idea is apparently possible and represents an innovation in weed control. The strategy would be a challenge for any organization to undertake, but the benefits that would be obtained economically as well as public relation-wise could be tremendous. The investigation and eventual implementation of using allelopathy to control tree growth should be encouraged.

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