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ALLELOPATHY IN ORNAMENTAL PLANT SYSTEMS

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Timothy A. Chick

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ALLELOPATHY IN ORNAMENTAL PLANT SYSTEMS

Ву

Timothy A. Chick

A THESIS

Submitted to Michigan State University in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

Department of Forestry

ABSTRACT

ALLELOPATHY IN ORNAMENTAL PLANT SYSTEMS

Ву

Timothy A. Chick

Allelopathy involves the chemical interaction between plants whereby one plant enhances its survival and growth to the detriment of another. Allelopathy in a forest context has been researched since the 1960's, but allelopathic influences in urban tree systems are virtually unknown.

An extensive review of the literature in allied disciplines has shown that allelopathy can be an important factor in shade tree survival and health. For example, ornamentals planted in right of ways can experience stagnation resulting from toxic ground covers. Street trees may experience chemically induced growth and vigor declines from tree or turfgrass associates in concert with competition and environmental stresses.

There are differences between both herbaceous and woody plants in their sensitivity to allelochemicals. Trees on poorly drained clay soils are more vulnerable than those on lighter-textured sites. Cultural treatments such as organic mulches for street trees and herbicides for right-of-way trees will mitigate allelopathic effects. To my Dad, who taught me the love of learning. Thank you for your wonderful gift.

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CHAPTER I

INTRODUCTION

Statement of the Problem

Foresters are traditionally trained to recognize and utilize plant competition as a regulator of succession, survival, and health. As a professional paradigm, competition is the basis for cultural treatments in both urban and forest contexts.

Competition theory, however, seems inadequate to explain some field observations in ornamental systems. For example, one of two adjacent trees may deteriorate inexplicably or trees planted in an open highway rightof-way (ROW) field may stagnate in spite of ample sunlight, rainfall, and nutrients.

Allelopathy, which involves the chemical inhibition of one plant by another, has been suggested as for unexplained possible reason tree growth а However, forestry textbooks give only retardation. cursory accounts about the role of allelopathy in woody plant ecology. The crop sciences, on the other hand, widely accept both competitive and allelopathic plant influences.

The goal of this study will be to determine the impact of allelopathy in ornamental plant systems by reviewing the literature in allied disciplines. After a foundation of knowledge about allelopathy is evaluated, applications for ornamental systems will be proposed.

Definition of Terms

The field of chemical ecology involves the relationships between organisms (plant and animal) that are chemically mediated in some manner. Chemical interactions by which one organism affects the growth, health, behavior, or population biology of another organism are termed allelochemic (Whittaker & Feeny, 1971).

Allelopathy, as originally coined by Molisch in to biochemical 1937, refers interactions (both stimulatory and inhibitory) between all types of plants including microorganisms (Rice, 1984). The word "allelopathy" is derived from the Greek root words "allelon," meaning "of each other" and "pathos," meaning "to suffer"--the injurious effect of one upon another (Mandava, 1985), or literally, mutual suffering (Putnam & 1986). Although it is often inferred that Tang, allelopathy involves only negative (inhibitory) effects between plants, Molisch (1937) meant it to mean positive (stimulatory) effects as well (Rice, 1987). This is an

important point as the difference in concentration levels may determine if an allelochemical is inhibitory or stimulatory. In general usage among scientists, however, allelopathy typically refers to a process in which a plant releases a natural chemical compound into the interfering which is capable of environment with germination or growth of another plant in the same or a neighboring habitat (Muller, 1969; Horsley, 1983). Further, it should be emphasized that allelopathy includes chemical relationships between higher plants and microorganisms.

Whereas allelopathy is a chemical process, there are two other physical processes which cause negative impacts on neighboring plants. Szezepanski (1977) describes them as allelomediation and allelospoly.

Allelomediation is the selective harboring of an herbivore that might selectively feed on one species, thus lending advantage to another. While this process may be important in some plant communities, it is rarely, if ever, a factor in ornamental plantings.

On the other hand, allelospoly, which is more commonly referred to as competition, is a very important factor in plant relationships. Competition is the process in which a plant reduces the level of some necessary resource to the detriment of another plant in that habitat (either simultaneously or sequentially).

Resources, such as light, carbon dioxide, mineral nutrients, water, and space are all subject to depletion by plants (Muller, 1969).

Historically, competition was considered to be the basis for conflict between plants and was typically cited by researchers as the rationale for explaining reductions in plant productivity. To discourage the inappropriate use of the word "competition" when chemical inhibition was suspected, Muller (1969) promoted the use of the term "interference" to include all negative influences between plants in a community.

In the current literature, interference describes the sum total of all the ways that a plant can prevent the germination and growth of other plants, including competition, allelopathy, and allelomediation. Competition is distinguished by a depletion of resources, whereas allelopathy entails the addition of a substance into the environment.

Early History and Background

The heightened, current interest in allelopathy would lead one to believe that the recognition of allelopathic effects is of recent origin. On the contrary, Rice (1984) provides a historical perspective which extends back in time over 2,000 years.

According to Rice (1984), Theophrastus (ca. 300 B.C.) provided the first stated account of allelopathic activity when he pointed out that chick pea (<u>Cicer</u> <u>arietinum</u>) "exhausted" the soil and also destroyed some weeds. Pliny (Plinius Secundus, 1 A.D.) reported "scorching" of corn (wheat) (Kielbaso, 1991) by other weeds and crops and "poisoning" of plants by walnut and several evergreens.

Lee and Monsi (1963) found a 300 year old Japanese document indicating rain or dew washings of leaves on Japanese red pine (<u>Pinus densiflora</u>) were harmful to crops growing under the pine. Subsequent experiments by these authors substantiated the earlier report.

A number of authors (Rice, 1984; Horsley, 1983; Muller, 1969; Mandava, 1985) point to DeCandolle (1832) as the person who first emphasized the importance of chemical inhibition in plants. According to Rice (1984), DeCandolle suggested that the soil sickness problem in agriculture might be due to crop exudates and that crop rotation might alleviate the problem. Muller (1969) underlined the importance of DeCandolle's work by noting recognition and into biochemical insight that his inhibition between plants far exceeded the experimental potential of his time. According to Mandava (1985), DeCandolle's theory was continually challenged until

research by Livingston, Schreiner, and others in the early 1900's supported his original work.

Of interest to woody plant specialists is work reported by Rice (1984) and done by Beobachter in 1845 showing that heath (probably <u>Erica spp</u>.) root "excrements" were instrumental in the death of planted trees and their poor vigor. Further, Stickney and Hoy (1881) observed the "poisonous" nature of black walnut (Juglans nigra).

Fales and Wakefield (1981) reported on a number of competition studies done in the early 1900's involving shade and fruit trees and their growth suppression from appears that woody-plant it turfgrasses. However, scientists didn't use DeCandolle's earlier work to test for allelopathy during this period. Muller (1969) credits the resurgence of interest in biochemical inhibition among plants, in all plant disciplines, to the work Molisch did in explaining the effects of ethylene production in apple orchards. This work was the basis for Molisch's coining of the word "allelopathy."

Mandava (1985) noted that a new interest in crop plant allelopathy arose by 1950. Peterson (1965) supports that view but emphasized that none of the new interest in allelopathy centered on forest research. It appears that the agricultural scientific community was more receptive to the concept of allelopathy and more

willing to assimilate it into their operational frame of reference than were woody-plant scientists, especially foresters. Agronomists deal with a short-term crop where they can regulate, to some degree, the resource inputs, monitor the responses to their adjustments, and get annual feedback as to their success. Correcting problems caused by allelopathy can bring rather immediate and substantial rewards.

Substantial work, however, was done in the fruit tree industry during the 1950's related to allelopathy and problems in replanting peach, apple, and citrus orchards (Rice, 1984). On the other hand, foresters have been trained to understand plant communities in terms of competition, and one of their primary management tools is the regulation of light, i.e., shade tolerance. The consideration of allelopathy in the management of longterm rotation timber stands may appear ethereal and unrealistic.

Whatever the reasons, it wasn't until the mid-1960's that forestry researchers were considering allelopathy as a viable factor in their work. Initially, the word allelopathy wasn't used in forestry. In fact, Brown (1990) indicated his early efforts to get funding for research in allelopathy were frustrated by funding committee members who refused to believe allelopathy even "existed." Instead, euphemisms, such as "water-soluble

substance" and "naturally occurring, biologically active compounds" were discreetly used to justify the work. By 1970, plant "phytotoxins" was in vogue. In the late 1970's, the term allelopathy appeared in the literature quite frequently and is now quite commonly referred to in studies on interference.

Although the concept of allelopathy has been recognized for more than 2,000 years, it has only been during the last 25 years that major, indeed logarithmic, progress has been achieved in this science (Putnam & Tang, 1986).

Allelopathy is a worldwide concern and is being researched in many types of plant systems. Extensive work has been noted in the literature in the United Kingdom, Soviet Union, Central America, Taiwan, India, and Australia.

While much is to be learned about allelopathy in the varied global plant systems, there is sufficient literature dealing with North American situations to concentrate efforts there. This paper will deal primarily with allelopathy related to temperate region plants. The reader is referred to Waller (1987) for an excellent overview of allelopathy research being done in other nations.

Allelopathy in the Plant Kingdom

Because allelopathy is really such a young science, there are numerous phyla of the plant kingdom about which we know virtually nothing, at worst, and very little at best. Rice (1984) details what is known, covering the spectrum from microorganisms to higher plants, for those interested in further study. A summary of his findings follows.

Many phyla of algae contain numerous species which have allelopathic potential or have demonstrated allelopathic effects. They include the following: bluegreen, green, cryptomonades, and denoflagellates, yellow green, golden brown, diatoms, brown, and red. Algae phyla that are not represented yet by allelopathic individuals include stoneworts and euglenoids. Rice (1984) explores the operation of allelopathy in algal systems in depth in a chapter of his book.

The Schizomycota (bacteria) have many species that produce antibiotics and marasmins. Many of these organisms are operable in higher plant inhibition and will be discussed further. Extensive literature is available elsewhere on this subject in relation to medicine, especially in regard to actinomycetes.

There are no research records identifying the slime molds as having allelopathic effects with higher plants. There may be some references relating to medicine. There

are many algae-like fungi that cause plant diseases which affect host plants. Ascomycetes (sac fungi) are represented by several genera for their antibiotic production related to plants. The club fungi and imperfect fungi include numerous species of ectomvcorrhizal basidiomycetes known to produce antibacterial and antifungal antibiotics.

Many allelochemicals that are inhibitory to some bacteria have been isolated from liverworts. Mosses, too, can produce both inhibitory and stimulatory allelochemicals. The very limited work done on whisk ferns reveals no information affirming allelopathy. Some evidence of allelopathic activity has been detected in horsetails.

There is a substantial body of research implicating some ferns as allelochemical producers causing inhibition in sporophytes and woody plants. On the other hand, no allelopathic implications have been shown in cycads, ginkgo, or gnetophyta.

Allelopathy is very common among many species of conifers and flowering plants. Much of what follows will focus on these two phyla.

The botanical recitation above is provided to give a sense of the scope of allelopathy in the plant kingdom. Much of the interest in plant-produced chemicals is in the areas of medicine and microbiology, but this paper

will concentrate on higher plants and microorganisms that have allelopathic interrelationships.

CHAPTER II

ALLELOPATHY IN PLANT SYSTEMS

Role--Philosophical

The role of allelopathy in plant physiology and communities is now considered. First, plants produce many chemicals, both primary and secondary metabolites. substances The primary include various proteins, carbohydrates, nucleic acids, and fats which are of general occurrence and metabolic importance in all The secondary substances, which include most plants. allelochemicals, do not occur in all living matter, but sporadically throughout living appear the world (Whittaker & Feeny, 1971).

According to Whittaker and Feeny (1971)allelochemicals occur in plants in ways that protect the plant against their own effects, e.g., neutralized by other chemicals. These secondary substances are treated like toxic wastes to be inactivated in or excreted by the plant, or both. In 1971, del Moral and Cates did empirical work on forest ecosystems in western Washington and concluded that allelochemicals are plant waste products.

Horsley (1983), on the other hand, characterizes allelopathy as an "interference strategy," implying that allelochemical activity is an evolutionary adaptation by plants. Whittaker and Fenny (1971) stated that chemical interactions may be essential aspects of niche differentiation, again implying an evolutionary rationale for allelochemicals. Muller (1969) also touts an evolutionary frame of reference. Putnam and Tang (1986) that the wealth of information accumulated say demonstrating the role of allelopathy in natural ecosystems lead us to speculate that allelopathy is a common ability acquired by the plant kingdom through the course of evolution. Gliessman (1976) explains that bracken fern has apparently evolved mechanisms of toxin release that allow it to effectively exert its dominance in each particular habitat in which it grows, whether it be southern California, the Pacific Northwest, or tropical Costa Rica.

Whether allelochemicals are simply waste products which affect other plants stochastically or whether they are evolved defense mechanisms awaits further study and debate. However, the evidence detailed in these reviews preclude the author from believing that allelochemicals are simply waste materials to be eliminated from a plant. Rather, I see them as evolved defense mechanisms and/or

adaptive devices to promote plant propagation and site dominance.

Role--Operational

At this point in time, most researchers are not addressing the theoretical/philosophical, but rather, the pragmatic and observable realities of allelopathy, namely, the "how" of allelopathic operation in plants and plant communities. Rice, Putnam, Mandava, and Muller have all been excellent "spokesmen" for the science at symposia, in proceedings, introductions in overviews, and in monographs and individual papers. A synthesis of their views on the role of allelopathy in plant systems follows, along with points made by other authors.

Aquatic

Rice (1984) provided insight into the importance of allelochemicals in determining algal succession (directly or indirectly) and productivity in aquatic ecosystems. Apparently, toxins from one species can slow the division rate of another species, thereby enhancing its niche in the system.

Plant Pathology

Another chapter by Rice (1984) detailed studies explaining the role of allelopathy in plant pathology including the promotion of infections by pathogens, development of disease symptoms, and host resistance to disease. Horsley (1983) mentioned that many plant diseases are caused by biochemical toxins released by pathogenic microorganisms. Rice (1987) also discussed how allelochemicals operate in assuring that parasitic fungi spores remain viable during dispersal and germination.

Higher Plant Systems

Higher plant ecosystems are categorized by Rice (1984, 1987) and Putnam and Tang (1986) as natural, including vegetation patterning and plant succession; and manipulated, which includes agriculture and forestry.

<u>Natural systems--patterning</u>. In natural systems of both herbaceous and woody plants, vegetation can show predictable patterns in the landscape. Putnam and Tang (1986) described bare soil zones around and under shrubs and trees where allelochemicals prevented germination of associated vegetation. Allelopathic herbaceous plants and shrubs influenced the density and distribution of jack pine (<u>Pinus banksiana</u>) forests (Brown, 1967). Lodhi (1976) found that some trees in a lowland forest such as sycamore (<u>Platanus occidentalis</u>), chemically exclude herbaceous understory plants. Rice (1984) stated that most ecologists have attempted to explain vegetation patterning and the general distribution of plants within

a community largely on the basis of competition. There is little doubt that competition plays a role in spatial distribution, but there is growing evidence that allelopathy also plays a role in most, if not all, spatial distributions of plants. While it is probably unwise to assign a primary role to either of these phenomena, it is very important to determine if allelopathy plays a role along with competition.

Natural systems--succession. Plant succession in natural systems is also influenced by allelopathy. Rice (1984) has done significant work in the tall grass prairie region of Oklahoma and Kansas. He identified four main successional stages on infertile, abandoned fields farm which were regulated by allelopathic Horsley (1977a) described how expected mechanisms. successional progression had been retarded for decades by herbaceous vegetation allelochemicals antagonistic to invading trees. Climax prairie in north central Oklahoma very well (Petranka invasion resists by trees & Rhus can invade the prairie, however, McPherson, 1979). by an allelopathic mechanism and the forest can then follow. Whittaker and Feeny (1971) summarized by saying that allelochemicals can speed the invasion of a plant into a new situation or retard the invasion of other plants into an established community.

Rice (1984, 1987) pointed out the importance of higher plant and microorganism allelopathy in succession. There is strong evidence that nitrogen fixation and nitrification are affected by allelochemic interactions. Species composition and successional stage are then influenced based on the types and amounts of nitrogen available in the soil. For example, as nitrification is inhibited, the net concentration of nitrogen is increased; as nitrogen fixation continues, a point is reached where climax species can invade.

<u>Manipulated systems--agriculture</u>. The bulk of the knowledge about allelopathy has been derived from agricultural studies. Both crops and weeds can produce allelopathic responses. Allelopathy is commonly a result of activity from both live, green plants as well as decaying plant residues.

According to Putnam and Tang (1986), there are about 90 weed species worldwide that have been identified as having allelopathic potential. Aggressive perennials, such as quackgrass (Agropyron repens), Johnson grass halepense) and yellow (Sorghum nutsedge (Cyperus esculentus) cause serious germination and productivity Weeds may cause indirect problems in field crops. allelochemic influences on crops too. Rice (1984)discovered that some weed species can inhibit the growth

of the nitrogen-fixing bacteria <u>Azotobacter</u> and Rhizobium.

Some crop plants, such as rye (<u>Secale cereale</u>) (Barnes et al., 1986) are known to produce antagonism allelopathically to weeds. Planting strategies that include crops that are inhibitory to common local weeds could reduce the need for herbicidal controls.

Both Putnam and Tang (1986) and Rice (1984) pointed out the role of allelochemicals in weed seed dormancy. Chemical inhibitors appear to be responsible for a seed's ability to withstand decay by soil microbes, an important consideration for weed control.

<u>Manipulated systems--forestry</u>. Earlier, it was noted that allelopathy has been strongly implicated in natural systems in both vegetation patterning and in plant succession. Although research efforts are not as extensive as in agriculture, increasing evidence of allelopathic influences which affect tree regeneration and growth are being accumulated. This information can be used in forest management.

Tubbs (1973) found that sugar maple (<u>Acer saccharum</u>) seedlings inhibited the growth of yellow birch (<u>Betula</u> <u>alleghaniensis</u>) seedlings. Eight to thirteen-year-old adlers (<u>Alnus glutinosa</u>) were affected severely by black walnuts (Juglans nigra) (Rietveld et al., 1983). Tall fescue (Festuca arundinacea) affects black walnut growth significantly (Schlesinger & Van Sambeek, 1986). These are just a few examples of how trees can affect other trees and herbaceous vegetation can affect trees using allelopathy as the tool. Agroforestry is based on using trees and crops that are compatible allelopathically (Horsley, in press).

Soil Microorganisms

Whether a soil is the substrate for a natural, manipulated, agricultural, or forest ecosystem, soil microorganisms are probably an important component in the allelopathy equation. Along with the secondary substances in the soil that are the result of higher plant activities and are subjected to microorganism degradation, bacteria and fungi are engaged in their own biochemical combats (Whittaker & Fenny, 1971). Their secondary substances are the antibiotics and toxins that are inhibitory, respectively, to other microbes and higher plants. Rhizosphere microbes concentrated near the root surface of plants are especially important in allelochemical interactions with the host plant. Although little is known about this facet of allelopathy, workers in the field think some it is immensely important.

Autotoxicity

The production of allelochemicals by a species that hastens its own demise or reduces its productivity is an anomaly among allelopathic donor plants. It is also an evolutionary paradox, with relatively few plants displaying this attribute (Whittaker & Feeny, 1971). Its ecological purpose has been difficult to interpret (Putnam & Tang, 1986).

hypothesized autotoxicity Some have that may function in perennial species as a mechanism to encourage further spreading of vegetative propagules, rather than allowing them to concentrate in one area (Putnam & Tang, Genetic inbreeding may be avoided by self-1986). destruction of most of the community members (Lange, This explanation is as logical as any this author 1990). has considered and is in line with Putnam and Tang's preceding comments.

(1969) states that auto-intoxication Muller is particularly suited to produce rapid disappearance of toxic pioneer species in а successional series. Whittaker and Feeny (1971) also say self-toxicity may not be a serious disadvantage for successional species, since these are vagabond populations that dominate a community for only a short time period in a given place. This line reasoning doesn't consistent of seem given our understanding of allelochemical inhibition as an

advantage in plants. But then again, allelochemical stimulation of other plants by a donor plant isn't consistent either.

One supposes that some selective advantage from production of toxic compounds outweighs the disadvantage of self-inhibition (Whittaker & Feeny, 1971), but we don't know that as fact. While a lack of understanding of autotoxicity need not limit observable advances in the science of allelopathy, more work in this area is desirable for a complete understanding of this phenomena.

An appropriate and poetic ending to this section is provided from the treatise by Whittaker and Feeny (1971).

Ecologists consider that ecosystems are given functional the transfer unity by of energy, inorganic nutrients, and foods between environment and organisms. To these two classes of materials in community transfer, inorganic nutrients and foods, should be added the third, allelochemics. An intricate pattern of exchanges of materials of all three classes relates the organisms of a community to the environment and to one another. If the organic inorganic nutrients provide and the essential fabric of this pattern, the allelochemics provide much of the color and detail of its design.

CHAPTER III

PLANT INTERFERENCE

Competition vs. Allelopathy

Practical Approaches to Differentiation

Interference involves the sum total of factors which influence the germination, growth, and survival of a plant, whether they be allelopathic (chemical) or competitive (nutrients, water, light). Of course, there are other very important factors that influence plant germination, growth, and survival, such as soil acidity (pH), soil texture, temperature, drainage, aspect, animal browsing, etc. These latter environmental factors regulate species survival and vigor.

Interference factors, on the other hand, deal with the struggle between plants capable of occupying a particular site. Plants that can compete for the limited resources of nutrients, water, and light are destined to succeed. The ability of a plant to produce allelochemicals to invade or repel invaders in plant communities gives it a significant advantage, either in concert with competitive abilities, in superseding competition, or it may be subordinate to competition.

Allelopathy has gained increased consideration and credibility in the last two decades because competition theory and research could not adequately explain the productivity differences and spatial patterns in plant communities. For example, Rice (1984) reported the work of Buchholtz (1971) with quackgrass, a weed which causes serious decreases in corn and potato yields. Even with heavy applications of nitrogen and potassium, only relatively small amounts of the added fertilizers were taken up by the quackgrass and at the same time crop yield decreases were only minimally improved by the nutrient additions.

I recall being shown sites in 1961 where jack pine had been clearcut and the slash burned to regenerate the jack pine. I remember being puzzled as to why different sites, which looked the same, had dramatically different regeneration successes. Ironically, it was in this same area that Brown (1967) did some of his pioneering work on allelopathy in forest communities. Brown couldn't explain why some jack pine sites had thousands of stems per acre while other similar looking sites (as well as environmentally similar based on testing) had small numbers of stems. He was subsequently able to show a relationship between allelochemical production by plants associated with jack pine and the germination and growth of jack pine seedlings.

During the past twenty years, I have observed vegetation along highways and utility corridors that seemed to grow much more slowly than the same species along city streets or in nearby forests. Traditional competition theory, along with the problems associated with soil texture and structure often found in these situations, was used to explain the slow growth. What was puzzling, though, was that trees planted in good, undisturbed native soils also showed slow growth.

In another situation, trees obtained from the same nursery by the same contractor were planted along a freeway service road; some in front of homes, and others within the freeway right of way. As expected, the trees in front of the homes grew dramatically faster than the right-of-way trees. But the large growth differences seemed to be greater than competition theory could explain. Not being able to explain the differences caused me "intellectual despair" until I found research by Horsley (1977a) and Fisher et al. (1978) which strongly implicated the right-of-way herbaceous species as being very allelopathic.

In spite of the above examples, and some researchers' studies of allelopathy as related to growth inhibition, it is still common for researchers to proclaim that "competition" is the reason for growth suppression. Both Rice (1984, 1990) and Muller (1969)
have stated that no research they have seen alleging that competition was the operable basis for plant inhibition has proven allelopathy was not involved; hence, the studies should more accurately be termed interference studies.

Glaring examples of recent misnomered "competition" studies in forestry include one by von Althen (1985) on black walnut plantation stagnation resulting from interference by herbaceous vegetation known to be very allelopathic. Another was a study by Fraedrich and Ham (1982) on tree mulching and growth. A third study by Watson (1988) discussed mulch and grass competition influences on tree root development. The authors of all three studies did not consider allelopathy while proclaiming competition the operable mechanism of growth inhibition.

Turfgrass allelopathic potential was recognized in three other studies of tree growth inhibition. However, all of the authors, Green and Watson (1989), Hensley et al. (1988), and Messenger (1976), conducted their experiments in such a manner that allelopathy was not tested.

A refreshing change in approach was displayed by Kolb (1988). Initially, he did work with Kentucky bluegrass (<u>Poa pratensis</u>) and its effect on northern red oak (<u>Quercus rubra</u>) and yellow poplar (Liriodendron

tulipifera). Because of reports by other researchers as to the allelopathic potential of bluegrass, he published mode allelopathy was the his assumption that of interference in the trees' growth. Unsatisfied with his tested conclusions, he further for competitive found them. Thus. possibilities and he proved competition after eliminating allelopathy as a possible factor.

Quite a number of forest and horticulture researchers have done allelopathy studies which test for and then eliminate competition as the causal factor for inhibition or put it in perspective as it relates to interference. Some examples follow.

Fales and Wakefield (1981) tested the effects of three turfgrass species on the growth of forsythia (<u>Forsythia intermedia</u>) and flowering dogwood (<u>Cornus</u> <u>florida</u>). Field studies were done on both species, while laboratory bioassay was done on forsythia only.

Various plots were set up to include combinations of turf surface fertilization and watering, turf subsurface fertilization and watering, and different sized turf-free rings around field-planted stock. The surface treatments showed slight growth, whereas the subsurface treatments showed an approximately 50% increase. The turf-free areas produced up to a 100% increase in growth. The strategy of the field study was to provide all the nutrients and moisture the turf and woody plants needed for growth so that competition was theoretically not a factor. It should be noted that the higher growth of the turf-free plots was achieved without the benefit of added fertilizer or irrigation.

The field studies didn't prove allelopathy, however. It was only implied. In this case, lab and greenhouse studies were subsequently conducted whereby leachates of the turfgrasses were applied to potted forsythia plants (no competition present). Significantly less growth occurred in the leachate-treated plants as compared to the controls. The authors concluded that allelopathy was operable in growth inhibition, but since specific allelochemicals were not recovered, their results were inconclusive.

Lodhi (1976) studied the herbaceous cover patterns under trees in a lowland forest. Relatively bare areas occurred under sycamore, hackberry, red oak, and white oak trees, but not under elm trees in the same habitat. Light levels were similar under all five species, however, as were nutrient levels. Soil moisture was consistently higher under the test species than the elm during the entire growing season. Other attributes, such as pH were tested and were not shown to be factors.

Although competition did not seem to be involved in the low herbaceous productivity under the test trees,

Lodhi took another approach to eliminate competition and demonstrate allelopathy. He transported intact soil samples from under the test species, put them in holes under elm trees, and transplanted associated herbaceous representatives to the new soil. At the end of the growing season, the transplants in the test plant soils relocated to the elm "understory" were significantly lower in weight than transplants in soils relocated from under one elm to another elm. Thus, toxic soils from the implicated as test species were seedling growth inhibitors.

Like Fales and Wakefield (1981), Lodhi obtained extracts from fresh and decaying leaves to test their effects on seedlings of associated understory vegetation. Significant reduction of radicle growth was observed, further implicating allelopathy. Lodhi then took another convincing step toward proving allelopathy that Fales and Wakefield did not. He actually identified toxins extracted from leaf litter and soil samples.

Fisher, Woods, and Glavicic (1978) conducted a novel field experiment in an effort to point both to allelopathic effects in tree-forb competitive and The authors observed that sugar maple interference. (Acer saccharum) was thriving in woodlots, but did not invade old fields inhabited by goldenrod seem to (Solidago spp.) and aster (Erigeron spp.).

Plots $(2m^2)$ were established in an old field. In addition to control plots, a second series was weeded and tilled and kept weed free for the duration of the twoyear study. A third series of plots had 15 cm of soil excavated and replaced with soil taken from the upper 15 cm of an adjacent woodlot. Remarkably, the pH, nutrient constituents, etc., were very similar in both locations.

Seeding was done in one set of plots while 2-0 seedlings were planted in a second set. The goal was to see how well a maple could grow with all old-field interference removed (forest soil), with competition removed (weeded old-field soil), and with the combined effects of allelopathy and competition (control).

germination survival rate The after two years (including rodent feeding) was 0% for the control, 4% for weeded plots, and 8% for the forest soil plots. Growth was 8 cm for weeded old-field plots and 15 cm in forest soils. Survival percentages for 2-year seedlings was 10%-control, 40+%-old-field weeded, and 85+%-forest soil. Two-year seedling growth was 25 cm-control, 34 cm-oldweeded, and cm-forest field 49 soil. The large differences in both germination and seedling growth between the old-field weeded plots and the forest-soil plots showed quite dramatically that something occurred other than competition to cause plant suppression.

Greenhouse studies were then carried out using leachates of goldenrod, aster, and other indigenous field plants to demonstrate growth inhibition in the absence of competition. These results supported the allelopathy hypothesis. It should be noted that the apparent allelopathic effects produced in the old-field weeded plots resulted from allelochemicals in the soil prior to The inhibitory effects resulted without weed removal. the continuous addition of toxins. In this situation. allelopathy accounted for a major portion of the interference.

In a classic study by Horsley (1977a) in an analogous situation to the previous study by Fisher et al. (1978), some very creative techniques were used to evaluate interference by old-field forbs and grasses on invading black cherry (<u>Prunus serotina</u>) and red maple (<u>Acer rubrum</u>). After a careful study of the logging and fire history and edaphic factors, Horsley conducted a thorough survey of the vegetation and deer browsing effects. Microclimate tests were done on both weeded and unweeded plots; soil temperatures were determined to be moderate while surface soil moisture was considered high for all plots.

An ingenious method for testing light competition in situ was devised after finding that the herbaceous vegetation canopies reduced light by 70 to 80% at ground level. Cherry seedlings were assigned to one of four treatments at the centers of 5 ft. diameter treated areas:

- Control-plot unweeded, seedling under natural shade.
- 2. Plot unweeded, shade removed by permanently restraining herbaceous vegetation behind a frame as it grew, thus providing a cone of direct light to the seedling without removing soil interference from the herbaceous plants.
- Plot weeded, cherry artificially shaded with cylinders of shade screen approximating the degree of natural shade in treatment (1).

4. Plot weeded, seedling unshaded.

A one-year lag occurred before much growth was observed on all four plots. Subsequently, the presence or absence of shade made little difference in growth. However, on the two plots with no weeds (both shaded and unshaded) growth was three times that of the plots with weeds (both shaded and unshaded). Competition for light, therefore, was discounted as a viable interference factor.

Competition for nutrients was dealt with in a more traditional fashion than Fisher et al. (1978) used. Three-year-old field-grown seedlings were transplanted into pots containing native soil from the old-field study area. Similar seedlings were transplanted into a siltloam soil of agricultural quality so the response of the seedlings could be tracked in a soil of known quality. After one growing season, the plants grown in the oldfield soil containing potential allelochemicals produced by the herbaceous vegetation grew only 10% as compared to the seedlings in the soil unexposed to herbaceous plants.

Theoretical Differentiation Protocols

The previous section gave examples of research work allelopathy and competition and implicated, on with varying degrees of success, one or both phenomena as the suspected reason(s) for plant interference. Many of the reported studies, as well as many others, have been pioneering efforts by intellectually bold scientists struggling to provide credibility to ideas that were received skeptically, if at all, by their peers. The methodology and measurement devices and techniques were usually crude or unavailable. Horsley (in press) stated that the complexity of interference phenomena combined with the potentially large number of interacting factors makes separating allelopathy from competition and other influences especially difficult. Thus, an unequivocal demonstration of allelopathy has rarely been achieved in practice.

In spite of the gloomy prognosis in differentiating between competition, allelopathy, and other influences on

plant growth, as well as proving whether one or more of the factors is causal or operative, this section will provide a structure for obtaining the sought-after proof. Fuerst and Putnam (1983) provided most of the theoretical basis for modern-day studies of interference, while Balke (1985), Putnam and Tang (1986), and Horsley (in press) provided additional insight to the subject. Horsley's work is especially useful because it deals with the field of agroforestry where an understanding of interference dynamics is essential.

Fuerst and Putnam (1983) first proposed criteria to be used to evaluate experimental evidence and indicate deficiencies in our technology. Their criteria were adaptations of "Koch's Postulates" formulated in 1890 by the German physician Robert Koch (Horsley, in press). Koch was having difficulty proving that microorganisms responsible for causing disease, and were hence. developed his now famous approach to solving the problem. First, he described the disease symptoms in a particular plant. The potentially causal organism was isolated from the diseased plant, grown in culture and characterized, inoculated into a healthy plant to produce the original and finally reisolated disease symptoms, from the diseased plant and compared to the identifying characteristics found in the first culture.

In order to avoid confusion, Horsley's work (in press) will be quoted primarily, rather than correlating his work with that of Fuerst and Putnam (1983). Horsley's work is basically a refinement of the above authors' presentation and differs mainly in the of evaluating interference designation steps in phenomena.

first step is to demonstrate interference The between plants and quantify it to the extent possible. The circumstances in which interference occurs should be described, including the stage of plant development affected (seed germination, growth on cotyledonary reserves, growth after the cotyledonary reserve phase) and the symptomology. Symptoms of interference should be as specific as possible because they will be used later to eliminate alternative causes of interference or to bioassay allelochemicals. Symptoms such as foliage discoloration, tissue nutrient content, loss of geotropic behavior, change in water potential, wilting, change in exchange rate, and epinasty are useful the CO₂ of growth descriptors. Gross measures that are influenced by many factors, such as a reduction in seed germination, plant height, dry weight accumulation, or survival, often are not specific enough to be used in separating components of interference or to act as discriminators in bioassays of fractions of natural

products. These gross measures, however, have been used extensively in most previous studies and were suggested for use by Fuerst and Putnam (1983).

Techniques, such as replacement series experiments, opportunity to quantify interference offer an and symptomology (Dekker et al., 1983). In experiments of this type, two species of plants are grown together either at a fixed plant density with varying proportions of each species (100:0, 75:25, 50:50, 25:75, 0:100) or with variable total plant density and а species proportion (double replacement). The effects of density and proportion of each species on total yield or other plant attributes can be measured and quantified. Given interference symptomology, additional experiments can be conducted that concentrate on reducing the number of alternative causes of the symptoms (Horsley, 1977a, 1987 in press).

Proving that competition is operative requires measuring the supply of each important resource and demonstrating increased utilization of the resource by the presumed aggressor species or decreased utilization by the presumed susceptible species. Demonstrating that symptoms of interference are caused by a change in supply of the resource within the range of change caused by the aggressor, but without presence of the aggressor, is an important element in determining competition. Lack of

symptom development with a change in a resource is evidence that deficiency of the resource is not a key factor controlling interference. By contrast, symptom development suggests involvement of the resource in interference but does not rule out interaction with other resources or allelopathy. For example, the addition of organic compounds to the soil may result in microbial immobilization of nitrogen. Experiments that restore the level of the presumed limiting resources, for example, through fertilization, irrigation, or supplemental lighting, in the presence of the presumed aggressor are useful in evaluating competition. Also valuable are the manipulative experiments that restrict access of aggressor to one resource but not to others (Horsley, 1977a; Fisher et al., 1978). Fuerst and Putnam (1983) suggested other useful have methods for studying competition.

Five steps are required to demonstrate that allelopathy is the cause of interference:

- One or more phytotoxic natural products must be released from the aggressor plant.
- Phytotoxic natural products must be identified and proved not to be artifacts (Putnam & Tang, 1986).
- 3. The presumed allelochemicals must be transported and accumulated in the environment in sufficient

quantities to account for the documented interference.

- Allelochemicals must be taken up by the susceptible plant.
- 5. They must reproduce the symptoms (physiological action) of interference in the susceptible plant.

While satisfying these conditions may seem a simple matter, there are enormous methodological problems, and few reports to date are free of deficiencies. Fuerst and Putnam (1983) go on to say that it is obvious that final proof of allelopathy or competition requires numerous experiments. For this reason, it seems likely that the most progress will be made when the interaction between two particular species is studied in greater detail, or when an extreme example of interference is studied in detail or in a model system. Furthermore, there is considerable need for development of technology to study The theoretical framework proposed by interference. Fuerst and Putnam and then refined by Horsley provides an ultimate goal to be worked toward by researchers, as there are major difficulties to be resolved before be provided for conclusive proof can interference mechanisms.

As will be shown later, there are many factors which influence allelochem transmission into the environment as

well as uptake by other plants. With competitive factors operating at the same time as allelopathic factors, and fact, influencing the intensity of one another, in determination of cause is very complex and difficult. Most researchers writing about allelopathy are very conservative in their conclusions and are reluctant to speculate that allelopathy is the primary, causal, or only mechanism of inhibition. Muller (1969) supported this careful approach when he challenged interference researchers to avoid "single-factor ecology." Other writers, such as Petranka and McPherson (1979) and del Moral and Cates (1971) displayed painstaking effort in their works by considering all variables possible. Thev objectively pointed out the interrelationships of the variables along with the importance of each variable under given circumstances. They were all careful about giving inordinate importance to allelopathy.

A Rationale for the Study of Allelopathy

A logical, valid, and reasonable question posed by anyone exposed to a presentation of allelopathy phenomena might be, "Why should we be concerned about allelopathy? It seems to be so complex, so difficult to prove, and seems to occur sporadically with only minimal impacts when it does occur. Further, competition theory is

relatively clearcut and easy to understand and seems to explain plant interactions satisfactorily."

I thought that students of the basic biological sciences would have recognized allelopathy as а before legitimate scientific entity practitioners. However, Muller (1969) said that agronomists and horticulturists preceded ecologists. In fact, he stated that ecologists discredited biochemical inhibition as a concept. They suggested that the burden of proof was on proponents of allelopathy to disprove competition. The development and relatively recent availability of powerful analytical chemical techniques has apparently changed that attitude among ecologists.

Rice (1990) and Brown (1990) related stories of skepticism and disbelief exhibited by other biological scientists when they made presentations about allelopathy. However, except for a very few writers on the topic of allelopathy, there seems to be little attempt to provide an apologetic basis for quelling critics. Muller (1969) and Fisher (1980) are the only exceptions noted in the ecology/forestry literature. Both authors challenged competition theory as the basis for interference.

In addressing the original question as to why it is important to differentiate competition and allelopathy,

it can be considered from several perspectives, philosophical and practical.

Philosophical Perspective

From a philosophical viewpoint, it is important to promote sound theories based on the most complete and accurate data available. To avoid pursuing "murky" areas because they are complex and difficult is certainly not indicative of sound and credible science, nor should they be ignored because they threaten conventional wisdom.

Kuhn (1962) pointed out that the primary advances in science have been made when seemingly minor inconsistencies which could not be explained by the accepted paradigms of a discipline were studied, eventually showing the paradigm to be in error.

Muller (1969) authored a classical paper entitled "Allelopathy as a Factor in Ecological Process," as a case in point. Specifically, he discussed the ecological phenomenon of dominance which is frequently invoked but less satisfactorily defined. If a pure, dense stand of a tree species is accompanied by shrubs and herbs of lesser stature, one says that the community is dominated by the tree. To the extent that the tree casts a dense shade to which the associated species are tolerant and other species are not, we perceive what is meant. But if the inducing powerful chemical changes tree is in the

environment to which shade-tolerant potential competitors are susceptible, the investigator has most likely not fully analyzed the dominance ascribed to the tree. The dominance that is operable may be allelopathic dominance rather than competitive dominance, or a combination of both.

Foresters, in particular, are guilty of this sin of omission, in my opinion. The concept of shade tolerance is very important in understanding forest succession and becomes a primary tool in regulating forest productivity. Lee and Monsi (1963) studied Japanese red pine stands in Japan where it was assumed that understory vegetation was regulated by pine density/shade. Light levels were checked and shown to be very high and more than adequate for plants common to the area. Further testing of the soil revealed allelochemicals that were inhibitory to the associated species; thus, allelopathy was operational and not light. Hence, managing light in this example would be futile.

Another philosophical aspect involves research misrepresentation. Although the motivation is certainly not analogous, the end result is similar to fraudulent research. A trail of research purporting to prove competition is being laid down which, in turn, fills bibliographies of new studies "proving" competition, with little reference to chemical inhibition and no testing to

eliminate it. I don't wish to seem melodramatic on this point, but I do feel that scientific integrity and credibility are at issue.

Practical Perspective

From a practical view, Fisher (1980) in his study "Allelopathy: A Potential Cause of Regeneration Failure," makes the observation that regeneration failures or delays in seedling growth sometime have no clearcut causes. Without knowledge of cause, foresters may attempt remedies that are unnecessarily costly or heavy handed, even when they succeed.

An example of costly and heavy-handed practices was evident in a study by von Althen (1985) concerning weed control in a walnut plantation. The understory herbaceous vegetation was comprised of species with well reported allelopathic potential. In spite of this widely published information, allelopathy was not considered a factor in the conduct of the experiment. Varying quantities of nitrogen fertilizer and simazine herbicide were applied separately and together. Substantial growth for simazine only plots was reported along with little additional growth with simazine/fertilizer plots, even at high rates of nitrogen. The author concluded falsely, in my opinion, that competition was eliminated by the herbicide, rather than chemical inhibition.

Fertilization in this situation would be futile as allelochems would probably impede nutrient uptake.

Another example of a practical situation where allelopathy and competition needed to be understood was in research done by Schlesinger and Van Sambeek (1986). vegetation studied herbaceous understory They interference in a black walnut plantation. Although the situation was primarily a forest products study, the site and planting was akin to some urban forest settings. While foresters, in general, recognize the need for protection from weed competition during the "establishment period" and apply mulch or herbicides accordingly, it is assumed that the established plant can compete adequately, if not ideally, after that period. In their five-year study, younger trees (10 years old) responded to vegetation control and resumed satisfactory growth after being released as compared to older trees (15 years old) which showed indications of irreversible vigor reduction. Whether it was from competition or allelopathy or both, the study did not show, but it would be helpful to know which factor to deal with culturally.

Ironically, both Fisher (1980) and Ponder (1986) point out that when foresters use selective weed control, they inadvertently eliminate both competition and allelopathy. Fisher (1980) goes on to say that if a forester knows which trees are particularly susceptible, which plants are most likely to produce toxic effects, and which site conditions contribute to interactions, most allelopathic problems can be avoided or easily dealt with by site preparation and weed control.

In concluding this introduction to the science of allelopathy, Muller (1969) and Fisher (1987) put the matter into perspective with conclusions from their respective papers.

Muller (1969) stated that allelopathy constitutes no simple panacea for the solution of unknown ecological problems. Also, it is a difficult and demanding subject of study. Its techniques are added to those of conventional ecology rather than substituted for them. The evidence we now possess indicates that biochemical products are widely, if not universally, involved in biotic interactions, and that allelopathic effects may singly, or in synergistic relation to other conditions, become limiting factors for species distribution and ecological processes in almost any natural or agricultural community.

In addressing forest regeneration failures, Fisher (1987) said that whatever the cause, allelopathy is not a problem for all plants nor at all locations where allelopathic plants occur. It should not be used as an easy explanation for any mysterious regeneration failure or poor stand growth. Rather, it should be considered as

a potential cause and analyzed as an explanation just as other possible causes are considered.

CHAPTER IV

STATE OF THE SCIENCE REGARDING ORNAMENTAL SYSTEMS

Ornamental Research Void

The focus now turns to the current state of knowledge about allelopathy as it relates to ornamental horticulture and urban forestry. With few exceptions, (Kolb, 1988; Nielsen & Wakefield. 1978; Fales & Wakefield, 1981), there is virtually no literature based on research done specifically about allelopathy in urban and/or ornamental systems. The classic text on arboriculture authored by Harris (1983) recognized allelopathy as a viable concern in urban landscape management but the coverage of the topic is minimal.

Except for the article by Kolb (1988), no other presentations about allelopathy have been made in the <u>Journal of Arboriculture</u> during the past 15 years. Rice (1984) made no specific mention of woody-plant allelopathy in ornamentals. None of the proceedings of the first four National Urban Forestry Conferences referred to allelopathy, either. On the other hand, Horsley presented a paper on "Allelopathy as a Stress for Urban Trees" at the 1983 Society of Municipal Arborists'

meeting. This is the only published paper I have found relating allelopathy to an urban context.

With the paucity of information specifically addressing the urban milieu, it becomes obvious that one must look elsewhere to obtain an understanding of how allelopathy operates in plant systems (both woody and herbaceous) and to find examples of species that might be allelopathic in urban systems.

Available Knowledge in Allied Disciplines

While avoiding quantum leaps about species between systems is prudent, the examination of research in other disciplines appears imperative in order to understand the physiology, chemistry, research methodology and techniques, microbiology, and environmental relationships applicable to allelopathy in all plant systems. In this latter regard, there is an increasingly sophisticated body of literature that is applicable to ornamental plantings.

The comprehensive monograph by Rice (1984) is the "Bible" of allelopathy. This book follows the first edition published in 1974 and will be updated again in 1994 (Rice, 1990). Grodzinsky (1965) has produced a monograph in Russian. The proceedings of the North American symposium on allelopathy was published as a special issue of the Journal of Chemical Ecology (Vol. 9,

No. 8) in 1983. <u>The Chemistry of Allelopathy</u> (1985) and <u>Allelochemicals: Role in Agriculture and Forestry</u> (1987) are the products of symposia conducted by the American Chemical Society. Putnam and Tang (1986) edited a valuable monograph entitled <u>The Science of Allelopathy</u>. The <u>Journal of Plant and Soil</u>, also published a special edition about allelopathy (Vol. 98, No. 3) in 1987.

Papers don't appear to be concentrated in a few selected journals. Rather, they are in 15 to 20 journals from the fields of forestry, botany, ecology, agronomy, and soils. Older textbooks in the plant sciences did not mention allelopathy, but the <u>Physiology of Woody Plants</u> by Kramer and Kozlowski (1979) and <u>Applied Weed Science</u> written by Ross and Lembi (1985) discuss the phenomenon, albeit briefly.

Major Contributors

Putnam and Tang (1986) recognized the major pioneer contributors to the science in contemporary history. McCalla et al. published a series of papers from 1948 to 1965 which created a greater understanding of plant residues and microbial relationships. C. H. Muller and E. L. Rice especially have contributed important research findings while training a large number of the scientists now engaged in the field of allelopathy. Notable efforts to determine the mode of action of allelochemicals have

been made by F. A. Einhellig, D. E. Koeppe, W. H. Muller, and N. E. Balke. K. P. Buchholtz, L. G. Holm, T. Kommedahl, and H. B. Tukey, Jr., have provided important efforts relating agriculture and allelopathy. A. R. Putnam has provided significant research contributions in agriculture and horticulture while training adherents and providing leadership in fostering the interests of the discipline.

In the forestry arena, R. T. Brown provided early research efforts as well as conducting the first conference on allelopathy (Rice, 1990). R. del Moral and J. W. Van Sambeek are doing substantial work, too. R. F. Fisher has produced progressive and significant work. In my opinion, S. B. Horsley has done the most exciting work relating forestry and allelopathy and has articulated the problems and needs of the field most clearly.

Interdisciplinary Research Cooperation

Although this thesis focuses on allelopathy in ornamental planting the need for systems, interdisciplinary research cooperation is emphasized literature, regardless repeatedly in the of the allelopathic topic under consideration. Waller (1987) and Thompson (1985), in the prefaces to their respective books, point out that symposia provide an expression of current work in the field, but equally important is the

the scientific of relationships among promotion disciplines required to utilize allelopathy for human And although organizing interactive working benefit. groups of scientists might create coordination and funding problems, it is necessary to overcome these obstacles to accomplish a thorough understanding of allelopathy. Putnam (1985) stated that the phenomenon of allelopathy may be unique in that it probably involves more scientific disciplines than any other single phenomenon.

In particular, the chemistry of allelopathy has been the Achilles' heel of the science for the following reasons, according to Putnam and Tang (1986).

 Early efforts went toward establishing allelopathy as a credible science.

2. The difficulty in isolating, identifying, and quantifying trace natural products in the soil without the availability of powerful modern instrumental methods of analysis. More refined methods for sample collection, improved methods of bioassay, and the increased availability of modern instruments for isolation and structural elucidation of compounds will correct this problem.

3. The difficulty of studying allelopathy without the combined efforts of organic chemists, biologists,

soil scientists, ecologists, etc., is only recently being
addressed.

Putnam (1985) goes on to challenge various disciplines to solve specific problems in their area which will enhance the entire science. These challenges will be addressed in following sections of this thesis.

Putnam and Tang (1986) summarized the state of the science of allelopathy quite clearly. They suggest that the flourish of activity related to allelopathy indicates the evolving of a maturing science. A state of rapid envisioned based on progress may be the existing knowledge and available research techniques, where enrichment of evidence and improvement of techniques, however, are still very much in need. In this stage, new directions research should abound. As а multidisciplinary science, it provides a fertile ground for both biologists and physical scientists to explore new opportunities of relevant research.

Allelopathy in Shade Trees

While this maturing science is already contributing to the solution of practical problems and providing explanations for observed plant-plant interactions in agriculture, woody plant scientists are lagging behind in their understanding of allelopathy in their sphere of

concern, especially those workers dealing with ornamental plantings.

The reason for this lack, in my opinion, is that the bulk of the research deals with the testing of seed germination and seedling growth in both agriculture and forestry. This approach is satisfactory for agriculture and in patterning, successional, and regeneration studies in ecology and forestry. However, it does not satisfy the questions of how allelopathy affects the survival, the growth, and vigor of larger planted trees characteristically used in ornamental plantings. Some researchers question the effects of allelochemicals on larger trees as they see them operable primarily at the regeneration stage of a plant's life.

It is my opinion, however, that allelochemicals do affect larger planted trees, although usually not as dramatically as seeds and seedlings. Furthermore, there is increasing evidence implicating allelopathy to support this claim.

There are a number of forestry studies pointing to larger tree-tree interactions. Gabriel (1975) observed the death or severe stunting of 15 inch planted white birches (<u>Betula spp</u>.) when placed in proximity to black walnuts that were 3 to 8 feet in height and 1 1/2 to 3 inches in stump diameter. Fisher (1978) observed the death of 22 to 25 year old white pines (Pinus strobus) adjacent to black walnuts. Reitveld et al. (1983) studied the sudden decline and death of black alder (<u>Alnus glutinosa</u>) 8 to 13 years after being interplanted with black walnut. Ponder (1987) also worked with mixed walnut-alder plantings, 15 years of age, with similar results obtained by Rietveld et al. (1983).

common large-tree allelopathy More has been implicated in conjunction with understory herbaceous vegetation, i.e., grasses and forbs. Walters and Gilmore (1976) studied the inhibitory effects of fescue sod (Festuca arudinacea) on 10-year-old sweetgum (Liquidambar styraciflua). Schlesinger and Van Sambeek (1986) also researched the effects of a fescue understory on 10 and 15-year-old black walnut plantations for a five-year period which resulted in irreversible stagnation of the walnut. Horsley (1977a, 1983) and Peterson (1965) observed poor growth of pulpwood-sized cherry and spruce trees from toxins produced by understory plants.

Much of the evidence for allelopathy in large trees is obtained by the extraction of allelochemicals from the larger plants or the herbaceous understory plants and tested on seedlings of the larger plants.

The results produce circumstantial evidence. As pointed out earlier by Horsley (in press), final proof can only be obtained when isolated allelochemicals can be added back into the larger tree's system with duplication

added back into the larger tree's system with duplication of the original symptoms. Clear proof of allelopathy in larger trees, in my opinion, must await techniques that test in situ over long time periods or that can test mature tissue samples in the laboratory for inhibition.

CHAPTER V

ALLELOCHEMICAL MOVEMENT

Environmental Routes of Entry

Chemicals with allelopathic potential are present in virtually all plant tissues, including leaves, flowers, fruits, stems, roots, rhizomes, and seeds. Whether these compounds are released into the environment in sufficient quantities and with enough persistence to affect a neighboring or a succeeding plant remains a critical question in many cases of alleged allelopathy (Putnam & Tang, 1986).

According to most authors, there are four primary routes of entry into the environment by allelochemicals released from higher plants. The processes include **volatilization**, leaching, root exudation. and decomposition of plant residues (Figure 1). I also identify a fifth category which I call indirect **Production.** Each mode of release is affected by a number of factors that may change the quantity and/or quality of the resulting allelochemicals (Horsley, in press), and these factors will be discussed in Chapter VI.



Figure 1. Environmental Routes of Entry.

Source: Modified from Burke, B. A. 1987. Allelopathy: a biotechnological-agrochemical approach. In: Waller (ed.), p 151. Drawn by Jay Fosgitt (1990).

Volatilization

A variety of plants either secrete or excrete metabolic products which are volatilized into the atmosphere where they may be absorbed directly by plants or adsorbed onto soil surfaces (Horsley, in press). Volatile toxins are produced most commonly from plants in arid and semi-arid regions of the world (Putnam, 1985; Rice, 1984). Representative genera include <u>Artemisia</u>, Eucalyptus, and Salvia (Whittaker & Feeny, 1971).

Molisch (1937) actually coined the term allelopathy while researching the volatile substance ethylene, which is produced by apple fruits and affects the growth of many plants (Rice, 1984). Muller and his associates have produced classic works which identify terpenoids, primarily monoterpenes and sesquiterpenes, which are volatiles that regulate plant patterning in semi-arid regions of southern California (Muller, 1969).

Eucalyptus is used as an ornamental in California. It produces volatiles that may effect lawns and understory vegetation (del Moral & Muller, 1969). Fruiting plants, such as crabapple, produce the volatile ethylene and may be suspect donor species.

Leaching

Leaching is the removal of substances from plants by aqueous solutions such as rain, dew, mist, and fog

(Horsley, in press). Some authors, such as Horsley (1983), specify living tissue as the source, while others allow leaching of senescent or dead leaves attached to the plant, or as litter, to their definition (Lodhi, 1978; Rice, 1984). In my opinion, these distinctions aren't critical. What is important and differentiates leaching from residue release is physical or microbial breakdown of the leaf tissue. This distinction is not made clear in the literature and it should be, as will be shown later. Hence, I define leaching to include water activity on live or dead above-ground tissue <u>prior</u> to cellular breakdown.

Various factors (discussed later) affect the amount of leached allelochemics. Vigorous, young, waxy leaves subjected to high-intensity rainfall of short duration, occurring at low temperatures tend to produce smaller quantities of leachates. In contrast, old, easily wet, senescent or dead leaves, and long, low-intensity rainfall occurring at high temperatures produce larger quantities of leachates (Horsley, in press). Seasonal variation is also a determinant of leachate quality (Dormaar, 1970; Lodhi, 1978).

The leaching of above-ground plant parts with water is by far the most common route of entry reported in the literature. This does not mean that it is the most common process of release in nature. Rather, it is the

easiest, at this time, to research. Above-ground parts are accessible and water-soluble compounds are relatively easy to extract from them.

According to Putnam (1985) leached chemicals include organic acids, sugars, amino acids, pectic substances, gibberellic acids, terpenoids, alkaloids, and phenolic compounds. Leachates of aster and goldenrod inhibiting black cherry and sugar maple are examples of this process (Horsley, 1977a; Fisher et al., 1978). Many other examples are cited throughout this paper.

Root Exudation

Root exudation is the release of substances into the sur rounding medium by healthy, intact plant roots (Horsley, in press). Numerous investigators have found that many kinds of organic compounds are exuded by many **Species** (Rice, 1984). For example, Smith (1976) examined exuded root chemicals in yellow birch (Betula alleghaniensis), beech (Fagus grandifolia), and sugar **mapl**e. He identified carbohydrates, amino acids, amides, organic acids, and nine inorganic ions in the exudate. Horsley (1983) stated that almost every class of chemical **Foun**d in plants can be exuded from the roots under **Ppr**opriate conditions. However, Hoagland and Williams (1985) stated that most of the compounds are simple • *** Ganics** of relatively low molecular weight.

Many factors can affect the quantity and quality of exuded chemicals: plant species, age or stage of development, temperature, lighting and nutritional conditions, soil microorganisms, rooting medium, soil moisture, and root damage (Horsley, in press). Tubbs (1973), for example, found that an inhibitor from sugar maple roots was only detectable when root growth was at Work by Ponder (1986) confirmed earlier its maximum. by Massey (1925), who concluded that work done **all**elopathic effects are more pronounced in the receiver **plant** when its roots come in contact with the donor plant.

An interesting example of the root exudation process is described by Petranka and McPherson (1979). <u>Rhus</u> <u>Copallina</u> rhizomes penetrate horizontally through prairie soils, exuding allelochemicals that inhibit the climax- **Pra** irie grass species. This allows its own invasion into the prairie.

The direct production of root exudates is well documented and understood. What is not as clear is the modification process that exudates undergo in the rhizosphere after release from the host plant. Soil microorganisms modify root-cell permeability and root metabolism, and rhizosphere organisms may absorb or excrete qualitatively different natural products than the plant roots (Horsley, in press). Hoagland and Williams
(1985) discussed soil microorganism-plant root associations in detail, which will be referred to later.

Residue Decomposition

When plant tissues age and die, cell membrane integrity is lost, resulting in the liberation of large quantities of water-soluble and partially water-soluble natural products (Horsley, in press). These compounds exist in the same form before and after cell deterioration so I consider them as "direct" allelopathic agents.

Horsley (in press) went on to say that substances, such as enzymes that normally are compartmentalized in li√ing tissue, released the immediate are into sur roundings and react with other natural products, resulting in qualitative changes in some of these **Products.** Horsley called these newly formed compounds "transformation products." Petranka and McPherson (1979) fourd a dramatic increase in toxicity in sumac leaves as they senesced. They believed the change resulted from the release of tannins into the cell sap through membrane degradation and the subsequent enzymatic oxidation of these compounds to form gallic and tannic acids.

Once natural products enter the soil in leachates or incorporated plant residues, additional qualitative changes occur as a result of physiochemical action of the

soil and the activities of resident soil microorganisms (Horsley, in press). Fisher (1987) stated further that it seems unlikely that the allelopathic chemicals that may be extracted from plant material are actually those that reach the receiver plant, yet nearly all our information on allelopathic compounds is derived from extracts that have never been exposed to the soil.

The previous paragraph exposes a major problem in the elucidation of allelopathic release processes that plaques virtually all authors dealing with this science. The conventional wisdom combines residue natural products released after cell wall deterioration with those produced by microorganisms after ingestion of host plant by-products as a nutrient source. I disagree with this approach, although its occurrence is understandable. Rice (1984) pointed out how difficult, or nearlv impossible, it is to determine if a natural product is toxic at release or changed by microorganisms. Many studies cited in this thesis support Rice's contention. But whether it is difficult or not, the distinction should be made between host plant metabolites and their soil-mediated products and new products produced by microorganisms. Hence, I propose a fifth route of entry to include allelochems produced by microbes, regardless of their origin.

The delineation of a fifth release process will be a much more accurate describer of allelochem release and will emphasize the importance of microbial processes. For example, Hoagland and Williams (1985) stated that the bulk of the literature about allelopathy has dealt with direct toxic effects on other plants. Their work, however, makes it obvious that allelochems may have a major impact on plant-root microbial interactions. Such interactions could lead to growth inhibition in the microorganisms (or in roots) and affect other factors of the root-microbe association resulting in effects interpreted as direct allelopathic effects. The authors noted that root exudates of a host plant can be readily changed to a different compound by microorganisms in the rhizosphere.

(in press) described the methods of Horslev microbial activity. Hydrolysis of glycosides, producing free sugar and aglycone, occurs readily in acid soils and as a result of microbial action. Further, microbial use of allelochems as carbon sources results in the compound to another transformation of one along a degradative route. For example, the phenolic ferulic acid is transformed by bacteria and fungi to vanillic acid, then to protocatechuic acid. The aromatic structure subsequently disappears with the formation of aliphatic organic acids. The speed and completeness of

these transformations depend on microbial species and factors that influence their activity, including soil properties such as texture, moisture, oxygen, organic matter, metals, nitrogen content (C/N ratio), soil reaction, species resistance to microbial attack, and concentration in the soil.

In addition to degradation, soil microorganisms synthesize new natural products from carbon sources released during residue decomposition. For example, the antibiotic patulin that is produced by <u>Penicillium</u> <u>urticae</u> following the addition of plant residues to the soil (Norstadt & McCalla, 1968).

Uptake and Translocation

According to Rice (1984), there is a large body of indirect evidence, but only a relatively small body of direct evidence, concerning the movement of allelochemicals from producing plants and the uptake and translocation of these compounds in neighboring plants. Fisher (1987) stated that a toxin that is free in the soil solution is available for uptake by the receiver Most, if not all, allelopathic chemicals are plant. taken up by plants, but plants may discriminate against certain toxins on the basis of size (molecular weight) or some other factor. However, it is poorly understood why

and how plants are able to discriminate against some chemicals.

Einhellig (1986) noted that, although little definitive work has been done regarding allelochemical uptake, many of the low molecular compounds can be expected to enter cells in ways parallel to foliar and root-absorbed herbicides. Phenoxyacetic acid (2,4-D), which is very closely related to several known allelochems, was taken up at a steady rate over a 24-hour period by Lemna minor (Rice, 1984).

Some work has been done directly on allelochem Winter (1961) placed horsechestnut (Aesculus uptake. leaves and bark containing hippocastanum) the allelochemical esculin in soil planted to wheat. The compound was later found to be present in both the soil and wheat roots. Einhellig et al. (1970) found tobacco and sunflower roots removed scopoletin from a nutrient medium with substantial quantities translocated to the leaves.

Once a toxin in absorbed, it must be translocated to the site where it is capable of interfering with metabolism (Fisher, 1987). Experimental evidence indicated that growth-regulating compounds applied to the tops of plants were translocated through the phloem (Rice, 1984). Rice stated further that soil-applied compounds move through the roots and xylem at a faster

rate than phloem, but this movement is dependent on the transpiration rate. Phloem translocation rates of 13 phenols and flavonoids were measured by Macleod and Pridham (1965) at 12 to 108 cm/hour.

Rice (1984) noted that bridges are formed between plants by natural root or stem grafts, mycorrhizal fungi, or haustorial connections of parasitic vascular plants. Further, he cautioned that allelochems may move between plants through these bridges rather than through the soil substrate.

Knowledge of uptake and translocation is the weakest link in the chain of information concerning allelopathy and there is an urgent need for careful research in this area (Rice, 1984). This research should include the tagging of suspected allelochems and tracing of their paths out of the donor plant and into and through affected acceptor plants.

CHAPTER VI

ALLELOCHEMICALS

Classification and Chemistry

Chemical compounds that produce allelopathic effects are termed allelochems or allelochemicals. Isolating and identifying these natural products is a critical barrier in proving that allelopathy is operating in a plant system (Horsley, in press).

Horsley (in press) says that since 1960 there has been a revolution in the methodology used in natural products organic chemistry. With the development of sophisticated instrumental methods has come the detection and identification of many allelochemicals. Swain (1977) reported the isolation of 10,000 low-molecular weight products from higher plants and fungi and estimated the possible existence of 400,000 chemicals.

In spite of the technological advances in the chemistry of allelopathy, woody plant scientists have rarely availed themselves of these techniques in performing their research. Lodhi (1976, 1978), Larson and Schwarz (1980), and Dormaar (1970) are exceptions, having identified tissue or soil allelochemicals. The point made earlier about multidisciplinary cooperation is

reiterated here. Because botanical scientists are seldom specialized in organic chemistry, it becomes incumbent on them to include natural product chemists in their research efforts.

There are several ways allelochems are classified. Whittaker and Feeny (1971) discussed a broad system used in chemical ecology based on the adaptive advantage of a releasing or receiving organism. Allemones, for example, give an advantage to the producing organism (e.g., repellents, venoms, attractants), whereas kairomones give an advantage to receiving organisms.

As described by Putnam and Tang (1986), Grummer (1955) classified plant inhibitors based upon their source of origin and upon the organism affected by their action (suspect). Kolines are produced by higher plants and affect other higher plants; marasmines from higher **Plants** affect microorganisms; phytoncides are from mic roorganisms and affect higher plants, while ant ibiotics are microbially produced and affect other microbes. Fuerst and Putnam (1983) proposed a similar nomenclature system but neither approach is commonly used.

Whittaker and Feeny (1971) classified secondary Chemicals on biosynthetic grounds (i.e., metabolic Cigin) into five major groups: phenylpropanes, Cetogenins, terpenoids, steroids, and alkaloids. These

chemicals primarily originate from amino acids and acetate and include most identified allelochemicals.

Rice (1984) felt a system needed to be developed that indicated chemical similarities. hence he devised an arbitrary arrangement with 14 categories. Most antibiotics, marasmins, phytoncides, and kolines which been identified fit one of these categories. have although some do not. Figure 2 depicts the probable major biosynthetic pathways leading to production of the various categories of allelopathic agents. From the diagram, it is apparent that inhibitors arise from, or come through, the acetate or shikimic acid pathways.

Rice's system seems to be the most acceptable to other scientists in the field. Hoagland and Williams (1985), Mandava (1985), Putnam (1985), Putnam and Tang (1986), and Rice (1987) have presented papers based on Rice's classification system. Hoagland and Williams (1985) provided a schematic outline of various products and associated enzymes from the shikimate and phenolic pathways in some plants and microorganisms. They also provided tables on the sources, i.e., species and plant parts and identity of allelochemicals from higher plants (Table A.1). Mandava (1985) provided a chart indicating the plant release source, e.g., leachates, and examples of allelochem classes isolated from those sources. He



Types of Chemical Compounds Identified as Allelopathic Agents

Figure 2.--Toxin Biosynthetic Pathways.

Source: Rice, E. L. 1984. Allelopathy. Academic Press, New York.

also provided diagrams of the molecular structure of allelopathic compounds.

The chemistry of allelopathy is a topic in its own right, and I am poorly qualified to elucidate it. Rather, I defer to the authors previously mentioned for a more thorough review of the subject. However, the chemical classes outlined by Rice (1984) will be and mentioned comments made where applicable to ornamental plants.

Chemical Classes

<u>Aliphatic compounds</u>. Several water-soluble simple organic acids and alcohols are common plant and soil constituents (Mandava, 1985). Under aerobic conditions, aliphatic acids are metabolized in the soil, and therefore, should not be considered as a major source of allelopathic activity (Hutchinson, 1975).

Simple unsaturated lactones. The less complex lactones are included in this category, while the more complex ones are discussed later. Parasorbic acid was identified from the fruits of <u>Sorbus aucuparia</u> and is very inhibitory to seed germination and seedling growth. It is also antibacterial (Evenari, 1949). Patulin is produced during the decomposition of apple root and leaf residues and may be important in the apple replant problem (Borner, 1963b).

Fatty acids and polyacetylenes. There is rapidly expanding evidence that these two groups of compounds are very important in allelopathy (Rice, 1984). He reported that a number of studies showed that decomposing residues of some common forbs produced chemicals inhibitory to other plants and microflora. Grummer (1961) reported that the polyacetylene, agropyrene is produced by Agropyron repens and that it is antimicrobial.

Naphthoquinones, anthraquinones, and complex

<u>quinones</u>. Juglone, a toxin of walnut trees, is the only inhibitor produced by higher plants that is definitely known to be a naphthoquinone (Rice, 1984). Skyrin is a dianthraquinone marasmin produced by the chestnut blight fungus Endothia parasitica (Owens, 1969).

Simple phenols, benzoic acid, and derivatives. This category and the cinnamic acid derivatives have been the most commonly identified allelopathic compounds produced by higher plants (Rice, 1984). The most commonly identified benzoic acid derivatives involved in allelopathy are p-hydroxybenzoic and vanillic acids Lodhi (1976) reported p-hydroxybenzoic (Rice, 1984). acid in bottomland forest soils. Compounds from this group have been reportedly produced by Celtis and Eucalyptus (Rice, 1984).

Cinnamic acid and derivatives. Rice (1984) stated that these compounds, which are clearly derived through the shikimic acid pathway, are widespread in higher plants and are implicated in many cases of allelopathy. Examples of compounds that are frequently involved with herbaceous and woody plants include cinnamic acid, transcinnimic acid, ferulic acid, p-coumaric acid, chlorogenic acid, and caffeic acid. These chemicals were found variously with such plant species as Sorghum, Bromus, Digitaria, Eucalyptus, Platanus, and Celtis (Rice, 1984). Lodhi (1976) found that caffeic, ferulic, p-coumaric, and acids p-hydroxybenzoic were the most persistent allelochemics in the soils he studied.

<u>Coumarins</u>. These lactones of o-hydroxycinnamic acid with the possible presence of various side chains occur in all plant parts and are widely distributed in the plant kingdom (Rice, 1984). Coumarin, esculin, scopoletin, and scopolin are commonly reported in the literature. <u>Celtis</u>, <u>Platanus</u>, <u>Aesculus</u>, and a number of oaks have been reported as producers of coumarins (Rice, 1984). Rice and Pancholy (1974) reported that scopolin is a strong inhibitor of nitrifying bacteria.

<u>Flavonoids</u>. Although widespread in higher plants, only a few flavonoids have been implicated in allelopathy, probably because of the difficulty in

identifying them and their numerous glycosides (Rice, 1984, 1987). Phlorizin in apple roots is toxic to young apple trees and often causes difficulty in replanting old apple orchards (Rice, 1987). Flavonoids and their glycosides are produced by species from the tall-grass prairie and post oak (<u>Quercus stellata</u>)/blackjack oak (<u>Quercus marilandica</u>) forest and are inhibitory to nitrifying bacteria and to seed germination (Rice & Pancholy, 1974).

Hydrolyzable and condensed tannins. Although unlike in their chemical structure, Rice (1984) included both types of tannins in the same category as they both are used in the tanning process. There are many kinds of hydrolyzable tannin molecules possible, and they are widespread in dicotyledonous plants. They are difficult to identify and only a few researchers have implicated them in allelopathy (Rice, 1984). They have been identified as growth inhibitors of Rhizobium from Rhus copallina (Blum & Rice, 1969), as reducers of seedling growth in Carpinus betulus (Mitin, 1970) and as reducers of nitrification from three Quercus species (Rice & Pancholy, 1973). These authors, along with Lodhi (1976), reported gallic, ellagic, and digallic acids as representatives of this category.

Rice (1984) indicated that there are fewer reports of condensed tannins being involved in allelopathy than hydrolyzed tannins, but nevertheless, the few that there are seem to involve trees. Rice and Pancholy (1973) found condensed tannins were involved in the inhibition of nitrifying bacteria in species in the tall-grass prairie, the post oak/blackjack oak forest and the oak/pine forest. Lodhi and Killingbeck (1980) identified condensed tannins in ponderosa pine (Pinus ponderosa) and these compounds inhibited soil suspensions of Nitrosomonas. Somers and Harrison (1967) found that all tannin fractions inhibited germination and hyphal growth of spores of the fungus which causes Verticillium wilt.

Terpenoids and steroids. These compounds have basic skeletons derived from mevalonic acid or a closely related precursor (Robinson, 1983). Higher plants produce a great variety of terpenoids, but only a few have been shown to be allelopathic (Rice, 1987). Isolation and identification of terpenoids is quite difficult as they show low solubility in water (Fischer, 1986).

Monoterpenoids are the major components of essential oils of plants, and they are the predominant terpenoid inhibitors that have been identified from higher plants (Rice, 1987). Camphene, camphor, cineole, α -pinene,

and β -pinene were identified by Muller and Muller (1964) as the volatile inhibitors produced by <u>Salvia spp</u>. Some of the same compounds are produced by <u>Eucalyptus</u> and result in pronounced allelopathic effects (del Moral & Muller, 1970).

Sesquiterpenes number ca. 2,000, but few are allelopathy, although the implicated in number is increasing (Fischer, 1986). Abscisic acid is а sesquiterpene, and is a well-known plant hormone involved in stomatal regulation and senescence. It is also a seed germination inhibitor present in the leaves of Fagus sylvatica (Mitin, 1971).

Amino acids and polypeptides. These groups include some of the best-known constituents of living matter, but only a few are implicated in allelopathy (Rice, 1984, 1987). Minor activity involving microbes, weeds, and crops in agricultural contexts has been reported.

Alkaloids and cyanohydrins. The logic for including these types of compounds together is that they are derived from amino acids and contain nitrogen (Neish, 1964). Rice (1987) said there has been little recent work done on alkaloids, but Evenari (1949) stated emphatically that all seeds and fruits that contain these compounds are strong inhibitors of seed germination. Scopolamine is a weak inhibitor noted in guite a few papers that is a member of this chemical class. The microbial alkaloid α-picolinic acid is toxic to plants (Owens, 1969). One of the more active synthetic herbicides on the market, Picloram (Dow's Tordon), is a chlorinated picolinic acid derivative (Rice, 1987).

The cyanohydrins are represented by chemicals important to ornamental plants. Benzaldehyde and HCN are produced by the breakdown of amygdalin (nontoxic) found peach root residues and are very inhibitory to the in growth of peach seedlings (Patrick, 1955). Evenari (1949) reported that seeds of many pomaceous fruits contain large amounts of cyanogenic glycosides and that **HCN** which is released slowly from the glucosides inhibits germination. He pointed out further that large quantities of HCN are released from Crataegus seeds just before germination and suggested that this may be the culmination of the period of after-ripening. Germination processes can proceed because HCN is liberated from the tissues.

Sulfides and mustard oil glycosides. The sulfides are derived from amino acids, are volatile, but are not reported as active in higher plant allelopathy (Rice, 1984). Mustard oils are products of the hydrolysis of Mustard oil glycosides and are produced by all organs of Plants belonging to the Cruciferae (mustard family) and are strong inhibitors of seed germination and microbial growth (Rice, 1987).

Purines and nucleosides. The purines are best known as constituents of nucleic acids (Rice, 1984). The only ones in higher plants which have been shown to be involved in allelopathy are caffeine and several lesser compounds produced by the coffee tree (<u>Coffea arabica</u>) (Chou & Waller, 1980a).

Identification

The extraction, collection, and identification of allelochemicals is a major concern and challenge. Extraction methods and techniques will be discussed in the section on research while identification will be addressed here.

The literature on allelopathy suggests that in temperate ecosystems, the phenolic, benzoic, and cinnamic acids and coumarins are the primary agents, while in arid and semi-arid environments, terpenoid compounds are most important (Horsley, in press). The most thoroughly studied and perhaps the most important allelochemicals are those derived from the shikimate biosynthetic pathway (Hoagland & Williams, 1985).

In many, if not most, research papers on allelopathy, there is an allelopathic mechanism shown to be operating, yet few attempts have been made to isolate

and identify the allelochemicals. Where identification has been made, it is usually the water-soluble phenolics, which are relatively easy to isolate. Where inhibitors have been distinguished, there are most likely others not vet identified.

According to Horsley (in press), mass spectroscopy and ¹H-nuclear magnetic resonance became available about 1960; ¹3C-nuclear magnetic resonance and single crystal x-ray crystallography came into use about 1970; high performance liquid chromatography has become increasingly available during the 1980s. Thus, the array of analytical techniques for identifying allelochemicals is expanding annually.

Once an inhibitory leachate or extract is obtained, a preliminary chromatographic separation is made (Horsley, in press). The "polarity" of the active allelochemical(s) is then obtained by extracting the leachate with a series of organic solvents ranging from nonpolar to polar. Bioassays are used at each step of the purification process to determine which fractions Contain allelochemicals and to monitor their activity (Horsley, in press). Bioassays will be discussed in the section on research.

Because of the lack of natural product organic Chemists working on allelopathy studies, Horsley (in Press) cautions readers to evaluate critically the

methodology for identifying allelochemicals before accepting the results of a study as authoritative. Rice (1984) noted that a knowledge of these compounds is very important in determining methods of escape into the environment, amounts present in the environment, amounts absorbed by affected organisms, and methods and rates of decomposition.

Factors Affecting Production

Factors affecting the amounts of allelochemics produced plants are extremely by important in allelopathy, but research on this subject was active only during a 15-year period starting in 1957, and very little research has been done since that time (Rice, 1984). For the horticulturist and urban forester, it would be useful to know what site conditions and stresses encourage toxin **Production** in donor species. This awareness would assist in the implementation of cultural practices to avoid or mitigate allelopathy conflicts. Rice (1984) provides a framework for this discussion, but it will be modified for the ornamental specialist.

Radiation Effects

Light quality, intensity, and day length all appear to have effects, both increasing and decreasing, on Chemical production. Rice (1984) found that greenhousegrown donor plants produced fewer inhibitors than fieldgrown plants. The addition of ultraviolet radiation increased chlorogenic acid and other phenolics. Red and far-red light as well as ionizing radiation have produced changes, too. Day length increases appear to increase the concentrations of phenolics, terpenes, and flavanoids.

stresses

Mineral deficiencies. Work done by Loche and Chouteau (1963) and Chouteau and Loche (1965) on tobacco showed decreases. plants increases and sometimes dramatic, in allelochemical production where nutrients were lacking. Scopolin concentrations increased when boron, calcium, magnesium, nitrogen, phosphorus, and potassium were deficient. Chlorogenic acid also increased where boron, nitrogen, and sulfur were inadequate, but decreased when calcium, magnesium, phosphorus, and potassium were in short supply. The great increases in concentrations of inhibitors in plants that result from nitrogen and phosphorus deficiency are probably extremely important in connection with allelopathic mechanisms operating in the revegetation of infertile old fields (Rice, 1984). In addition to right-Of-way corridors that are ecologically analogous to old **fields**, the urban plant manager should consider the low **fertility** tree-planting sites in the city where

allelochemical production from grasses and forbs may be increased to damaging levels.

<u>Water stress</u>. Variable increases and decreases of chemicals from water stress have been demonstrated, but little conclusive evidence has been developed (Rice, 1984).

Temperature. The results of studies with temperature are inconclusive, too. Martin (1957) found more than seven times as much scopoletin exuded from oak roots at 30°C as compared to 19°C. Koeppe et al. (1970b) chilled (8°C) tobacco plants and got concentration increases in scopolin and chlorogenic acids in some plant parts and decreases in others.

Herbicides. Rice (1984) describes studies of 2,4-D Sprayed on tobacco and sunflowers and allelochemical interactions. Thirty-one fold increases of scopolin Concentrations and lesser amounts of scopoletin and chlorogenic acids were reported. New phenols were also produced that do not normally occur in certain species. Spraying of herbaceous vegetation under trees with some herbicides may increase allelopathic risk to the trees.

Seasonal Variation

Neither Rice (1984) nor other authors discussed Seasonal variation as a chemical production factor per

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se, but the literature is rife with examples of the importance of timing and chemical release, and of timing and concentration levels, especially in forestry. Tubbs (1973) found that inhibitors exuded from sugar maple roots were produced only from rapidly growing roots and not from dormant roots. Dormaar (1970) studied the presence of allelochems in the leaves of Populus cultivar Northwest and found that simple phenolics present earlier the growing season were transformed to more complex in phenols as the season progressed. Brown (1967) also found seasonal differences in jack pine germination resulting from Populus spp. leaf leachates. Petranka and MCPherson (1979), Lodhi (1978), and Feeny and Bostock (1968) reported similar results in Rhus, Platanus, <u>Cel</u>tis, and Quercus. The changes can occur in active green leaves, senescent foliage, and litter. A better understanding of the seasonal production of allelochems may teach us to modify practical activities for some plants, such as planting season and fall leaf pickup.

Concentration Levels and Synergism

This section will consider the concentration levels in the environment that are necessary for allelopathic activity to occur in receiver plants i.e., sensitivity. Chemical combinations and stress factors that tend to

magnify the potency of the available allelochemicals will be discussed also.

One of the few facets of allelopathy that seems to universally agreed upon by scientists is that be allelochemicals are concentration dependent in their effects on receptor plants. Dose-response curves with show inhibition compounds either above the known threshold level or even stimulation occurring below the threshold level (Einhellig, 1987).

Although the concentration of a compound required to exceed the threshold varies greatly due to different sensitivities among species and among phases of the growth cycle for higher plants, the concept of an inhibition threshold seems consistent (Einhellig, 1987). For example, del Moral and Cates (1971) did a study in which 40 plant species were tested against two herbaceous and one woody plant to determine the threshold concentration levels for inhibition. Peters and Luu (1985) isolated all the allelochems from tall fescue leachates and tested each against birdsfoot trefoil (Lotus comiculatus) to determine threshold levels.

Larson and Schwarz (1980) attempted to find the degree of toxicity produced by varying concentration levels. They found variable responses of inhibition in different plant parts, e.g., roots, stems, nodules, etc. Einhellig (1987) found in tests with sorghum seedlings

grown in nutrient solution amended with p-coumaric and ferulic acids, that the threshold for growth reduction was less than 1/20th the level required to reduce germination.

other fairly obvious factors affecting Two concentration levels are the proximity of a receptor to a donor plant and the biomass of the donor. Gabriel (1975) showed а direct relationship between the arowth inhibition and/or death of white birch trees and their distance from black walnut trees. Rietveld et al. (1983) reported that the growth of black alder was inversely related to the density of interplanted black walnut. They proposed that allelopathy resulted partially from the accumulation of sufficient walnut biomass to contribute substantial amounts of juglone to the environment.

In nature, however, it is rare that a single allelochemical is responsible for inhibition. Rather. allelopathic effects normally occur from the combined actions of several allelochems, often with each below a threshold concentration for impact (Rice, 1987). For example, Lodhi (1975) found that the combined effect of P-COumaric, ferulic, caffeic and acids at the concentrations found in soil under hackberry was much more inhibitory to seed germination than the effect of each chemical (at its soil concentration) tested

separately. Einhellig (1987) reported that up to 100fold enhancement was found using two compounds simultaneously, demonstrating that biological activity could occur with concentrations two orders of magnitude below the threshold for a single compound.

Additive and synergistic effects do not only occur with chemical combinations, they also develop with a combination of chemicals and environmental stresses. Allelopathy may be more severe when chemicals are enhanced by low fertility levels, moisture, temperature, and herbicide stress (Einhellig, 1987). According to Einhellig, as the stress factor increases, less chemical is needed to produce equal inhibition or a lower threshold of inhibition is the result. Further, this may even occur when these stresses are insufficient to have any measurable effect on growth.

Synergistic effects are particularly important under field conditions (Rice, 1984). The conditions that cause low fertility in soils, such as excessive erosion, often result in soils with lower infiltration rates and thus in soils that are often deficient in available water. These combinations would increase the allelopathic potentials of inhibitory species. Thus, the potential impact of an allelochemical on plant growth should be evaluated with regard to both the presence of associated allelopathic

compounds and the influence of other chemical and physical conditions in the environment (Einhellig, 1987).

Factors Determining Efficacy

The focus in this section is on the factors that determine the availability of allelochemicals for uptake in receiver plants. Rice (1984) emphasized the great importance of this topic in the overall phenomenon of allelopathy and the critical need for more research on the subject.

Edaphic Elements

Except for volatile compounds that are released and received directly through the atmosphere, all allelopathic responses are mediated through the soil (Horsley, in press). The availability of toxins to receptor plants is determined by their fate in the soil. Fisher (1987) provided a useful schematic showing the potential fate of an allelochemical released into the soil environment (Figure 3). Various works by Fisher and work by Horsley (in press) and Hoagland and Williams (1985) are the most authoritative about this topic, and their ideas are confirmed by other significant studies. Forestry researchers have contributed much of the knowledge about soils and allelopathy.

Each of the major authors approaches the topic from a different perspective but covers essentially the same



Figure 3.--Allelochemical Fate.

Source: Fisher, R. F. 1987. Allelopathy: a potential cause of regeneration failure. In: Waller (ed.), p 176-84.

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material. For example, one author may emphasize moisture regime as a determinant of microbial populations, whereas another may say soil texture and drainage determine microbe numbers and species. In order to avoid confusion, arbitrary categories were chosen and the salient points of the various writers were incorporated. The units will include pool size, the adsorption complex, decomposition, soil texture, persistence, and depths.

<u>Pool size</u>. The amount of chemical available for uptake by a receiver is determined by what Hoagland and Williams (1985) term the "pool size." Rice (1987) explains it as the attainment of active concentrations of allelochemicals in soil, which in turn, depend on the relative rates of addition and inactivation. Pool size can be affected by the adsorption of allelochems by inorganic and organic soils and decomposition by both abiotic and biotic processes.

Hoagland and Williams (1985) provided an in-depth microbiology/inorganic-organic chemistry perspective which went well beyond the scope of this paper, but provided intriguing background to allelochemical complexes, pool sizes, turnover, phenolic binding, and availability in soils. The next two units will address these topics in a manner that is useful to woody-plant scientists.

Adsorption complex. The biological activity,

persistence, and movement of natural products in soil depends on their interaction with the soil adsorption complex and soil microbial populations (Horsley, in press). The adsorption complex includes both inorganic (colloidal) and organic (humic) surfaces.

Fisher (1987) described chemical-soil adsorption in a concise manner and the following descriptions are credited to him. Soil colloids (usually clays) are capable of adsorbing most allelopathic chemicals. Such adsorption would result in temporary loss of toxin activity. Chemical changes could occur during adsorption that would permanently deactivate the toxin. The adsorption reactions are usually reversible, however, so that some or all of the toxin would still be available for uptake by the receiver plant.

Toxins are also likely to be adsorbed or complexed by soil humic acids. If the reaction is a simple adsorption reaction, all or part of the toxin might later become available for absorption by a receiver plant. If the toxin is complexed or precipitated by its reaction with soil humic substances, then it would be deactivated. Inactivation in humic soils can be deceptive, however. Blum and Rice (1969) added known amounts of tannic acid to a prairie soil and a minimum of 400 ppm had to be added before any could be immediately recovered.

However, as little as 30 ppm added to the same soil reduced the nodule number of heavily inoculated legumes, indicating that some of the bound tannic acid remained biologically active.

Decomposition. The decomposition of allelochems can be accomplished by biotic or abiotic processes (Rice, 1987). Tubbs (1973) reported the breakdown of sugar maple leachate without the aid of microorganisms even at cool temperatures. After five days storage in a sterile, sealed container, the inhibition of growth of seedlings was 18% compared to 38% for "fresh" inhibitors. Unfortunately, no explanation was provided for the abiotic degradation.

Soil microorganisms have a tremendous capacity to reduce the quantity of natural products in the soil (Horsley, in press), but microbial decomposition can result in new compounds which may be more toxic than the original substance, either by itself, or in synergistic combination with other chemicals (Rice, 1987). Hence, allelopathic activity can increase as well as decrease from chemical decomposition.

Fisher (1987) described the edaphic factors that largely control the reactions that a toxin undergoes in the soil. Moisture regime helps to determine whether aerobic or anaerobic decomposition occurs, which, in

turn, helps to fix the quantity of toxin metabolized and the nature of the decomposition products. The spectrum of species also controls degradation. Soil nutrient status and temperature help to determine the rate of microbial activity. Microbes are capable of degrading adsorbed toxins, too, but at a slower rate. One of the most important understandings about allelopathy for the practitioner is that different things will happen to the same toxin introduced into different soils or even into the same soil at different times.

Soil texture. It is in the area of soil texture and its ramifications that forest researchers have advanced the science of allelopathy. DeBell (1970) was the first to report the effects of soil texture on allelopathy, but it was Fisher (1978, 1980) who did dramatic research on the subject. A number of other forestry authors have produced results confirming the importance of this variable.

In his 1978 study, Fisher attempted to show that "wet moisture regimes" played a role in the suppression (and death) of 22-25 year-old white pines by black walnut toxins. He found that pines on well-drained sites were unaffected by adjacent walnuts. On the imperfectly drained sites, survival and growth were severely restricted where walnuts were adjacent to pines as

compared to pure pine stands. On poorly drained sites, pine could not coexist with the walnut, i.e., 100% mortality.

The interdependence of edaphic factors is very evident from this study. Heavier-textured soils tend to have adsorptive colloids which bond allelochems and enhance pool size. The poor drainage associated with these soils results in slow leaching (Norby & Kozlowski, 1980) and probably alters microbial breakdown (Fisher, 1978). Rietveld et al. (1983) believed that wet soil greatly restricts aerobic metabolism by microorganisms, allowing juglone to build up to toxic levels.

On the other hand, well-drained, coarse soils do not provide ample adsoptive surfaces, and solutions of allelochems leach readily. Adequate soil aeration provides the necessary oxygen for aerobic metabolism of toxins. Rietveld (1982) observed that soil drainage was а Consistent factor affecting the occurrence of allelopathy in а survey of 46 mixed, even-aged plantations of various species with black walnut.

<u>Persistence</u>. The rapidity of allelochemical breakdown is obviously important to pool size, concentration levels, and availability of a chemical at critical inhibition times. The persistence of an allelochem in the soil depends to a large degree on the

degradation factors discussed in the previous sections as well as on the molecular bonding of the toxin. Very little literature directly addresses the persistence level of specific toxins under varying field conditions. There are, however, some indications and opinions of how long secondary products exist, when considered as a group of compounds.

Tubbs (1973) reported as few as five days of effectiveness of sugar maple leachates. Brown (1967), while testing germination of jack pine seeds in soils previously planted to known inhibitor-producing plants, concluded that the germination-influencing compounds produced by these plants quickly break down and must be consistently replenished if they are to influence field germination.

At the other end of the spectrum, lengthy persistence has been reported. Petranka and McPherson (1979), in a study of Rhus copallina, believed that gallic and tannic acids require "a very long breakdown period," although the timeframe was not defined. This study, along with work by Lodhi (1976, 1978), implied that leachates of green materials do not produce highly toxic or persistent toxins as compared with senescent or decaying leaf litter. Apparently, the bound compounds that are released during decay or transformation by

microbes are quite persistent compared to easily leached toxins.

Gabriel (1975) observed a general depression of tree vigor in 15-inch-tall, white birch seedlings planted on a former black walnut plantation site some years earlier. The difference between the trees growing on the juglone persistent soil and those on soil free of juglone was dramatic. The former remained stunted at 2 ft. in height while the latter were 6 to 10 ft. in height, 2 to 3 inches in diameter, and with crowns that were 5 to 8 ft. wide. The toxin persistence was more than 5 years.

Earlier in this paper, a study by Fisher et al. (1978) was described in which forbs, such as goldenrod and aster, were removed from old-field plots, and sugar maple seeds and seedlings were planted. Although the allelochems were not identified and no toxins were added to replenish the pool size, significant inhibition was evident over two full growing seasons.

These results suggest that allelochemicals can be very persistent in the soil, even after herbaceous vegetation has been removed for a considerable time. There may be many allelochemicals besides juglone that are antagonistic to trees over a period of time.
<u>Depth</u>. Little work has been done on the depth that allelochems persist in the soil. However, Brown (1967, 1990) and others imply that toxins occur in the top several inches of soil and primarily regulate species and spatial patterning by affecting germination and seedling growth. But feeder roots of large trees would also be able to absorb allelochemicals in surface soils (Horsley, 1977a; Peterson, 1965; Walters & Gilmore, 1976).

Blum and Rice (1969) detected tannic acids as deep as 70 cm in soils under shallow-rooted clones of Rhus copallina during the growing season. They found a definite zone of accumulation at the 45-55 cm level. Gant and Clebsch (1975) studied soils under sassafras (Sassafras albidum) clones. The depth of the first root zone varied from 1-5 cm depending on stand age. Four terpenes were present in the soil. Leachates from aboveground sources and root exudates provided soil inputs. Samples from the top 3 mm of soil contained the fewest and lowest concentration of terpenes. Concentration levels increased to a depth of 10 cm (not tested deeper). The increase in concentration with depth could result from leached exudates from the first root zone and upward movement of exudates from deeper roots.

It is important that urban plant managers recognize that phytotoxins can leach or be exudated to a level where they are readily available for root uptake by shade

trees. When inhibition is not evident in a tree it does not mean that toxins are not present in the root zone. Rather, some other factor, such as receptor biomass or concentration level, is most likely operating.

Genetic Elements

The genetic makeup of a receptor plant appears to have a bearing on whether it is resistant to allelopathic influences from another plant. Gabriel (1975) noted that some strains of white birch remained alive, while others were killed by black walnut.

Rink and Van Sambeek (1987) tested four white ash (<u>Fraxinus</u> <u>americana</u>) families for resistance to tall fescue leachates while under different moisture stress regimes. They found a significant difference in height and weight between families, which implies that genetic selection for allelopathic resistance may be possible. However, another study by Rink and Van Sambeek (1985) using black walnut with tall fescue leachate found no such relationship between tree families.

Peters and Luu (1985) presented a study demonstrating genetic control of phytotoxin inhibition as well as providing an exciting example of how allelopathy can be utilized as a practical tool in higher-plant management. The authors noted that tall fescue fields often had no weeds in them and lab experiments confirmed

fescue leachates significantly reduced the that germination and growth of several weed species. Further, at a grass breeding nursery, tall fescue genotypes from around the world showed varied infestation of large crabgrass (Digitaria sanguinalis) in their respective The authors concluded that allelopathy may be plots. genetically controlled, and it may be possible to select fescue with a high amount of allelopathy to exclude other plants from the stand or to select fescue with less allelopathy so that a certain species could be grown with tall fescue.

The possibilities of collecting appropriate genotypes from other turf species could result in allelopathically weed-free lawns in the future. What a dramatic possibility for weed control without environmentally suspect chemicals!

CHAPTER VII

PHYSIOLOGICAL RESPONSES TO ALLELOCHEMICS

This section will describe the reasons for the plant inhibition resulting from allelochemical uptake. Mode and mechanism of action are interchangeably used in the literature to identify this facet of allelopathy. Some authors refer only to processes intrinsic to a plant when dealing with this subject while others include external influences such as nitrogen fixation and the influence on disease-producing organisms. This thesis will deal with metabolic process and mycorrhizal symbionts.

Although Rice (1984) has provided an up-to-date review of the subject, both he and Hoagland and Williams (1985) noted that, in spite of an increase in research activity in this area since 1966, there is a general void of knowledge. Frank Einhellig seems to be the authority on this subject with many cited papers to his credit.

Mandava (1985) pointed to several reasons why it is very difficult to understand mechanism of action. First are the complications in separating the primary and secondary effects of natural plant products. Second is the uncertainty of translating the observed effects in

isolated enzyme and other biochemical systems to intact plant systems. Third is the lack of understanding of the effect of allelopathic agents on whole-plant photosynthetic processes. Einhellig (1986) also noted that clarification of allelochemical action is further hampered because so many different compounds are usually involved.

Einhellig (1986) and Hoagland and Williams (1985) agree that the sites of action for allelochemicals should be similar, if not identical, to those for herbicides (Tables A.2, A.3, and A.4). The work by Einhellig (1986) will be used as a basis for the following discussion on plant processes (Figure 4).

Sites of Action

Regulation of Growth

Cell division and elongation are necessary for size and weight increases of organisms. Most inhibitors of growth modify these events (Rice, 1984; Einhellig, 1986). Organic synthesis of major plant constituents or the distribution of carbon in cellular pools is modified by phenolic compounds (Einhellig, 1986). The alteration of enzyme synthesis or function and the disruption of hormones regulating plant growth by several phenolic products was reported by Einhellig (1986).





Figure 4.--Mechanisms of Action (Model).

Source: Einhellig, F. A. 1986. Mechanisms and modes of action of allelochemicals. In: Putnam and Tang (eds.), p 171-188.

Respiratory Metabolism

Muller et al. (1969) found that volatile monoterpenes (cineole, dipentene, etc.) from Salvia leucophylla were potent inhibitors of 0, uptake by mitochondrial suspensions. Also, a wide range of interfere compounds with mitochondrial phenolic functions, including quinones, flavonoids, and phenolic acids (Einhellig, 1986). Keoppe (1972) reported that juglone-induced reduction of respiration in vivo resulted from inhibition of the coupled intermediates of oxidative phosphorylation, slowing electron flow to 02. The literature on adverse effects on respiration at the level of enzymes, isolated mitochondria, excised tissue, and the whole plant argues for respiratory metabolism dysfunction as one mode of action of allelochemicals (Einhellig, 1986).

Photosynthesis and Related Processes

The increase of dry matter of higher plants is linked to carbon fixation, so any loss in efficiency of photosynthesis might be detrimental to growth (Einhellig, 1986). Photosynthesis may be altered by a variety of mechanisms, both direct effects at the chloroplast level and indirect actions, such as stomatal closure and chlorophyll content. Scopoletin, p-coumaric, caffeic, and ferulic acids are some of the implicated compounds.

Nutrient Uptake

Results of a number of field and laboratory studies that interference with root membrane suggests permeability could affect a plant's ability to take up nutrients and water, even when these resources are present in adequate supply in the soil (Horsley, 1983). This mechanism of action is likely a primary reason for allelopathic inhibition in ornamental plants. For example, Walters and Gilmore (1976) showed that sweetgum subjected to leachates from the rhizosphere or residue of tall fescure had less PO_{A}^{3-} content and more K^{+} than controls, but N was not different. Brown and Mikola (1974) showed that reindeer-moss lichens (Cladonia spp.) inhibited the growth of jack pine seedlings by affecting phosphorus uptake via the roots and/or mycorrhizae. Buckholtz (1971) suggested that quackgrass inhibitors can reduce K⁺ uptake by corn. It is my opinion that quackgrass allelopathy may be responsible, at least in part, for the slow growth of ornamental trees in utility and transportation corridors in the Lake States where quackgrass is so prominent.

Balke (1985) has written the most thorough paper about mineral uptake. He stated that phenolic acids and flavonoids inhibit mineral absorption by excised plant roots. The physiological mechanism of action of these allelochemicals involves the disruption of normal membrane functions in plant cells. These allelochems can depolarize the electrical potential difference across membranes, a primary driving force for active absorption of mineral ions. Allelochems can also decrease the ATP content of cells by inhibiting electron transport and oxidative phosphorylation, which are two functions of mitochondrial membranes. In addition, allelochemicals can alter the permeability of membranes to mineral ions. allelochemicals mineral lipophylic alter Thus, can absorption by several mechanisms as the chemicals partition into or move through cellular membranes. Which mechanism predominates may depend on the particular allelochem, its concentration and environmental conditions (especially pH).

Hoagland and Williams (1985) and Horsley (1983) emphasized the important role of microorganisms in the mineral uptake of higher plant root cells. The rhizosphere microorganisms (mycorrhizae) can be significantly affected by allelochemicals. Balke (1985) and Hoagland and Williams (1985) both provided tables listing donor plants, chemical classes, receptor effects, etc., involved in inhibition of mineral uptake (Table A.5).

A logical outcome of some of the observed effects on ion uptake and membrane functions would be changes in plant-water balances (Einhellig, 1986). Rice (1984)

summarized observations indicating that allelopathic compounds may interfere with xylem flow by clogging the Certainly an interdependence between water vessels. balance and allelochemical effect seems likely, since even mild water stress can be very detrimental in conjunction with allelochemical stress (Einhellig, 1987). Einhellig et al. (1985) performed tests on grain sorghum (Sorghum bicolor) using ferulic acid, p-coumaric acid, and extracts from several allelopathic weeds. Stomates almost closed and water potential changes resulted from reductions both osmotic potential in and turgor Dry weights were reduced even pressures. at low allelochem concentrations. They also noted that the effects on water balance are likely to impede other physiological processes, with the combined action causing growth reduction. The authors cited a study by Lodhi and (1973) which reported that Celtis laevigata Nickell produced allelochems which interfered with water content in receptor plants, with concurrent growth suppression.

Cell Destruction

Virtually all the literature discusses plant inhibition based on a perturbation of a plant process. The only exception is a study by Peterson (1965) which described actual root cell destruction in black spruce (Picea mariana) by leachates from the leaves of sheep

laurel (<u>Kalmia</u> <u>augustifolia</u>). The dead terminal portion of the root often curled to one side and remained a side projection as a new growing tip pushed forward. Hence, the tree remained alive, but with a reduced growth rate.

Symptoms of Activity

The correlation of plant symptoms with allelopathic activity has not progressed very fast or far, especially under field conditions. Putnam (1987) said that, although many highly respected plant ecologists say it is virtually impossible to separate interference mechanisms in the field, instead we must be more creative in solving this problem. It was pointed out previously that stresses, like water, magnify allelochemical effects, but we have not learned to differentiate the presumed wilting as water stress or allelopathic symptoms.

In the field, it may be necessary to identify the understory species, its allelopathic potential, water availability, soil type, and nutrition levels before physical symptoms can be judged as allelopathic. At present, the elimination of other possible causes seems to be the primary way of attributing observed field symptoms to allelopathy

Several documented studies do give a sense of how to determine if allelopathy is operable in a forest setting. Schlesinger and Van Sambeek (1986), knowing that tall

fescue can be allelopathic, surmised that the slower than "normal" growth of black walnut had to be something that competition theory couldn't explain. Top dieback occurred even with satisfactory levels of water and nutrients.

Gabriel (1975) noted "a general depression of vigor" in a white birch plantation that had been preceded by a black walnut planting. Peterson (1965) compared the site conditions and growth of black spruce and found obvious suppression on sites with sheep laurel understories. No suppression existed on similar sites where laurel was absent. Similarly, Horsley (1977a) compared black cherry of the same age growing in old fields and in an adjacent The open-grown trees in the field should wooded area. have been much larger than their counterparts in the forest, but were, in fact, similar in size. These researchers went on to study and implicate allelopathy as the operable inhibition mechanism.

Fales and Wakefield (1981) reported foliage color variation from dark green to very chlorotic in forsythia plants. Nitrogen content correlated with color which was, in turn, controlled by an allelopathic mechanism. Unfortunately, the same color spectrum could result from N competition, too.

Muller has done some of the most useful work in the area of symptoms, according to Putnam (1987), and he

suggested that Muller's approaches be imitated. Muller (1969) demonstrated a relationship between allelopathic species and very observable spatial growing patterns, such as bare zones adjoining thickets of <u>Salvia</u> and Artemisia.

Although it is an uncommon occurrence, plant death is a dramatic symptom of allelopathy. Black walnut is the only temperate zone tree to be reported as a potential lethal donor plant to receptor trees. White and red pine (Fisher, 1978), black alder (Rietveld et al., 1983), and white birch (Gabriel, 1975) are all quite easily killed by walnut.

Detection of allelopathic symptoms in the laboratory advanced and greenhouse is compared field to identification. Symptoms in the lab include can physiological actions as well as morphological changes. They might include foliage coloration, tissue nutrient content, loss of geotropic behaviors, change in water potential, wilting, change in CO, exchange rate, and epinasty (Horsley, in press). As an example, sorghum plants grown with extracts from several common weed species produced effects including chlorosis, necrotic spots on leaves, leaf folding, and reduced root development (Einhellig et al., 1985).

Horsley (in press) warned that gross measures of growth are unreliable because they are influenced by many

factors. However, these growth measures are used frequently and are very convincing if used in the proper context. Larson and Schwarz (1980) used gross growth measures, root nodulation and N-fixation rates very effectively in implicating the allelopathic potential of herbaceous weeds inhibiting the growth of black locust (Robinia pseudoacacia) and black alder.

CHAPTER VIII

RESEARCH METHODS AND TECHNIQUES

The chemical nature of allelopathy and the difficulty of correlating external symptoms with allelopathic activity will probably mean that research methods and techniques will be necessary for both the initial discovery and the diagnostic identification of allelopathy by researchers and practitioners. This chapter will serve as a review of the methods and techniques used by researchers in their attempts to substantiate allelopathic activity.

In Chapter III, plant interference was discussed in great detail. In order to point out the differences between allelopathy and competition, field studies were described, Koch's postulates were set forth, and Fuerst and Putnam's steps for proving allelopathy were outlined. This chapter will complement the earlier field research discussion by providing background on laboratory and greenhouse investigations. The use of bioassays in detecting the presence of allelochemicals in a plant and the importance of understanding allelopathic potential are the key issues in this unit.

Allelopathic Potential

When allelopathy is suspected as a possible problem in plant growth under natural conditions, laboratory studies are usually conducted to determine the presence of toxic soil and/or plant chemicals. The isolated compounds are tested utilizing an arbitrary species, such as lettuce, radish, or brome grass. Seed germination percentages and/or some facet of seedling growth, such as radicle length, are usually measured. The testing is usually done with varying concentrations of extracts from different plant parts. In these approaches, edaphic factors and soil microorganisms are not accounted for.

Horsley (in press; 1990) emphasized the flaw in concluding that lab proof of allelopathy equals operable field activity. For example, Mergen (1959) obtained hot water leaf extract of ailanthus (<u>Ailanthus altissima</u>) and applied it to stem wounds on slash pine (<u>Pinus elliottii</u>) seedlings. Wilting occurred at low concentrations and death at high levels. In this example, Horsley's point is well taken. Ailanthus and slash pine neither grow together in nature, nor are chemicals injected directly from donor to receiver. Hence the lab results don't appear to be applicable to natural systems.

While I share Horsley's view that laboratory studies of allelopathic potential seldom have relevance in understanding interference phenomena in natural systems,

there is some benefit to be gained by the urban forester/horticulturist in manipulated systems. First, trees which do not occur together in nature, such as ailanthus and slash pine, may be planted together in an ornamental setting. Secondly, many ornamental trees may be planted in farm or yard settings with crop and turf species identical to lab receiver species. For example, Petrushenko et al. (1974) determined that the membrane permeability of wheat (Triticum vulgare) was affected by the leaf litter extracts of horsechestnut (Aesculus hippocastanum) and Austrian pine (Pinus nigra). Black walnut, on the other hand, while allelopathic to tomatoes is not to beans (Ponder, 1986). Agronomists and urban foresters can utilize this type of information in designing compatible plantings. Thirdly, studies of species' allelopathic potential give us clues to broad groups that may be a problem. The previously mentioned example of horsechestnut-wheat may lead us to suspect potential damage to rye or other grasses. And lastly, as del Moral and Muller (1969) pointed out, plants that may not be allelopathic to natural associates in one system, such as Eucalyptus in Australia, may be very allelopathic as an exotic in a new system, such as California.

Bioassays

According to Leather and Einhellig (1986), bioassays are an integral procedure in all studies of allelopathy. They are necessary for evaluating allelopathic potential of species and following the activity during extraction, purification, and identification of bioactive compounds. Webster defines a bioassay as "The use of biological material to test the relative activity of a substance (as a drug) against a standard of known activity."

Ackoff (1962) defines a technique as ". . . a way of accomplishing a scientific objective, a scientific course Techniques, therefore, are ways of using of action. scientific tools." A method is ". . . the way techniques are selected in science; that is, . . . the evaluation of alternative courses of scientific action. . . . methods are rules of choice; techniques are the choices themselves." The procedure for selecting appropriate experiments would be a method whereas the field test or bioassay chosen for a project would be a technique.

In Leather and Einhellig's (1986) paper entitled, "Bioassays in the Study of Allelopathy," they noted that nearly all the published reports on allelopathy describe some type of bioassay that was used to demonstrate allelopathic activity. However, the lack of standardized bioassays, including incomplete information on the allelochemical source, method of extraction,

fra com act are emp: in must chos alle Jece clos susp or p <u>Coll</u> of e neth be o Mille SUSCe plant Whole recei. fractionation concentrations, and the absence of comparisons with known compounds with demonstrated activity in the bioassay, is a major difficulty.

Although bioassays are nearly universally used and are useful in studies of allelopathy, Horsley (in press) emphasized that the initial definition of interference is in terms of symptoms of plant injury, and these symptoms must be preserved in all phases of the work. Improperly chosen techniques can lead to incorrect suggestions of allelopathy in the field. To avoid this problem, it is necessary to simulate field conditions in the lab as closely as possible. This includes the extraction of the suspected allelochem and testing of the same plant part or phase as in nature.

Collection and Bioassay Preference

The discussion on bioassays is based on the routes of environmental entry. For each source, the collection methods, field/lab analogy, and bioassay techniques will be outlined.

<u>Volatilization</u>. Horsley (in press) describes how Muller (1969) tested seed germination of plants susceptible to plant volatiles. Seeds of the receiver plant were germinated in closed containers along with whole foliage or foliage extract. The control containers received no foliage or extract and the difference in germination percentage was attributed to the secondary metabolites. Horsley (in press) reports that volatiles can also be quantified directly from air samples by gas chromatography. However, Leather and Einhellig (1986) reported that seed germination bioassays are the preferred choice for tests of volatiles.

Volatiles are probably the only agents of allelopathy that are not soil mediated; therefore, the should correlate closely with results lab field conditions. Volatiles that are adsorbed on soil particles would need to be tested and the results interpreted as other allelochems subject to edaphic and microbial activity.

Leaching. The collection of allelochems by soaking fresh (live) or dried (dead) leaves with water is relatively simple. But duplicating the quality and quantity of leachate in the lab as in nature is more difficult.

Horsley (in press) states that the amounts of tissue or the leaching conditions that occur in nature have often not been considered when protocols for leachate preparation were developed. Brown (1967), for example, produced and tested extracts from 56 plants common to jack pine forests. To make the extracts, 20 g dry weight of fresh materials were reduced with distilled water in a

blender and centrifuged until 600 ml of extract was produced. No attempts were made to relate natural conditions to subsequent seed germination tests and yet the results were presented as suggesting a relationship to field situations.

Mandava (1985) listed various methods for extracting allelopathic agents, including soaking and dripping with hot and cold water or organic solvents of intact or cut up foliage. It is doubtful that extract quantity and quality similar to nature can be obtained from some of these procedures. Fortunately, there are many examples of studies where natural conditions were simulated, often by very creative means.

For example, Dormaar (1970) picked fresh leaves of poplar at 3-week intervals and placed them in water for 1 hour to simulate canopy drip. The 3-week interval tests provided data on the seasonal variation in allelochem release. However, no field basis was explained for choosing a 1-hour soaking time. Petranka and McPherson (1980) went a step further in their study of the effects of <u>Rhus</u> on associated vegetation. They determined the amount of plant material to be leached by actual field measurements and then soaked the material with water amounts equivalent to natural rainfall. Horsley (1983, 1987, in press) also determined the field biomass of

ferns at different seasons and leached them with water quantities based on 25-year records of rainfall.

Seed germination and root hypocotyl growth seem to be the bioassays most commonly used for testing foliage leachates. Although it is conceivable that leachates in nature contact and are absorbed by seeds on the soil surface without being subjected to microbial transformation, it seems more logical that leachates would be modified by edaphic conditions and microorganisms prior to contact with either seeds or root systems. Therefore, tests of laboratory extracts which may provide insight into allelopathic potential may be very suspect in explaining operational allelopathy under field conditions.

<u>Root exudation</u>. The collection of exudates is complicated by the soil medium that contains the roots. Root washings which may contain dead root tissue, microbial rhizosphere products, and other transformation chemicals are often obtained by treating the soil with a solution of water or organic solvents using a "stair step apparatus" or direct extraction (Horsley, in press). Isolating the source of the allelochemical is obviously difficult using these techniques. Further, soil adsorption may complicate the determination of how much exudate is plant produced. Tang (1986) described a number of early attempts to collect root exudates as well as some recent innovations which have had varying levels of success. They pale by comparison to a system developed by Tang and Young in 1982 called the Continuous Root Exudate Trapping System (CRETS). As described by Tang (1986), CRETS is a method for the collection of natural products from an undisturbed root system. The approach is quite simple and is capable of producing sufficient quantities of rhizospheric exudate for chemical analysis and bioassay (Figures 5 and 6).

Donor plants are grown in a sterile sand/bluerock substrate. A nutrient solution is circulated through the substrate and an Amberlite XAD-4 resin which adsorbs and accumulates all the hydrophobic and partially hydrophobic compounds which are soluble secondary metabolites, i.e., allelochemicals (Tang, 1986). The plants' primary chemicals, which are hydrophilic or insoluble, pass through the system. Bioassays can then be conducted with plants treated with effluents receiver containing hydrophobic plus inorganic compounds or organic compounds only. Growth differences and symptom development are attributable to presence of hydrophobic the the allelochemicals (Horsley, in press).



The root exudate recirculating system. A = silica sand, B = crushed basaltic rock, C = glass wool, D = perforated Teflon disk, E = robber stopper wrapped with Teflon sealant tape, F = glass tubing, G = Teflon sleeve connector, H = glass tube, I = Teflon tube to air pump, J = vermiculite. K = perforated Teflon tube. Arrows indicate direction of flow. A glass column containing XAD-4 resin was attached to the bottom of the donor pot for resin controls

Figure 5.--Root Exudate Recirculation System.

Source: Tang, C. S. 1986. Continuous trapping techniques for the study of allelochemicals from higher plants. In: Putnam and Tang (eds.), p 113-131.



Figure 6.--Root Exudate Trapping System (Donor).

Source: Tang, C. S. 1986. Continuous trapping techniques for the study of allelochemicals from higher plants. In: Putnam and Tang (eds.), p 113-131. Residue decomposition. At this juncture of the science's progress, there are no definitive techniques to differentiate between the donor plant residue, transformation products, and microbial natural products in the soil. As with root exudates, it is difficult to extract allelochemicals from the soil without the possibility of producing artifacts (Putnam, 1985).

The following are examples of ways to test for residue decomposition products in the soil. Fisher et al. (1978) extracted phytotoxins by leaching putrefied herbaceous residues and then used the effluent as a soil moisture source. These authors also placed residue on the soil surface and watered to simulate field conditions. Walters and Gilmore (1976) incorporated fescue leaves and roots into the sand substrate of the donor pots of a stairstep design which was then leached and carried into the receiver pots.

Because microorganisms appear to play such an important role in the array and quantity of natural products present in the soil, testing in sterile strata has limited value in determining the cause of inhibition in field situations (Horsley, in press). He also suggests that organic materials, such as glucose, excelsior, and chromatography cellulose be used in controls rather than horticultural peat, which can

distort the test results, i.e., through nitrogen immobilization.

I'm unaware of any studies that used actual field soils and compared them with sterile soils with added allelochemicals to determine the difference that microorganisms produce during inhibition. All studies that tested for soil natural products activity used "sterile" soils, with the implication that microorganisms produced activity once organic matter was introduced.

Allelochem Isolation and Characterization

Putnam (1985) detailed techniques that are used to separate chemicals, such as partitioning on the basis of polarity, molecular size, or adsorptive characteristics. Various chromatography methods are used also. In the past, detection of specific functional groups was the norm, whereas a series of spectroscopic analyses is in current usage.

The use of bioassays at each step in the process of isolating and identifying natural products is emphasized and then diagramed by Leather and Einhellig (1986). Horsley (in press) questions the value of standard bioassays in the purification process and their Correlation with natural conditions. He suggests that new bioassays be devised that preserve the original Symptoms and are sensitive, repeatable, quantitative, fast, easily performed, and use tissue of the susceptible species. Electrolyte leakage from leaf disks, cell cultures, or protoplasts of susceptible plant leaves may be favored techniques. Unfortunately, Horsley did not describe these latter approaches, and they might be useful in dealing with allelochem concerns in large ornamental trees.

Bioassays--Types

Leather and Einhellig (1986, 1988) provided the only comprehensive discussions of bioassays in the literature, but even these papers give minimal insight into the topic. The authors categorize bioassays into sections on seed germination, plant growth and development, and microbes, etc., and their views are the basis for this section.

Seed germination. Many papers alleging allelopathic activity used seed germination bioassays to confirm field observations, but in many, if not most cases, there was little correlation. Further, there was little standardization governing the bioassays.

However, seed germination has been the bioassay of Choice historically since field observations supported the view that absence of a species in an area was due to inhibition of germination of its seed (Rice, 1984). Other positives for germination bioassays include species

availability of seed, simplicity, rapidity, and the relatively small volumes of solution necessary.

In general, these bioassays are conducted in Petri dishes by placing the seed on substrate (e.g., sand, felt, sponge, filter paper) saturated with the test solution. Incubation, which includes light/dark sequences, is usually done, too. Germination is usually defined as the emergence of the radicle 2 mm beyond the seed coat over time.

number of There are а variables. such as that affect germination, but temperature, osmotic potential seems to be a unique problem in seed bioassays, not explained in the literature. Whatever the basis for the problem, Leather and Einhellig (1986) reported that osmotic potentials greater than 75 milliosmoles inhibited early radicle growth and pressures greater than 150 milliosmoles may delay germination. Therefore, osmotic adjustment to the controls must be used.

Another concern expressed by del Moral and Cates (1971) is the importance of using local seed sources, especially when doing patterning studies. The work by Gliessman (1976) on the regional adaptation of bracken fern allelochems to the localized habitat seems to support the seed-source view.

<u>Radicle elongation</u>. Radicle elongation is a more sensitive assay for allelochems than seed germination (Leather & Einhellig, 1988). As with germination, there is extreme sensitivity to high (100 mosmol) osmotic potentials. Because of the crooked growth of radicles, measurement is difficult and often unreliable. A technique developed by Putnam (Leather & Einhellig, 1986) has improved measurement accuracy. A plate is placed in contact with the radicle and marked at the beginning and end of a 24-hour growing period. Measurements are made directly from the plate.

According to Leather and Einhellig (1988), radicle afford elongation does greater possibilities for mechanism studies than seed germination. It is particularly well suited for determining effects of allelochems on cell growth hormones as well as on respiration and cell division.

Lemna bioassays. Leather and Einhellig (1988)

described a recent addition to the bioassay arsenal. The <u>Lemna</u> species (duck weeds) are angiosperms that provide a versatile and extremely sensitive assay for phytotoxicity. Photosynthesis and overall respiratory metabolism are particularly sensitive to natural product effects. Relating the results of this bioassay, however, to terrestrial plants does pose some drawbacks.

<u>Seedling growth and development</u>. As described by Leather and Einhellig (1986, 1988), seedling growth assays are more sensitive than germination tests, and because they use relatively easy dry weight and growth measurements, they are less tedious and more reliable than radicle tests. A variety of mechanism studies are possible using this technique, such as nutrient uptake, water relations, and photosynthesis. The downside to this test's use is that it requires a greater quantity of chemical than is usually available during initial isolation and identification of allelochemicals.

<u>Miscellaneous bioassays</u>. There are a number of assays which are applicable to ornamental plants that require special note.

First is the Stairstep Method. This method is intended to differentiate between competition and allelopathy. Walters and Gilmore (1976) and Horsley (1977a) used and described this system (Figure 7). Four tiers of pots are arranged so that the donor plants are on the top and third row, while the receptor plants are on rows two and four. A control set of pots consisted of receptor plants on all four rows. Nutrient solution is circulated from pot one (top) to pot four (bottom) sequentially. Allelopathy is indicated if the receptor plants (donor/receptor series) grow less than their



Figure 7.--Stairstep Method.

Source: Walters, D. T., and A. R. Gilmore. 1976. Allelopathic effects of fescue on the growth of sweetgum. Journal of Chemical Ecology 2: 469-79. control counterparts (receptors only) (Horsley, in press). Conversely, competition is suggested if the receptor plants on row four of the donor/receptor test grow at a lower rate than on row two of that series with respect to the controls. In their tests, Horsley (1977a) showed a reduction in the growth of black cherry from root washings of fern, goldenrod, and aster, while Walters and Gilmore (1976) produced growth inhibition in red gum from fescue allelochems.

Van Sambeek (1990) and his colleagues have developed modified stairstep approaches in which a vacuum system pulls leachates from under grass sods in large wooden boxes. The leachates are then added to the soil surface of the receiver plants. In a second version, an in vitro test using micropropagated plantlets of black walnut is used, since both seed and seedling bioassays have been impractical for testing for phytotoxins that inhibit black walnut growth.

The second technique is the Split-Root Technique. This is another useful technique used to differentiate between allelopathy and competition utilized by Buchholtz (1971) and Peters and Luu (1985). The basic approach involves the slicing of a single root of a plant or the root system of a plant "clump" and placing it on the edge of two adjacent containers. The plant's split roots are nourished by a nutrient solution in one container and

distilled water in the other. By varying the position of donor and receptor species, the operable interference mechanism can be determined.

Both studies mentioned were able to show that ample availability of nutrients was not able to overcome the inhibition apparent from allelochems of the donor plants. The tests with two receiver plants grown together showed growth suppression typical of competition but not the additional reductions from natural products.

Last is Nitrogen-Fixation Assays. Larson and Schwarz (1980) were concerned about the possible reasons for inhibition of black locust and black alder by common allelopathic grasses and forbs. They suspected allelochem damage to mycorrhizal fungi with resultant reduced nodulation and N-fixation rates.

"Typical" bioassays were set up with the receiver species growing in containers in a greenhouse with donor leachate added in prescribed doses. In addition to the height and weight variables, N-fixation was checked to determine the mechanism of action on intact plants. Chambers were placed over the plants and a procedure which makes use of the capability of nitrogenase to reduce acetylene to ethylene in proportion to the fixation of atmospheric N was used. Nodules were also counted after harvest as additional evidence.
<u>Comments</u>. While the aforementioned review of bioassay methods shows their importance in implicating allelopathy, proof in large trees has been difficult. Leather and Einhellig (1986), while addressing the future of natural product research, pointed to the need for standardizing bioassays so that the results can be related to field observations. While this is applicable to all areas of allelopathy research, the use of advanced technology, such as tissue cultures, should promote advancements in understanding the involvement of allelochemicals in large ornamental plants.

CHAPTER IX

IMPLICATIONS FOR URBAN FORESTRY/HORTICULTURE

Ecological Right-of-Way Management

utility corridors Transportation and encompass immense acreages in this country. The infrastructure vegetation is usually intensively managed. Although ornamental plants are not considered in this section, urban foresters and companies specializing in arboriculture are very involved in right-of-way (ROW) management. It is my opinion that allelopathy will be an integral part of future management concepts.

Based on my 25 years of involvement in this field, it appears that early construction of roads and highvoltage transmission lines destroyed vegetation and landforms. Subsequent maintenance of these facilities was frequently heavy-handed in the use of both mechanical cutting equipment and broadcast chemical sprays to severely limit or eradicate herbaceous and woody plants.

More recently, political pressure and financial constraints have prompted agencies to consider environmental and aesthetic concerns. Although not in widespread use presently, there is increasing awareness among professionals of the need to incorporate ecological

principles into management strategies. Putnam (1985) challenged forest scientists to exploit allelopathy in ROW management in hopes of reducing herbicide use. Unfortunately, it is doubtful that many managers are aware of the role that allelopathy plays in plant regulation. This section addresses that void.

The eminent ecologist, Elroy Rice, has provided the scientific basis for the consideration of allelopathy as a primary element in ecological management of right of Rice and his colleagues have dedicated their ways. careers to understanding old-field succession which is analogous to many right-of-way situations. In contrast to Rice's basic ecological research, the works of W. C. Bramble, concentrate on the more practical aspects of applied ecology by identifying species, and measuring and classifying plant communities. Both approaches seem meritorious. Between these extremes are the works of Horsley and Fisher and his associates.

The development and maintenance of a low, stable plant cover which resists tree invasion is an important goal in right-of-way management (Bramble, 1980; Bramble et al., 1990). In natural systems, environmental conditions, such as precipitation patterns, fire frequency (Petranka & McPherson, 1979), edaphic factors, and deer browsing (Horsley, 1987) have important roles in the establishment and maintenance of old-field systems. Allelopathy has a major influence, too, on old-field creation and continued regulation (Rice, 1987). Manipulated systems, such as a right of way, are subject to many of the same successional factors and processes as old fields.

Depending on the region (environment) and site (edaphic factors), allelopathy may regulate succession in one of several ways: toxicity between later and earlystage plants (Rice, 1984); autotoxicity, allowing laterstage plants to replace the earlier ones (Rice, 1984); inhibition of tree-root mycorrhizae necessary for growth (Horsley, 1983); and control of microorganisms which transform nitrogen to the form needed by a particular plant species (Horsley, 1983).

In his work on prairie succession in Oklahoma and Kansas, Rice (1984, 1987) recognized four stages: a pioneer weed stage that persists for 2-3 years, an annual grass stage that continues for 9-13 years, a perennial bunchgrass stage that remains for 30 years or longer after abandonment, and the climax prairie.

The second-stage dominant, <u>Aristida</u> <u>oligantha</u> is able to invade because of its resistance to allelochem inhibition by pioneer-stage plants. Because <u>A. oligantha</u> inhibits growth of <u>Rhizobium</u> nitrogen fixers, available nitrogen is lacking for the needs of higher stage plants. This enables it to delay succession and its own demise. Rice and Pancholy (1973, 1974) believed they had strong evidence which indicated that nitrification was slowed in the later stages of succession. As available nitrogen eventually increased in concentration, later species with higher nitrogen requirements could invade.

Rice (1984) further discussed the nitrogen cycling role of allelopathy in depth and Horsley (1983) and Putnam and Weston (1986) synthesized this very complicated subject. Although some ecologists disagree with Rice on the subject (Rice, 1984; Hoagland & Williams, 1985), his works are necessary reading for an understanding of this topic.

Other authors described situations similar to Rice's but with different herbaceous plants in other places. Asters and goldenrods in Ontario and the Allegheny Hardwood Forest dominate forest openings for 60 years or more with little tree invasion (Horsley, 1987; Fisher et I have noted abandoned fields in southern al., 1978). Michigan infested with aster and goldenrod that have remained as stable, fallow land for many years. Many of these same fields are inhabited by tall fescue and quackgrass, which are known toxin producers (Putnam & Weston, 1986; Walters & Gilmore, 1976). Although stability and timeframes were not investigated, Brown (1967) described low-growing vegetation that inhibited the establishment of jack pine in Upper Michigan. Norby

and Kozlowski (1980) determined that red pine may be repressed in its growth by aster and goldenrod.

Another way that herbaceous vegetation excludes woody plants allelopathically is by interference with the symbiosis of mycorrhizal fungi and tree roots (Horsley, 1983). Perry and Choquette (1987) suggested that a very high percentage of forest trees form mycorrhizal relationships which are essential to normal growth. The evidence indicates that allelochems play a role in survival of mycorrhizal fungi in the soil, their ability to form large populations, and their functioning once established (Horsley, 1983). Persidsky et al. (1965) noted that prairie soils act as storehouses of toxic excretions of grass roots, or by-products of root decay, which being accumulated in a high concentration may preclude the survival of free-living symbionts of trees.

There are some tree species noted in the literature that are associated with old-field ecology. Sassafras is an early invader of abandoned farmlands and can remain as a stable clonal inhabitant for a century (Gant & Clebsch, 1975). Black locust (<u>Robinia pseudoacacia</u>) is also allelopathically maintained in stable, pure stands according to Waks (1936). I have observed <u>Crataegus</u> scattered as the lone tree species in old fields in southern Michigan. It is possible that the large amounts of cyanogenic glucosides produced by Crataegus seeds

(Evanari, 1949) may interfere with herbaceous growth, thus allowing the hawthorns to establish and thrive.

The encouragement and maintenance of sassafras, black locust, and hawthorn would often be compatible with ROW management. Conversely, discouraging the infringement of sumac may be advisable, as Petranka and McPherson (1979) found that <u>Rhus copallina</u> was a necessary preceder of tree invaders in prairie-forest ecotones in Oklahoma. While excluding sumac from areas where trees are inappropriate, the planting of sumac in protected areas of a highway ROW, such as a ditch backslope, would enhance tree invasion and growth.

For the ROW manager, the preceding background is important to the understanding of old-field succession, although nitrogen cycling and mycorrhizae are not quantifiable under field conditions. However, cognizance of site conditions (e.g., poor drainage, high colloidal and low humic soil content) which magnify allelochem concentrations and a knowledge of species that are copious donors of toxins is a prerequisite to ecological manipulation.

In addition to the allelopathic grasses, forbs, and ferns mentioned throughout this thesis, Putnam and Weston (1986) listed 90 common agroecosystem weeds with alleged allelopathic potential (Table A.6). Their presence, especially in large areas of the right of way, should

alert the specialist to the possible benefits of their retention as nontarget species during chemical spray operations. Bramble et al. (1990) listed some additional herbs and shrubs, such as panic grass (<u>Panicum spp</u>.) and blueberry (<u>Vaccinium spp</u>.) that resist tree invasion, as well as some that do not.

The approach used by Bramble et al. (1990) to determine the stability and tree invasion resistance of species is probably the most useful to managers. Cover types were developed based on the kind of maintenance techniques to be used as well as the indigenous species Various ROW treatments of target and composition. species (e.g., hand cutting, selective basal sprav, broadcast pellet application, etc.) were performed on the different cover types and the results were classified as high, variable, and low in their resistance to tree Blueberry, fern, and fescue were highly invasion. resistant, while blackberry (Rubus alleghaniensis) and witchhazel (Hamamelis virginiana) were low in resistance. It appears that the use of Bramble's method by ROW specialists is the most practical in implementing ecological management of right of ways. This approach is silvicultural techniques familiar similar to to environmental, foresters. Along with site. and competition factors, allelopathy is added to the

management equation to make it increasingly accurate and valid.

Ornamental Planting in Right of Ways

The landscaping of interstate highways and utility corridors in and around cities is an effort to make infrastructure development and use more compatible aesthetically and environmentally for users and adjacent landowners. The planting of trees and shrubs on fallow right-of-way land is also applicable to other green-space sites, such as low-use/maintenance parks.

An understanding of allelopathy as it relates to the establishment and culture of woody plants on fallow land is necessary to both short-term and long-term ornamental management. While consideration of allelopathic influences in this milieu is virtually unknown in practice, the literature is rife with research results, albeit addressed to other questions, that implicates its role and importance.

In my opinion, it is in this area that the most immediate and fruitful advances can be made related to allelopathy in ornamental systems. Further, the literature this topic provides on the strongest foundation for authoritative hypotheses and conclusions regarding ornamental plants and allelopathy.

As with ecological right-of-way management, oldfield ecology is the basis for dealing with ornamental right-of-way landscapes. The distinction between the two pivots on the enhancement or repression of allelochems. For ecological management, allelopathy is utilized to exclude invading trees and shrubs. In ornamental management, the goal is to mitigate allelopathic effects on planted trees. Put another way, donors are encouraged at the expense of the receptor species in the former case, while donor eradication is necessary for the sake of the receptor in the latter case.

As with ecological ROW management, allelopathic influences on ornamentals are donor species and site dependent. However, early allelopathic successional processes that influence invasion, e.g., germination and seedling growth, are not relevant to ornamental establishment, although they may be later in regard to nitrogen cycling.

Goldenrod, aster, fern, and tall fescue have all been implicated as allelopathic inhibitors of tree seedlings, as well as older trees (Fisher, 1987; Horsley, 1977a, 1987; Walters and Gilmore, 1976; and Norby and Kozlowski, 1980). Quackgrass, which is highly inhibitory to corn (Buchholz, 1971) and legumes (Weston & Putnam, 1986), is a common constituent of old fields and right of

ways in the Lake States, and should be suspect in ornamental inhibition.

Early studies (Brown, 1967; Fisher, 1980) implied that allelopathy only influenced patterning and regeneration by inhibiting seed germination. But polyacetylenes produced by goldenrod and asters (Numata et al., 1973) apparently operate by using some mechanism of action other than inhibition of seed germination. Horsley (1977a) and Fisher et al. (1978), for example, observed allelochemically induced slow growth in larger trees under field conditions that was also shown by seedlings.

Walters and Gilmore (1976), while not identifying the toxins in fescue, determined the mechanism of action to be nutrient uptake inhibition of nitrogen and phosphorus in the receiver plant (10-year-old sweetgum). Black walnut growth was inhibited by fescue in the same manner (Ponder, 1986). Like fescue, quackgrass toxins produce phosphorus uptake inhibition (Buchholtz, 1971; Weston & Putnam, 1986).

Agropyrene is a polyacetylene produced by quackgrass (Grummer, 1961) which is classified by Rice (1984) in the same compound group as allelochems produced by <u>Solidago</u> and <u>Erigeron</u>. Although Grummer (1961) attributed antimicrobial action to agropyrene, Weston and Putnam (1986) found that quackgrass extracts inhibited root-hair formation in legume field crops rather than <u>Rhizobium</u> symbionts. The damage, however, resulted in the prevention of infection by rhizobia with subsequent growth reductions and nodulation (Putnam & Weston, 1986).

The foregoing studies suggest that old-field grasses forbs common to the Lake States region produce and allelochemicals that limit tree growth. Implication is also made that the inhibition mechanism may involve impaired root hairs and mycorrhizae, resulting in reduced nutrient uptake. Because so many trees have mycorrhizal dependence (Perry & Choquette, 1987), it is likely that many tree species, untested to date, may also be subject to old-field herbaceous vegetation toxicity. The evidence for allelopathy via a nutrient uptake mode is compelling, but not definitive. It is in this area that further research would benefit the science of allelopathy substantially.

dependence is the second factor Site which right-of-way influences allelopathic effects on ornamentals. This is not to say that all site situations are primarily regulated by allelopathy. Willow and cottonwood on wet, marsh sites, for example, are still regulated by edaphic and environmental conditions. It is within the necessary site parameters of a species that allelopathy functions, just as competition.

Horsley (1977a) pointed out the "poorly drained soils along stream bottoms or high flats underlain by fragipans" as constituents of the old fields he studied. However, it was the work of Fisher (1978) and Rietveld et al. (1983) that suggested that well-drained, lighttextured soils mitigate toxin presence, while poorlydrained, colloidal soils tend to build up and retain toxic compounds at damaging levels.

Based on available evidence, it is my opinion that tree growth can be inhibited by many old-field species, to varying degrees, and that site factors are secondary. To the practitioner, priority of cultural treatments should be directed initially to ornamentals planted on heavy-textured, poorly-drained sites.

The planting, establishment, and ongoing cultural care could be classified as successional and intrinsic design strategies. Successional plans are aimed at immediate visual impacts with the use of landscape plantings pending eventual successional attainment of advanced or climax forest types to meet landscape goals. Intrinsic plans involve the planting and maintenance of the original design throughout the life of the plants.

Because of the ecological stability of old fields, successional designs usually fail to meet their goals based on the predictable, ecological progressions experienced in a forest setting. One practical solution to this problem is the interplanting of trees with sumac (Petranka & McPherson, 1979). They found that sumac clones can encroach into prairie at the rate of 2.5 m/yr. and that forest trees follow.

Another tactic that can be used to attain the visual impact goal of successional designs is the use of "oldfield resistant species." Larson and Schwarz (1980) found that black alder resisted old-field weeds' allelopathic influences and sassafras (Gant & Clebsch, 1975) can invade old fields and develop large, long-lived clones. Ailanthus is another choice (Mergen, 1959).

The planting of traditional ornamentals in an intrinsic design requires the exclusion of "volunteer" with ecological trees. As ROW management, the perpetuation of a stable, herbaceous ground cover by selective removal of target plants (mechanical cutting spray or selective chemical and stump spray) is necessary. And obviously, sumac planting should be avoided.

Arborists readily recognize the unusually slow growth and apparent stagnation of ROW ornamentals after establishment, but competition for nitrogen is usually the diagnosis. Mulching and fertilization are the usual prescription for correction of the problem, but because this activity is labor intensive and costly, it is rarely

performed. The study of old-field ecology and experience working in this discipline have convinced this author while competition is certainly operable, that, allelopathy is the primary reason for stagnation of In fact, Walters and Gilmore ornamental tree growth. (1976) found that almost all interference of 10-year-old sweetgum by tall fescue was a result of natural product toxicity. The work of Fisher et al. (1978) with sugar maple, goldenrod, and aster also implied that allelopathy, and not competition, was the primary vehicle of interference with tree growth.

Although I am unaware of any direct research on the stagnation of ornamental plantings in right of ways, many parallel studies have been done on around cover interference in black walnut plantations. Von Althen (1985) studied an 8-year-old stagnating black walnut plantation in Ontario with a goldenrod, aster, and quackgrass ground cover during a 4-year period. Annual bareground simazine treatments resulted in 153% and 222% increases in diameter and height growth, respectively. and nitrogen fertilizer combinations added Simazine minimal growth compared to simazine alone.

Schlesinger and Van Sambeek (1986) attempted to revitalize two black walnut plantations in Illinois that were 10 and 17 years old and had tall fescue ground covers. Annual cultivation in both stands over 5 and 3

years, respectively, yielded a 69% diameter increase in the younger stand and little increase in the older stand, compared to controls. Their study did not differentiate between interference mechanisms but pointed to the work of Ponder (1986), and Rink and Van Sambeek (1985) in confirming that tall fescue leachates do interfere with black walnut growth.

Both studies by von Althen, and Schlesinger and Van Sambeek make salient points about right-of-way ornamental growth and culture. First, ornamentals with old-field ground covers that do not receive cultural treatments after establishment will probably be affected adversely by interference mechanisms. For a period of perhaps 5 to 15 years after establishment, growth rates would be expected to decline and result in stagnation which may be irreversible. Die-back problems and mortality increases would most likely follow.

Secondly, cultural treatments after establishment are necessary to attain the design goals and maintain plant vigor. Lack of treatment may result in the lack of achievement of goals and a waste of capital investment as plants stagnate and die.

Thirdly, allelopathy appears to be the primary mechanism and not competition (contrary to von Althen's interpretation). This distinction is very important because adding fertilizer to improve growth will be to no

avail as it is ground-cover allelochems that disrupt normal nutrient uptake through the roots.

And lastly, marked improvements in growth can be achieved by eradicating ground covers with herbicides rather than costly and time-consuming mulching and fertilization. By identifying the causative factor, clarifying its role in plant interference, emphasizing its importance in tree growth and survival, and pointing to the relative ease of solving the problem, practitioners may see the value of post-establishment treatment and implement weed control programs. Ironically, herbicides will resolve both allelopathic and competition problems (Ponder, 1986; Fisher, 1980) while reducing the need to fertilize.

Another tactic in intrinsic design would be the use of "self-herbiciding" species where follow-up care is not feasible after establishment. Species, such as black locust (Larson & Schwarz, 1980) and ailanthus (Mergen, 1959), which are unlikely to invade old fields, could be established as ornamentals. Clones of these species are very resistant other plants' to invasion and Lodhi (1976, 1978) found a paucity of interference. herbaceous plants under sycamore, hackberry, and red and white oaks in lowland forest resulting а from interference by the trees' natural compounds. Whether these trees would be toxic to old-field ground covers is

speculative, but the notion that they might eliminate interfering understories after establishment is fascinating.

A final intrinsic design tactic would be the use of genotypes that are resistant to allelochems produced by old-field grasses and forbs. Rink and Van Sambeek (1985, 1987) are pursuing that goal in black walnut and white ash plantation management in order to minimize the need for cultural treatments.

Shade Tree Management

The purpose of this section is to synthesize the preceding information into a cogent text on shade-tree management and allelopathy. It should provide a basis for learning by professionals and focus on potential areas of research. Consideration will be given to residential street and private-property trees as well as central-city tree sites.

Recognition of Allelopathy

I have attempted to point to research which implicates allelopathy as a credible factor in shade tree physiology. The works of Gabriel (1975), Fisher (1978), Reitveld et al. (1983), Ponder (1987), Walters and Gilmore (1976), Schlesinger and Van Sambeek (1986), Horsley (1977a, 1983), Peterson (1965), and Jobidan and Thibault (1981) provide descriptions of observations as well as field and laboratory research related to allelopathy in larger trees. Reference is made to Chapter IV for details.

It was not the large-tree studies that convinced the author of allelopathic involvement in shade trees; rather, it was mode-of-action. The emphasis in much of the literature, particularly agriculture and ecology, revolves around seed germination and seedling growth. That emphasis implies a role, primarily, in regeneration. However, Einhellig (1986), Hoagland and Williams (1985), and Balke (1985) pointed to dysfunction in the nutrient uptake of plant roots resulting from allelochem influence on root cells, mycorrhizae, or rhizospheric flora as an important mechanism in plant growth inhibition.

Horsley (1983), Brown and Mikola (1974), Einhellig et al. (1985), Walters and Gilmore (1976), Buchholtz (1971), Weston and Putnam (1986), Putnam and Weston (1986), Peterson (1965), and Ponder (1986) provided convincing evidence that this mode-of-action is a powerful inhibition process. There is no reason to believe that this mechanism cannot be operable in large tree roots as well as in tested seedling roots, and it could explain growth repression in larger plants. Refer to Chapter VII for a more thorough explanation of allelopathy and nutrient uptake. As allelopathy gains recognition among woody-plant specialists, there may be increasing peer pressure to reassess "competition" studies because of the absence of an evaluation of possible allelopathy (see pages 25 and 26). For the purposes of this thesis, competition studies are viewed as interference research with implications and interpretations for allelopathy, too.

These three aspects--large tree studies, research in and nutrient uptake, the incomplete nature of interference work--lead the author to suspect that allelopathy has an important role in shade tree management.

Interference in Shade Trees

Anyone who has looked at a large elm stump in a city and observed the wide growth rings might wonder if interference affects trees at all, either competitively or allelopathically. It is possible that some large, mature trees have such extensive and deep root systems and sufficient biomass that they are unaffected by any interference variables. But for smaller and/or younger shade trees and shrubs, both interference mechanisms most likely affect them.

Tree-tree interactions have not been commonly documented in the past, but they do occur. For example, balsam poplar (Populus balsamifera) affects green alder

(<u>Alnus crispa var. mollis</u>) according to Jobidan and Thibault (1981). Black walnut antagonism has been reported in white birch (Gabriel, 1975), black alder (Reitveld, et al., 1983), and red and white pines (Fisher, 1978). Compatibility testing for trees is even less reported, but Ponder (1987) noted that black walnut did not affect autumn-olive (<u>Elaeagnus umbellata</u>).

Turfgrasses in highly maintained lawns, as well as grass and broadleaf weeds in low maintenance areas, are the more probable donors of toxins in woody-plant inhibition. Perennial ryegrass (Lolium perenne), red fescue (Festuca rubra), and Kentucky bluegrass were reported to be allelopathic to forsythia and flowering dogwood (Fales & Wakefield, 1981). Tall fescue is an inhibitor of growth in sweetgum (Walters & Gilmore, 1976) and black walnut (Schlesinger & Van Sambeek, 1986). On the other hand, Kolb (1988) determined that Kentucky bluegrass did not affect northern red oak and tulip popular allelopathically.

Poorly maintained turf areas may contain weeds with allelopathic potential. Familiarity with the species listed by Putnam and Weston (1986) should provide a basis for consideration of possible natural product conflicts (Table A.6). I have observed many examples of downtown planting sites where wild carrot, chickory, ragweed, chickweed, goosegrass, quackgrass, ragweed, and crabgrass

dominated the ground cover at the trees' base. All these plants are common allelopaths in agricultural systems (Putnam & Weston, 1986) and should be suspect when growing with woody plants. Wild carrot, for example, has been implicated as an inhibitor of growth in black locust (Larson & Schwarz, 1980).

In spite of many well-documented reports about the negative effects of turfgrass on tree growth, lawns continue to dominate the urban landscape (Green & Watson, 1989). Competition for water, nutrients, and space, along with possible allelochem toxicity make the presence of lawns a potential bane to tree health and vigor.

Harris (1977) showed that diameter and height growth were positively influenced in <u>Eucalyptus</u> <u>camaldulensis</u> and <u>Magnolia</u> <u>grandiflora</u> when released from bahiagrass and alta fescue, respectively, and fertilized. Turf removal had a greater influence on diameter growth, whereas fertilizer had more of an affect on height growth. Hensley et al. (1988) obtained similar growth increments and patterns in their study of <u>Magnolia</u> <u>grandiflora</u> growing with a tall fescue ground cover, except that mulch was used instead of herbicides.

Green and Watson (1989) studied the effects of unnamed turfgrass species and mulch on the establishment and growth of bare-root "Green Mountain" sugar maples.

Mulched trees had 2.5 times more diameter growth and 75% more crown development than grass controls.

Root density in seven common ornamental shade tree species was compared between bare soil, mulch, and grass treatments (Watson, 1988). Compared to grass controls, fine-root development in bare-soil treatments ranged from a -8% to 113% while mulching resulted in a 6% to 195% increase.

The results of the preceding turfgrass-woody plant studies were attributed to competition. That competition interfered with tree growth without toxin influences is doubtful. The lack of natural product testing leaves the conclusions uncertain.

Fales and Wakefield (1981) have provided the only credible interference research which differentiates between competitive and toxin factors in turfgrass/ woody-plant interactions. Flowering dogwood in turf-free plots had greater diameter growth than in plots with turf that were subsurface fertilized and irrigated to compensate for competition.

Whether interference of tree growth by turfgrasses results from competition or allelochemicals, and to what degree, is open to discussion. However, if some form of nutrient uptake allelopathy is the operable mechanism, then surface fertilization may be costly and/or futile, as turfgrass phytotoxins can interfere with tree-root abilities to absorb minerals.

In spite of all the evidence pointing to the disadvantages of trees growing with turf, there remains an intractible marriage between the two in American culture. Green and Watson (1989) state the problem well.

It is difficult to overcome the common expectations of landscapes with manicured lawns right up to the base of every tree. This presents a challenge to landscape professionals to make attractive landscapes without grass around trees.

Where mulch is not acceptable, shrubs and perennial ground covers might be an appropriate alternative.

If turf cover is mandatory, an awareness of allelopathy should provide additional impetus for deep watering and feeding care, especially for younger and smaller plants, to encourage two-tier root systems with minimal interference.

Environmental Influences

In addition to the intensive interference from turf and weeds, ornamental trees and shrubs exist in an environment where soils disturbed, are typically compacted, and structureless compared to the well developed soils with litter layers in forests (Watson, 1988; Fraedrich & Ham, 1982). There are no allelopathy studies on urban soils to my knowledge. Instead, the works of Fisher (1978, 1987) and Reitveld et al. (1983)

provide the basis for understanding allelochemical-soil interactions and their effects on woody plants. The works of Rice (1984) and Einhellig (1986, 1987) establish the background on environmental stress and physiological responses. Portions of Chapters VI and VII are used as references for this topic.

The interdependence of allelochems, environmental stress factors, and edaphic elements makes a cause-effect relationship for allelopathy difficult to determine and explain simply. Components of allelopathy that are relevant to shade tree environments, as well as their relative importance, will be discussed.

After ascertaining the species and donor-receiver roles, biomass and proximity should be considered (Rietveld et al., 1983). They studied a black alderblack walnut plantation which grew satisfactorily in its early stages. Then from ages 8-13 abrupt and rapid decline and death occurred in the alder, in part because substantial amounts of juglone were introduced into the soil by the larger walnuts. The more common possibility, however, is ground cover antagonism to woody plants. Complete tree root-zone coverage over a number of years by the donor turf could cause interference compared to short-term, minor coverage.

Leachate quality and quantity varies as vegetation condition and seasons change (Petranka & McPherson, 1979;

1978; Dormaar, 1970; Fisher et al., 1978). Lodhi. Senescent foliage and decaying litter, as a rule, produce more potent phytotoxins than actively growing, early season foliage. Walters and Gilmore (1976) found that decaying tall fescue litter was much more inhibitory to sweetgum than green foliage. One could speculate that frequently cut lawns with little thatch buildup would produce relatively small amounts of benign toxins. On the other hand, poorly maintained sites, such as vacant lots and passive park areas, may develop a substantial layer of decaying litter resulting from infrequent mowings which produce large quantities of effectual inhibitors.

Under field conditions, single toxins are rarely responsible for inhibition (Rice, 1987; Einhellig, 1987). In fact, a specific compound may be present below its threshold for inhibition and still be active by its acting in concert with other allelochemicals. It is conceivable that mixed stands of grass and broadleaf weeds could contribute a variety of relatively toxic compounds that additively or synergistically achieve the threshold for inhibition in a receiver.

Allelochem production in the donor plant is also influenced by stress. Various allelochems may either increase or decrease in quantity when subjected to nutrient deficiencies, and water or temperature extremes (Loche & Chouteau, 1963; Rice, 1984; Martin, 1957). Removal of highly allelopathic weeds, such as tall fescue, quackgrass, wild carrot, and foxtail from downtown tree pits might be considered a higher priority during hot, dry periods because of the possibility of higher toxin concentrations. The same stresses that promote natural compound production in donors reduce the threshold level for damage in the receiver plant (Einhellig, 1987).

Mitigation of Allelopathy

In ornamental systems, almost all donor plant toxin production is made available to receptor plants via the soil. Thus, the fate of allelochemicals in the soil is of paramount importance. Fisher (1978, 1987) and Reitveld et al. (1983) found that poorly-drained, high clay-content soils produced severe dieback or mortality in red and white pines from juglone produced by black walnut. Conversely, pines growing on well-drained sandy soils showed no damage. These results are probably critical to understanding allelopathy in urban soils.

Clay (colloidal) soils adsorb most allelochemicals potentially available for uptake by a receptor plant (Fisher, 1987). Because clay soils drain poorly, leaching of toxins is minimal (Norby & Kozlowski, 1980), thereby enhancing allelochem pool size. The wet-moisture

also limited oxygen necessary for the regime by aerobic microorganisms decomposition of toxins (Fisher, 1987; Horsley, in press). Persistence may a result of adsorptive bonding as well. accrue as Conditions in well-drained, coarse soils resulted in dissipation of toxins below threshold levels. Thus, to avoid plant antagonism in urban soils, provision must be made for well-drained, sandy loams that are well aerated contain active microbial populations. and Poorlydrained, compacted clay soils should be considered "atrisk" sites and it might be prudent to assess the species and stress factors that were reviewed previously to evaluate the potential for allelopathic problems.

Correction of allelopathy in urban soils is consistent with efforts to remedy other associated problems by the use of traditional cultural treatments. Clarification and emphasis of allelopathy's role and importance may provide additional weight for implementing treatment and establishing priorities.

The eradication of all herbaceous plants that could be potential donors is obvious. That step is universally accepted for newly planted trees to prevent competition. Chemical weed control or mulching with organic or inorganic materials can rectify both interference problems. Herbicides are acceptable when used by competent applicators, especially when treatment resources are limited. While tree growth is not as dramatic as with organic mulching, bare-ground treatments are substantial improvements over turf cover (Watson, 1988).

Inorganic mulches also solve both competition and allelopathy concerns, although the initial cost and time are extensive. However, replenishment and heterotroph fertilization are minor concerns. Organic mulch is the recommended choice by the author. Besides control of interfering turf, organic mulch increases infiltration, reduces evaporation, and increases soil organic matter, resulting in improved soil structure, water holding capacity, and nutrient availability (Watson, 1988). The reduction of stress factors mitigates toxin production and lowered threshold levels (Einhellig, 1987). The increased microbial populations fostered by the presence material could of organic result in more rapid decomposition of phytotoxic compounds (Fisher, 1978; Horsley, in press).

In an effort to mimic forest conditions, mulching a relatively large area (out to the dripline) around trees could establish a larger zone which is conducive for root growth and provide ultimate long-term benefits for tree growth and vigor (Fraedrich & Ham, 1982). Obviously, the eradication of all ground-cover donors will result from this practice.

Mulching during establishment is a standard planting practice. However, the continued use of organic mulch following establishment can be important to plant health for many commonly recognized reasons, as well as the control of allelopathic factors. The works of Watson (1988) and Fraedrich and Ham (1982), using established ornamental shade trees (20 years old and 2 1/2" to 6" diameters) indicated significant growth increases in organic mulch plots compared to grass control plots. Top growth and root development were both affected positively.

The duration of continued mulch treatment is open to question, but is most likely determined by site as well as receptor species and potential donors. For example, infestation by potent species, such as tall fescue, may require long-term control to prevent severe growth inhibition (Schlesinger & Van Sambeek, 1986). And trees on compacted clay sites may require continuous treatment to repel any invading ground covers as well as minimize stress factors and encourage the microbial breakdown of toxins (Fisher, 1978). A tree-tree conflict, such as walnut and white birch, may require increased mulch treatment as the trees age and add biomass.

Three additional theoretical possibilities exist for dealing with allelopathy. The first involves the breeding of trees for allelochem resistance (Putnam,

1985; Rink & Van Sambeek, 1987). Secondly, mycorrhizae could be added to soils to reduce toxicity effects (Perry & Choquette, 1987). Lastly, foliar fertilizer spraying could be done, similar to spraying for iron deficiency in pin oak (<u>Quercus palustris</u>), thereby bypassing nutrient uptake damage from allelochems.

Landscape Design

This unit is intended as a resource for designers and caretakers of ornamental plant systems for locating information on species conflicts and compatibilities. First, comments will be made about studies that have lists of tested species or review other topical works. A catalog of species common to designed landscapes and strongly implicated to be allelopathic by field and/or laboratory study will follow (Table 1). A list of ornamental plants with allelopathic potential is provided and is a compendium of studies reviewed by Rice (1984) and other authors cited in this thesis (Table 2). And lastly is a list of allelopathically compatible species (Table 3).

Fisher (1980, 1987) provided a one-page list (Table A.7) of some allelopathic plants important in forestry, the toxins they produce, and examples of plants they affect. He also reviewed allelopathy in the forestry literature. Bramble (1990) listed ground covers and

Receiver Species Reference Donor Species Tree-Tree Conflicts Black Walnut White pine Fisher, 1978 Red pine Fisher, 1978 Schreiner, 1949 Austrian pine Schreiner, 1949 Schreiner, 1949 Schreiner, 1949 Scotch pine Japanese red pine Schreiner, 1949¹ Japanese black pine Bruner, 19691 Bruner, 19692 Massey, 1925 Loblolly pine Shortleaf pine Apple Black locust Ponder, 1986 White birch Gabriel, 1975 Black alder Rietveld et al., 1983 Balsam poplar Green alder Jobidan & Thibault, 1981 Sassafras Boxelder Gant & Clebsch, 1975 Elm Gant & Clebsch, 1975 Silver Maple Gant & Clebsch, 1975 Black cherry Norby & Red pine Kozlowski, 1980 Brown, 1967 Jack pine* Tubbs, 1973, Sugar maple Yellow birch Tubbs, 19766 Tubbs, 19766 Tubbs, 19766 Tubbs, 19766 Black spruce White spruce Jack pine Tubbs, 1976⁶ Tamarack DeBell, 1979^2 Southern Red Oak Sweetgum Gambel Oak Ponderosa pine Harrington, 1981 Sargunova, 1969^{\perp} Birch & Aspen Larch*

Table 1.--Allelopathic Interactions

Donor Species	Receiver Species	Reference
Sycamore maple	Yellow birch	Mensah, 1972 ²
Apple	Autotoxic	Borner, 1959 ²
Monterey pine	Autotoxic	Chu-Chou, 1978 ²
	Shrub-Tree Conflic	ts
Heather	Euro. wh. birch Norway spruce	Handley, 1963 ³ Robinson, 1972 ³
Lambkill	Black spruce	Peterson, 1965
F	ern/Grass/Forb-Tree Co	onflicts
Bracken fern	Black cherry	Horsley, 1977a
Hayscented fern	Black cheery	Horsley, 1987
Interrupted fern	N. red oak	Hanson & Dixon, 1987
Wild carrot	Black locust	Larson & Schwarz, 1980
Tall fescue	Black locust	Larson &
	Black walnut Sweetgum	Ponder, 1980 Walters &
	White ash	Rink & Van Sambeek, 1987
Orange Hawkweed	Balsam Fir	Dawes & Marayolo,
	White pine	Dawes & Marayolo, 1973

Donor Species	Receiver Species	Reference
Foxtail	Populus spp.	Walker ₄ et al.,
	Loblolly pine	Gilmore, 1980 ⁴
Smooth brome	Populus spp.	Walker ₄ et al., 1982
Broomsedge	Loblolly pine	Priester & Pennington, 1978
	Black walnut Black locust	Ponder, 1986 Larson & Schwarz, 1980
Goldenrod	Jack pine Black locust	Brown, 1967 Larson & Schwarz, 1980
Goldenrod/aster	Sugar maple	Fisher et al.,
	Red pine	Norby & Kozlowski,
	Tulip poplar Virginia pine Black cherry	Haney, 19691 Haney, 1969 Horsley, 1977a
Perennial rye	Apple	Good & Hyrycz,
	Forsythia	Fales & Wakefield, 1980
	Dogwood	Fales & Wakefield, 1980

Donor Species	Receiver Species	Reference
Red fescue/ Kent. bluegrass	Azalea	Nielsen & Wakefield, 1978 ⁵
	Jap. barberry	Nielsen & Wakefield,
	Yew (hybrid)	Nielsen & Wakefield, 1978
	Forsythia	Nielsen & Wakefield, 1978
	Fl. dogwood	Nielsen & Wakefield, 1978
Colonial bentgrass	Azalea	Nielsen & Wakefield, 1978 ⁵
	Jap. barberry	Nielsen & Wakefield, 1978 ⁵
	Yew (hybrid)	Nielsen & Wakefield, 1978 ⁵
	Forsythia	Nielsen & Wakefield, 1978
Arizona fescue	Ponderosa pine	Rietveld, 1975 ²
	Tree-Understory Conf.	licts
Sycamore	Understory	Lodhi, 1976
Hackberry	Understory	Lodhi, 1976
Red oak	Understory	Lodhi, 1976
White oak	Understory	Lodhi, 1976

Donor Species	Receiver Species	Reference
Japanese red pine	Understory	Lee & Monsi, 1963
Eucalyptus	Understory	Del Moral & Muller, 1969 ²
Cherrybark oak	Understory	Hooks & Stubbs, 1967 ²
Swamp chestnut oak	Understory	Hooks & Stubbs, 1967 ²
Shumard oak	Understory	Hooks & Stubbs, 1967 ²
Shining sumac	Prairie grass	Petranka & McPherson, 1979
Aspen	Red fescue	Younger et al.,
	Tall fescue	Younger et al.,
	Perennial rye	Younger et al.,
	Kent. bluegrass	Younger et al.,
	Rough fescue	Dormaar, 1970
Black locust	Understory	Waks, 1936 ²
Juniper	Grass	Jameson, 1961 ²
Pinyon pine	Grass	Jameson, 1961 ²
Post oak	Understory	McPherson & Thompson, 1972
Blackjack oak	Understory	McPherson & Thompson, 1972
Table 1.--Continued.

Donor Species	Receiver Species	Reference .
Black locust	Grass	Matveey et al., 1985 ²
Smoketree	Grass	Matveey et al., 1985 ²
Sycamore	Kent. bluegrass Ryegrass	Al-Naib, 1968 ² Al-Naib, 1968 ²
Grand fir	Understory	Del Moral & Cates, 1971
Noble fir	Understory	Del Moral & Cates, 1971
Engelmann spruce	Understory	Del Moral & Cates, 1971
Rhododendron	Understory	Del Moral & Cates, 1971

*Germination tested only.

¹Cited from Gabriel, W. J. 1975. Allelopathic effects of black walnut on white birches. Journal of Forestry 73: 234-7.

²Cited from Rice, E. L. 1984. Allelopathy. Academic Press, New York.

³Cited from Rice, E. L. 1987. Allelopathy: an overview. In: Waller (ed.), p 8-22.

⁴Cited from Ponder, F., Jr. 1986. Effect of three weeds on the growth and mycorrhizal infection of black walnut seedlings. Canadian Journal of Botany 64: 1888-92.

Table 1.--Continued.

Donor Species	Receiver Spe	ecies Reference	

⁵Cited from Fales, S. L., and R. C. Wakefield. 1981. Effects of turfgrass on the establishment of woody plants. Agronomy Journal 73: 605-10.

⁶Cited from Norby, R. J., and T. T. Kozlowski. 1980. Allelopathic potential of ground cover species on Pinus resinosa seedlings. Plant and Soil 57: 363-74. Service Product of the Service State

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Table	2Species	with	Allelopathic	Potential ⁺

Species	Reference
Acer platanoides A. pseudoplatanus A. campestre A. tataricum A. laetum A. laetum A. urkestanicum A. ginnala A. mandschuricum A. saccharinum A. saccharinum A. negundo Quercus robur Fraxiinus excelsior Tilia cordata Picea pungens Pinus sibirica P. sylvestris Abies sibirica Picea odorata Larix sibirica Catalapa bignonioides Albizzia julibrissin Aesculus hippocastanum Pinus nigra Sophora japonica Berberis Rosa Syringa Philadelphus Viburnum Sorbus aucuparia Juniperus spp. Pinus edulis Betula verrucosa Fraxinus pubescens Bus typhina	Kokino et al., 1973 Kokino et al., 1973 Barnasketsky, 1973 Barnasketsky, 1973 Barnasketsky, 1973 Barnasketsky, 1977 Stephanov, 1977 Stephanov, 1977 Stephanov, 1977 Stephanov, 1977 Chumakov & Aleikina, 1977 Chumakov & I970 Oleksevich, 1970 Oleksevich, 1970 Oleksevich, 1970 Stephanov, 1961 Jameson, 1961 Roshchina, 1974 Roshchina, 1974 Roshchina, 1974
Pherrodendron amurense	RUSHCHINA, 1974

¹All references cited from Rice, E. L. 1984. Allelopathy. Academic Press, New York. ٦,

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Table 3.--Compatible Species*

Species	Reference
Fern, aster, goldenrod, yellow and black birch	Horsley, 1977a, 1987
Blackberry and black walnut	Ponder, 1986
Black walnut and autumn olive	Ponder, 1987
Shining sumac, red bud, oak, elm, and hackberry	Petranka and McPherson, 1979
Kentucky bluegrass and N. red oak	Kolb, 1988
Kentucky bluegrass and tulip poplar	Kolb, 1988
Wild carrot, goldenrod, crownvetch, and black alder	Larson and Schwarz, 1980

*No allelopathic conflicts when grown together.

shrubs with variable resistance to tree invasion. Although an interference study, many of the plants are suspected allelopaths.

Del Moral and Cates (1971) surveyed 40 species of ferns, conifers, and hardwoods in western Washington for inhibition in the field and lab (against Douglas fir and downy brome). Nine species (some used as ornamentals) showed both field/lab interference, sixteen showed lab inhibition (allelopathic potential), and five showed field interference (competition).

Mergen (1959) tested 46 species of trees with ailanthus extract in the lab and greenhouse in an allelopathic potential experiment. **A**11 species experienced growth inhibition except white ash. Fourteen hardwood species were tested against slash pine with no inhibition demonstrated. Brown (1967) studied the effects of 56 species against jack pine. Extracts from nine species caused significant reduction of germination.

Lee and Monsi (1963) examined Japanese red pine forests in Japan and South Korea for suppression of understory plants. Many are the same species or genera found in North America. A list of seed rain species found ungerminated in sassafras clones was presented by Gant and Clebsch (1975). Ninety weeds with allelopathic potential were enumerated by Putnum and Weston (1986) and are listed in Table A.6. Rietveld (1982) noted 16 species affected by juglone.

A review of pertinent literature was done by Gabriel (1975), Norby and Kozlowski (1980), Rice (1987), and Ponder (1986). Rice (1984) provided the most comprehensive review of virtually all studies addressing allelopathy in woody plants including forestry and horticulture.

Toxin Contaminated Soils

The use of topsoil as a planting-hole backfill material to provide a beneficial root-growing medium is a common practice in ornamental systems. To my knowledge, consideration of possible contamination of these soils by allelochemicals is unknown to practitioners or researchers.

The degree of influence of tainted soils on a recently planted tree is certainly debatable and in need of further study. The literature, however, is replete with evidence that leads me to believe that along with other stresses, toxins in topsoil may serve as another negative factor related to plant survival and vigor.

To carry out urban planting projects, topsoil is typically stripped from abandoned farm fields or "mined" from marsh areas. The old-field sites are usually inhabited by herbaceous species that are copious producers of secondary metabolites that contribute to soil pool size (Fisher et al., 1978; Horsley, 1987; Buchholtz, 1971; Walters & Gilmore, 1976). In lowland, marshy areas, tree species, such as sycamore, hackberry, various oak species, boxelder, and balsam poplar are all reported to produce inhibitors of woody plants and/or herbaceous associates (Lodhi, 1978; Kokino et al., 1973; Jobidon & Thibault, 1981).

Currently, there are no practical ways to determine if allelochemicals exist in a soil and to what degree they might affect a plant. There are, however, some general suggestions noted in the literature and gleaned from this author's experience which may be helpful in ameliorating toxin levels without undue research or effort.

Went (1957) speculated that charcoal added to tainted soils might absorb toxins, but as Brown (1967) pointed out, the charcoal itself may also contain problem This author wonders whether charcoal may substances. result in adsorption of toxins increasing pool size and lengthening persistence. However, Putnam et al. (1983) did autotoxicity of asparagus (Asparagus overcome officialis) by amending with charcoal, so the prospects for practical usage appear possible.

Whittaker and Feeny (1971) and Rice (1984) each point to work by C. H. Muller and others whereby phenolics from manzanita (<u>Arctostaphylos</u>) in the California chaparral inhibited herb growth. After destructive fires, the herb seeds proliferated as the toxins were "denatured," as Rice puts it.

The experience in California would suggest that phenolics, at least, can be detoxified in old-field settings. From a practical standpoint, it would seem logical to burn off the accumulated dry litter prior to spring green-up before stripping the topsoil. This practice would serve the dual purpose of denaturing toxins already in the soil and consuming the debris on the surface which would normally be decomposed into additional transformed toxins.

It is conceivable that dark-colored topsoils exposed to extended periods of midsummer sun might experience reductions in allelochem levels similar to those resulting from fire. Fire (and heat) may be a method with relatively high return from little effort and cost.

As a general rule, soils that are stripped, piled, and kept free of newly established weeds should be expected to have decreased toxin concentrations over time. Periodic disturbance of the pile, with a front-end loader for example, will till the weeds while providing aeration and stimulating microbial buildup, both resulting in allelochem degradation. Conclusions derived from the work of Fisher and others (1978) suggest that

allelochems in lighter loams and in soils with high humic content will degrade considerably faster than in soils with higher clay compositions.

An interesting corollary example of time correction of tainted soils resulted from work on a different problem by highway right-of-way landscape contractors and this author. The contractors were experiencing difficulty gaining access to back-slope planting sites through flooded ditches. In order to avoid equipment and roadside damage, they requested permission to dia planting holes in late summer prior to fall rains while ditches were dry and the surface firm. The holes were backfilled with topsoil to prevent wall drying and to be ready for spring planting. Along with solving a logistical difficulty, a technical problem may have been resolved unknowingly; the topsoil allelochems were allowed to degrade through the winter. It might be useful to specify this approach to enhance toxin degradation whenever possible.

Soil microorganisms have a tremendous capacity to reduce the quantity of natural products in the soil (Horsley, in press). Fisher (1978) and Rietveld et al. (1983) have suggested that more coarsely textured soils provide the degree of oxygen necessary for aerobic microbes to flourish. It would follow, then, that any activity that encourages microbial populations, such as

aeration, would likely reduce allelochem concentrations. This microbe/ aeration principle is applicable for established trees with allelochem problems as well as for new plantings.

Regulating Plant Growth

Even with a limited understanding of allelopathy, it is easy to imagine the practical use of allelochemicals as agents for controlling plant growth. This section presents a cursory review of the literature and its application to ornamental systems.

A number of authors have championed the use of natural products as herbicides in manipulated systems, particularly agriculture (Putnam, 1985, 1987; Rice, 1987; Mandava, 1985; Bentley, 1987; Putnam & Tang, 1986). However, it was Mergen (1959) who provided the first account noted in the literature proposing the use of an allelochemical (ailanthus toxin) for weed control.

Agricultural scientists are currently using residues of field crops that provide exceptional suppression of a number of weed species (Putnam & Tang, 1986). Further, allelopathic rotational crops or companion plants are utilized in annual or perennial cropping systems. Barnes et al. (1986) found that spring planted winter rye (<u>Secale cereale</u>) reduced the biomass of some weeds by 90%. One progressive Midwest nursery reported using rye on a trial basis for weed control (Myers, 1990). Horsley (in press) is preparing a paper on allelopathy for use in agroforestry. Further research on intercropping systems should provide valuable information on plant compatibilities in ornamental systems too.

Exploiting natural resistance to pests by plants has proven to be one of the safest and least costly ways to protect cultivated plants that are under attack (Bentley, 1987). The utilization of allelochem resistant genotypes of trees (Rink & Van Sambeek, 1985, 1987) and turf (Peters & Luu, 1985) are examples of ornamental applications to this type of research.

The new techniques available in genetic engineering, such as recombinant DNA, molecular biology, and tissue culture offer potential great for identifying allelochemicals and their function (Bentley, 1987). Further, they offer opportunities to more readily incorporate the capacity to produce or resist specific allelochems into given plants.

An important contribution from allelopathy research may be the discovery of novel chemicals either useful as structural models herbicides for herbicide or as development (Putnam, 1985; Rice, 1987). The need for cost-effective, efficacious, selective, more and environmentally safe herbicides which can counter

herbicide-resistant weeds may be satisfied by natural product applications (Duke, 1986).

Putnam (1985) noted that a cineole derivative was being developed as an herbicide by a major chemical company. Duke (1986) presented a thorough discussion of natural product herbicides, specifically microbially produced phytotoxins. Although Duke's work focused on agricultural applications, it is relevant to woody-plant weed control as well. That allelochems can use different sites of action, compared to synthetic compounds, makes them especially valuable for use on herbicide-resistant weeds (Duke, 1986).

Putnam and Tang (1986) and Rice (1984) noted the importance of allelopathy in preventing seed decay and controlling germination. It is conceivable that allelochems that are involved in plant patterning may regulate these functions, such as in jack pine (Brown, 1967), and might be useful as natural product herbicides. Solidago and aster extracts, or their synthetic counterparts, would appear to be useful in right-of-way management where woody plant suppression is important. Allelochems from oaks, sycamore, and hackberry, which are self-herbiciding to understory herbs, might be useful in weed control around trees.

Although the issue is unaddressed in the literature, it would appear logical that natural products could be

used as plant growth regulators, or PGRs as they are referred to in the landscape industry. For utility companies that chemically treat pruning wounds to retard regrowth, the use of allelochemical growth retardants might be useful on the wound as well as a systemic to slow overall tree growth into overhead wires. Landscape architects might want to retain a juvenile-sized tree in a design, such as in a restricted urban space. The of allelochem which acts application an on а photosynthetic site of action may be appropriate to negate excessive growth and frequent plant replacement.

While most researchers are dealing with the inhibitory effects of allelopathy, few are examining stimulatory effects. The concentration levels of allelochemicals determine the effects on receiver plants. Frequent reports suggest that low dosage levels of a "toxin" actually stimulate growth (Lodhi, 1976; Navarette et al., 1989). While the mechanism of action is unknown, the ability to improve plant growth with allelochem treatments is an exciting prospect. Larson and Schwarz (1980), for example, were able to stimulate growth in black alder with crownvetch solutions.

Rice (1986) found that ground ivy (<u>Glechoma</u> <u>haderacea</u>) stimulated growth in some herbaceous plants. He theorized that mineral uptake was enhanced by root exudates. If the theory is correct, it is possible that

treatment of trees on nutrient-deficient sites with allelochemicals may result in more efficient uptake of the available minerals when fertilization is not feasible.

Bentley (1987) stated that an understanding of allelopathy provides a basis for using specific chemicals that produce desired reactions with a minimum of undesirable effects.

CHAPTER X

SUMMARY AND CONCLUSIONS

The purpose of this thesis is to determine if allelopathy is a viable factor in shade tree physiology, and if so, what is its role and magnitude. This chapter summarizes the procedures and findings of this study, and then draws conclusions. Also, implications of the investigation are discussed and recommendations are made for further study.

Summary of Procedures

The minimal recognition of allelopathy in arboriculture writings and the paucity of research involving large-sized shade trees prompted a thorough search of allelopathy literature in the fields of agriculture, ecology, plant physiology, horticulture, forest resources, and organic chemistry. Fundamental concepts about allelopathy were gleaned from each discipline to provide a foundation for understanding its possible role in shade tree physiology. Particular attention given to examination was an of plant competition as the determinant of interplant growth. Of

great importance was the question of allelopathic activity in large trees.

Summary of Findings

The chemical influence between plants has been known for two thousand years, but its importance has only been recognized during this century (Rice, 1984; Mandava 1985). Allelopathy is operable in all plant systems but has received prominence primarily in medicine and agriculture. In the 1960s, research into allelopathy commenced in the ecological and forest resource sciences.

Early allelopathy research in ecology and forestry centered on germination and seedling growth. Allelopathy was seen as a factor in the spatial patterning and early successional stages of natural systems and in the regeneration of managed forests.

In 1965, Peterson recognized that growth in large black spruce trees was being retarded by some mechanism other than competition but implicated chemical inhibition only in seedlings. Horsley (1977a) and Fisher et al. (1978) produced similar studies. Walters and Gilmore (1976) were the first to demonstrate that natural products did, in fact, inhibit growth in larger woody plants (10 year-old sweetgum). Studies in black walnut plantations have further implicated allelochemicals as inhibitors of tree growth (Schlesinger & Van Sambeek, 1986) or even agents in tree death (Ponder, 1987; Fisher, 1978). The affected trees were 10-25 years old.

The research by Walters & Gilmore (1976) suggested that allelopathy can comprise most of the interference causing growth reduction. The data resulting from a study of old-field weed chemicals on sugar maple seedling growth confirms the earlier study (Fisher et al., 1978). Fortunately, highly allelopathic old-field weeds, such as goldenrod and aster, do not usually grow in urban landscapes, except in low maintenance parks or right of Fales and Wakefield (1980), however, showed ways. chemical inhibition of forsythia and flowering dogwood by cool-season turfgrasses. All reviewed studies alleging competition as the basis for reduced growth in trees caused by turfgrasses failed to test for allelochem interference.

Allelochems enter the soil primarily by leaching of above-ground foliage and by exudation from plant roots. Decaying vegetation generally produces more toxic products than green foliage. Microorganisms may produce their own toxins or transform other toxin inputs. Most research has centered on the easily extractable phenols from foliage. Lesser study has been done on root exudates and microbial products.

Natural product chemistry has emphasized the readily available phenols, so little is known about many

allelochems. In most research, the toxins are not identified. Juglone is a highly toxic metabolite of walnut trees, while phenols have been isolated from oaks and hackberry (Lodhi, 1976). Asters and goldenrods are known to produce polyacetylenes (Nuamta et al., 1973), which are constituents of extracts which dramatically reduce tree growth. Quackgrass, a common ground cover in Lake States' right of ways, also produces a polyacetylene (Grummer, 1961).

Temperature, water, and nutrient stresses are reported to increase toxin production dramatically. However, small concentrations of individual chemicals can combine to produce a synergistic reaction which surpasses the inhibition threshold level of a receiver plant. Stresses can also lower the threshold concentration level necessary for damage to occur in the receptor.

In addition to chemical, biological and climatic factors that influence allelochemical production by the donor plant and sensitivity in the receiver, edaphic elements impact the fate and availability of toxins. Poorly-drained, clay soils tend to collect allelochems while toxins are leached and microbial decomposition enhanced in sandy soils (Fisher, 1978).

Germination and early growth associated with cotolydonary reserves are important stages of development which are controlled by allelopathy. Other physiological

processes such as cell division and photosynthesis are also affected (Einhellig, 1986). Nutrient uptake can be limited by allelochemical damage to roots or rhizospheric microbes, resulting in retarded plant growth. Reduced potassium uptake in corn caused by quackgrass (Buchholz, phosphorus uptake in conifer seedlings 1971). bv Mikola, and reindeer-moss lichens (Brown & 1974), phosphorus uptake in sweetgum ornamentals (Walters & Gilmore, 1976) suggests that this mechanism of action is important to growth regulation.

Conclusions

Based upon the findings of the study, allelopathy can be regarded as a factor in shade-tree physiology and growth. Nutrient uptake is most likely an important mechanism of action which retards growth.

While tree-tree antagonism is possible, it is more likely that ground-cover species will determine allelopathic potential. Environmental stresses and site conditions ultimately determine the fate of an allelochemical and its potency in the affected plant.

It is doubtful that maintained residential lawns will allelopathically affect mature shade trees. However, trees in poor health for other reasons, e.g., compaction, moisture stress, and insect infestation, may be susceptible to allelopathic impacts. Newly planted trees may be vulnerable, too. Shade trees on poorly maintained street lawns, in central-city tree pits, and in parks may be more susceptible to allelopathic ground cover species and/or stresses. Mulching is an excellent deterrent to allelopathy in urban trees and shrubs.

Ornamentals planted in right of ways can be greatly affected by highly toxic old-field weeds, especially on poorly-drained sites. Trees in this setting may experience very slow growth which may be irreversible unless corrected at an early stage.

Allelopathy is certainly not the only factor affecting tree growth. Rather it is an interactive element which may vary in importance over time as environmental stresses, site conditions, and involved species change.

Discussion

The applied allelopathy presented in Chapter IX is essentially an extrapolated conclusion from the foundational material examined in Chapters I-VIII. There are some important implications for ornamental plant systems that can be derived from these conclusions. The first consideration is the recognition of two distinct subcategories of ornamental trees: the urban environment and the right of way. In urban environments, ground covers do not seem to be a dominant allelopathic factor. However, allelopathy may be operable interactively with environmental and competitive stresses so as to be indistinguishable symptomatically. As Horsley (1983) put it, "allelopathy may tip the stress load in favor of decline or mortality of the affected tree."

The obsession with turfgrass around trees, with its concurrent use of fertilizer, needs to be challenged. The fertilizer is probably unavailable for uptake by the tree anyway, as a result of ground cover toxins. Rather, a "mulching ethic," which eliminates ground covers and minimizes stress conditions, needs to be promoted by the landscape profession.

In right of ways, the eradication of highly toxic herbaceous vegetation is paramount for the health and survival of ornamental trees. After establishment, fertilization can usually be eliminated, but herbicides need to be applied throughout the juvenile stage, which may be 10-15 years.

Field symptoms of allelopathy in trees are meager at best, hence, the forgoing preventive measures are recommended for use by landscape managers. Without the benefit of symptoms it would appear difficult to prioritize cultural treatments. In this case, attention

should focus on trees on poorly-drained clay soils and proceed toward plants on superior sites.

Recommendations for Future Study

1. Re-evaluation of misnomered competition studies to confirm the operable interference mechanism to insure diagnosis and treatment of the correct problem.

2. Identification of symptoms of allelopathy that are distinguishable by field observers.

3. Confirmation of allelopathy in mature trees by tissue culture or similar advanced techniques.

4. Study on sites of action in shade trees, such as confirming nutrient uptake inhibition.

5. Further study on cool-season grass effects on shade trees.

6. The study of quackgrass as a possible inhibitor of shade tree growth.

7. Identification of tree species or genotypes within species resistant to allelochems in specific situations.

APPENDIX

(Examples)
Allelochemicals
Higher Plant
able A.1I

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		Charles Class
Method of Isolation	Species and lissue	
Extraction - ethanol	Cyperus esculentus, tubers and leaves	Ferulic acid and other phenolics
	Cyperus rotundus, tubers and leaves	Ferulic acid and other phenolics
- 19787	Abutilon theophrasti. leaves	Phenolics
	Aeronyron Smithil. litter	Phenolics
-	Ambrosis artemisifolia. Shoots	Chlorocenic and caffeic acids
	Arter bilosus, shoots	Chlorogenic and caffeic acids
	Avena fatua. dead litter	Ferulic and coumaric acids
	Ridens piloss, leaves	Phenylheptatriyne
	Brachlaria mutica, dried leaves	Vanilite, p-hydroxybenzoic,
		o-hydroxyphenylacetic acids
	Chloris gayana	Phenolics - ferulic acid
	Cypodon dactylon, dried leaves	Phenolics - p-coumaric acid
	Digitaria decumbens, dried leaves	Ferulic acid and other phenolics
	Diefraria sanguinalis. whole plant	Chlorogenic, isochlorogenic and
		sulfosalicylic acids
	Erica arborea, leaves	Salicylic acid, scopoletin,
		<u>p</u> -hydroxybenzaldehyde
	Hellanthus annuus, root	Chlorogenic, isochlorogenic
		acids; scopoletin
	Kochia scoparia, leaves	Feruitc acid, wyricetin,
		quercitin
	Panicum maximum, dried leaves	o-Hydroxyphenylacetic acid
	Paspalum plicatulum, dried leaves	Ferulic acid, other phenolics
	Polygonum orientale, roots, stems,	Flavone glycosides
	leaves	
	Rumex crispus, leaves	Phenolics
	Setaria sphacelata, dried leaves	Ferulic acid, other phenolics
	Sorghum halepense, leaves, rhizomes	Chlorogenic, p-coumaric acids,
		p-hydroxybenzaldehyde
	Tripsacum <u>laxum</u> , dried leaves	Ferulic acid, other phenolics

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Exudates - root	Ambrosia artemisifolia	Chlorogenic and caffeic acids
	Chenopodium album	UTALIC ACID
	Bellanthus annuus	Chlorogenic, isochlorogenic
		acids; scopoletin
	Bemarthria altissima	Cinnamic and benzoic acids and
	Polygonum aviculare	Phenolic glucosides, fatty acids
- root and	Sorghum halepense.	Chlorogenic, p-coumaric acids;
rh120me		p -hydroxybenzaldehyde
Leachates - leaves	Cyperus esculentus	Ferulic acid, other phenolics
	Deture stremonium Polyconum aviculare	Scopolamine, hyoscyamine Phenolic glucosides, fatty acids
- fronds	Pteredium aguilinum	Phenolics Consists familia and A athere
	ITEN BTOSTES	ARECTETIN' TELETIC SETA' ALIALE
- fruite	Amni majue	Xanthotoxin, (furanocoumarin)
	Aburdlen theoshyaeti	Phenol 1ca
	Datura stramonium	Scopolamine, hyoscyamine
		•
- roots and	Agropyron Tepens	Acetic, butyric acids Familie and ather abanalies
rhizo ne e	Cyperus esculentus	reruits acid, other prenotics
<u>Volatiles</u> - leaves	Artemisia tridentata	Terpenes, camphor, pinene,
	Salvia leucophylla	Various volatiles

Source: Hoagland, R. E., and R. D. Williams. 1985. The influence of secondary
plant compounds on the associations of soil microorganisms and plant
roots. In: Thompson (ed.), p 301-25.

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Plant Function or Condition	Test Species	Concentration (μM)	Action	Reference
Protein synthesis	Lettuce	200	Inhibited	Cameron and Julian (1980)
-ipid synthesis	Cell culture	100	Increased	Danks et al. (1975a)
AA-Induced growth	Pea	S00	Increased	Tomaszewski and Thimann (1966)
ABA Inhibition	Amuranthus			
	cundatus	10	Released	Ray et al. (1980)
Respiration rate	Yeast	500	Increased	Van Sumere et al. (1971)
Photosynthesis	Suybean	1000	Decreased	Patterson (1981)
stomatal conductance	Sorghum	500 200	Decreased	Einhellig et al. (1985)
Chlorophyll content	Suybean	500	Decreased	Einhellie and Rasmussen (1979)
^b hosphorus content	Sorghum	250	Decreased	Kubza (1980)
on uptake	Barley	500 200	Decreased PO ₄ ¹	Glass (1973)
	Oats	S00	Decreased K ⁺	Harper and Balke (1981)
Membrane potential (mv)	Barley	250	Decreased	Glass and Dunlop (1974)
Vater potential	Sorghum	250	Lowered	Einhellig et al. (1985)

Table A.2.--Ferulic Acid Metabolism Effects

Einhellig, F. A. 1986. Mechanisms and modes of action of allelochemicals. In Putnam and Tang (eds.), p 171-188. Source:

Table A.3.--Mechanisms of Action (Examples).

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Mechanism	Allelochemical
Cell extension	Phenolic acids, tannins
Cell division	Volatile terpenes, coumarins
Membrane permeability	Phenolic acids
Nutrient uptake	Phenolic acids
Chlorophyll synthesis	Coumarins
	Phenolic acids
Photosynthesis	Phenolic acids
Protein synthesis	Phenolic acids, coumarins
Enzyme activity	Phenolic acids
Respiration	Juglone, volatile terpenes, phenolic acids
Water relations	Phenolic acids

Source: Leather, G. R., and F. A. Einhellig. 1988. Bioassay of naturally occurring allelochemicals for phytotoxicity. Journal of Chemical Ecology 14: 1821-8.

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Table A.4.--Sites of Action (Examples).

Affected Site (Enzyme)	Herbicide (Reference)	Microbial Toxin (Reference)
	Amino Acid Metabolism	
Methionine synthesis		Rhizobitoxine (Giovanelli et al., 1971)
(B-Cystathionase)		
Aromatic amino-acid synthesis	Glyphosate (Duke, 1985a)	
(EP3P syntnase) Arginine synthesis		
(Ornithine carbamovl transferase)		Phaseolotoxin (Gilchrist, 1983)
Histidine synthesis	Amitrole (Duke, 1985a)	
(Imidazoleglycerol phosphate dehydratase)		
Glutamine synthesis	Methionine sulfoximine" (Duke, 1985a)	Tabtoxinine- β -lactam (Thomas et al., 1983)
(Glutamine synthetase)		Bialaphos (Fischer and Bellus, 1983) Overin (Omura et al. 1984)
Valine and isoleucine synthesis (Acetolactate synthase)	Sullonyl ureas (Duke, 1965a) Imidazolinones (Duke, 1985a)	
All Transaminases	Benzadox (Duke, 1985a)	
Glutamate synthesis		
(Aspartate aminotransferase)		Gostatin (Nishino and Murao, 1983)
	Plastid Functions	
Electron transport	Many (e.g., triazines) (Gressel, 1985)	
		Total 10 10 10 10 1000 T
Energy transfer		Lentoxin (Steele et al., 19/0)
Uncoupring (LT1)		

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Fusaric acid (D'Alton and Etherton, 1984) Mevinolin (Bach and Lichtenthaler, 1983) Cercosporin (Daub and Hangarter, 1983) Tentoxin (Vaughn and Duke, 1984b) Ophiobolin A (Leung et al., 1985) CBT-toxin (Macri et al., 1983) Fusicoccin (Gilchrist, 1983) AAL-toxin (Gilchrist, 1983) Dichlobenil (Montezinos and Delmer, 1980) Many (e.g., benzonitriles) (Moreland, 1985) Many (e.g., pyridazinones) (Duke, 1985a) Bipyridiliums (Vaughn and Duke, 1983) Dinitroanilines (Hess and Bayer, 1977) Rose bengal" (Knox and Dodge, 1984) Diphenylethers (Kenyon et al., 1985) Plasma Membrane Thiocarbamates (Duke, 1985a) Thiocarbamates (Duke, 1985a) Mitochondrion **Other Sites** Oxadiazon (Duke, 1985a) Ioxynil (Moreland, 1985) Asulam (Duke, 1985a) Continued. (Aspartate carbamoyl transferase) Nuclear-coded protein uptake Alters membrane potential Coupled electron transport Singlet oxygen production 'Not a commercial herbicide. **Fubulin polymerization** Chlorophyll synthesis **Carotenoid synthesis Calmodulin function Terpenoid synthesis Pyrimidine synthesis** K +-ATPase activity Microsomal ATPase Table A.4. Folic acid synthesis **Cellulose synthesis** Alternate oxidase Energy diversion Lipid synthesis

Putnam and Tang (eds.) 1986. Microbially produced phytotoxins as In: a perspective. herbicides -Duke, S. 0. p 287-304. Source:

Source		Identity	Effect
Species	Tissue-isolation		
Camelina sativa	H ₂ 0-leaf wash	2	stim d. radicle elongation in
	4		presence of N ₂ -fix. bacteria
Cassia fistula, C. occiden-,	non-nodulating roots	2	inhib'd. <u>R. jāponicum</u> growth
talis. Leucaena leucocephala,	and root extracts		
Trifolium alexandrinum	fungi and bacteria	2	antagonistic and stim. to \underline{R} .
	of T. elexandrinum		Japonicum
Hyparrhenia filipendula.			•
Cynodon dactylon,	root extracts	6	inhib'd. growth of NO ₃ & NH ₄
Rhynchelytrum repens.			oxidizers
Sporobolus pyramidalis.			
Eragrostis curvula, Themeda			
triandra, Pennisetum			
purpureum			
Populus balsamifera	H ₂ O-extracts of all	6	red'd. growth, nodulation &
	plant parts		acetylene red'n in Alnus crispa
Abries balsames. Populus	extracts & leachates	6	inhib'd. nitrification
balsamifera	of leaves and buds		
Pinus ponderosa	extracts-needles,	caffeic,	red'd nitrification
	bark	chlorogenic	
		acids, tannin	
Artarida adacensionia	extracts & leachates	~	inhib'd. Rhizobium& Azotobacter
	roots, shoots, litte		nodulation
Atriblex confertifolia.	H_O-extract, leaves	~	inhib'd. N ₂ -fixation
Eurotia lanata, Artemisia	7		7
tridentata			

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Table A.5.--Rhizosphere Interactions (Examples).

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SOURCE		TURNETLY	112117
Species	Tissue-isolation		
Various plant	volatiles fr. plant	1	Inhib'd. Rhizoctonia growth,
species	residues		inc'd pigmentation in mycelium,
			dec'd saprophytic activity
Pseudomonas spp.	growing v.	acid end-	inhib'd. A. chroococcum
	Azotobacter	products	
Trachypogon plumosus	H_O-extract, roots	۰.	1nh1b'd. E. col1, Bacillus
	7		subtilis; Staph. aureus, Strep. haemolyticus
Oryza sativa	decomposing straw	phenoli cs	toxic in lettuce & rice seed
			bioassays; mungbean root assay
Solls	extracts of soil	humic 8	stim'd plant growth & nodule mass;
		fulvic acids	dec'd nodule no.
Trichoderma viride.			
Rhizobus nigricans. Mucor	m ycelial exudates	••	1nh1b'd. R japonicum; T. veridi
vestculosis	•		inhib'd. nodulation & M.
			vestculosis
			Inc d nodule no.
Calluna vulgaris	root leachate	۰.	inhib'd. mycorrhizal fungi growth
Various plant species, ex.	extracts, exudates,	sugar-	Inhib d. Nitrosomonas, Nitrobacter;
Ambrosia elatir, Euphorbia	leachates of	phenolic	red d noaule size a no.; red u bammalabin in madulas
corrollater, Hellanthus	plants & soll	complexes,	SATADON HT HTODIAD
annus		Cantus	
Possilie tremila	H_O-extracts.	benzoic	inhib'd. mycorrhizal fungal growth
		acid.	
	leaves	catechol	

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Hoagland, R. E., and R. D. Williams. 1985. The influence of secondary plant compounds on the associations of soil microorganisms and plant roots. In: Thompson (ed.), p 301-25. Source:

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Table A.6.--Weeds with Allelopathic Potential.

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Abuilion theophrasti Velvetleaf Gressel and Holm (1964) Agropyron repens Quackgrass Kommedahl et al. (1959) Agrostemma githago Corn cockle Gajić and Nikočević (1973) Allium vineale Wild garlic Osvald (1950) Annaranthus dubius Amaranth Alteri and Doll (1978) Annaranthus dubius Amaranth Alteri and Doll (1978) Annaranthus spinosus Spiny amaranth Vander Veen (1935) Annbrosia arreimisi/glia Common ragweed Jackson and Willemsen (1976) Ambrosia arrifida L. Giant ragweed Letourneuu et al. (1956) Anternaia microphylla Pussytoes Selleck (1972) Artemisia obsinthium Absinth wornwood Bode (1940) Artemisia oulgaris Mugwort Mann and Barnes (1945) Scelepias syriaca Common milkweed Rasmussen and Einhellig (1975) Avena fatua Wild oat Tinnin and Muller (1971) Aremisia valgaris Downy brome Rice (1964) Bromus japonicus Japanese brome Rice (1964) Bromus japonicus Japanese brome Rice (1964) Grummer and Beyer (1960) Candin	Scientific Name	Common Name	First Reference"
Agropyron repensQuackgrassKommedahl et al. (1959)Agrostemma githagoCorn cockleGajić and Nikočević (1973)Allium vinealeWild garlicOsvald (1950)Annaranthus dubiusAmaranthAlteri and Doll (1978)Amaranthus retroflexusRedroot pigweedGressel and Holm (1964)Amaranthus spinosusSpiny amaranthVander Veen (1935)Ambrosia artemisii/oliaCommon ragweedJackson and Willemsen (1976)Ambrosia cumanensis—Anaya and DelAmo (1978)Ambrosia cumanensis—Anaya and DelAmo (1978)Ambrosia cumanensis—Anaya and DelAmo (1978)Ambrosia trifida L.Giant ragweedLetourneau et al. (1956)Amtennaria microphyllaAbsinth wormwoodBode (1940)Artemisia absinthiumAbsinth wormwoodBode (1940)Asclepias syriacaCommon milkweedRasmussen and Einhellig (1975)Asclepias syriacaCommon milkweedRasmussen and Einhellig (1975)Boerhovia diffusaSpiderlingSen (1976)Bromus japonicusJapanese bromeRice (1964)Commus tectorumDowny bromeRice (1964)Cannelina sativaLargeseed falseflaxGrummer and Beyer (1960)Candenia sativaSandburSen (1976)Cenchrus bjflorusField sandburRice (1964)Cenchrus bjaciforusField sandburRice (1964)Cenchrus bjaciforusSpoted knapweedFletcher and Renney (1963)Cenchrus bjaciforusField sandburRice (1964)Ce	Abutilon theophrasti	Velvetleaf	Gressel and Holm (1964)
Agrostemma githagoCorn cockleGajić and Nikočević (1973)Milum vinealeWild garlicOsvald (1950)Annaranthus dubiusAmaranthAltieri and Doll (1978)Annaranthus retro/lexusRedroot pigweedGressel and Holm (1964)Annaranthus spinosusSpiny amaranthVanderVeen (1935)Ambrosia cumanensis—Anay and DelAmo (1978)Ambrosia uramensis—Anay and DelAmo (1978)Ambrosia trifida L.Giant ragweedLetourneau et al. (1956)Anternaria microphyllaPussytoesSelleck (1972)Artemisia absinthumAbsinth wormwoodBode (1940)Artemisia absinthumAbsinth wormwoodBode (1940)Artemisia vulgarisMugwortMann and Barnes (1945)Sclepias syriacaCommon milkweedRasmussen and Einhelig (1975)Saclepias syriacaCommon milkweedRasmussen and Doll (1979)Bidens pilosaBeggar-ticksStevens and Tang (1985)Soorhova diffusaSpidertingSen (1976)Branus tectorumDowny bromeRice (1964)Calluna vulgaris—Salas and Vieitez (1972)Cannelina astivaLargeseed falseflaxGrummer and Beyer (1960)Cenchrus bjflorusField sandburSice (1964)Cenchrus bjflorusSandburSen (1976)Cenchrus bjflorusSandburSen (1976)Cenchrus bjflorusField sandburStecher and Renney (1963)Cenchrus bjflorusField sandburRice (1964)Centaurea diffusaDiffuse knapweed	Agropyron repens	Quackgrass	Kommedahl et al. (1959)
Allium vineale Wild garlic Osvald (1950) Annaranthus dubius Amaranth Altieri and Doll (1978) Amaranthus retroflexus Redroot pigweed Gressel and Holm (1964) Amaranthus spinosus Spiny amaranth VanderVeen (1935) Ambrosia artemisiifolia Common ragweed Jackson and Willemsen (1976) Ambrosia psilostachya Western ragweed Neill and Rice (1971) Ambrosia rifida L. Giant ragweed Letourneau et al. (1956) Antennaria microphylla Pussytoes Selleck (1972) Artemisia vulgaris Mugwort Maan and Barnes (1945) Saclepias syriaca Common milkweed Rasmussen and Einhellig (1975) Avena fatua Wild oat Tinnin and Muller (1971) Berteroa incana Hoary alyssum Bhowmik and Doll (1978) Solerhowid diffusa Spiderling Sen (1976) Bromus japonicus Japanese brome Rice (1964) Calluna vulgaris — Salas and Vieitez (1972) Cannelina alvsum Flax weed Grummer and Beyer (1960) Cannelina sativa Largesced falseflax Grummer and Reney (1963) Cenchrus paucifforus	Agrostemma githago	Corn cockle	Gajić and Nikočević (1973)
Amaranthus dubiusAmaranthAltieri and Doll (1978)Amaranthus retroflexusRedroot pigweedGressel and Holm (1964)Amaranthus spinosusSpiny amaranthVander Veen (1935)Ambrosia artemisiifoliaCommon ragweedJackson and Willemsen (1976)Ambrosia ratemisiifoliaWestern ragweedNeill and Rice (1971)Ambrosia ratifida L.Giant ragweedLetourneau et al. (1956)Amtennaria microphyllaPusytoesSelleck (1972)Artemisia absinthiumAbsinth wormwoodBode (1940)Artemisia vulgarisMugwortMann and Barnes (1945)Sceleias syriacaCommon milkweedRasmussen and Einhellig (1975)Anena fatuaWild oatTinnin and Muller (1971)Berteroa incanaHoary alyssumBhowmik and Doll (1979)Bidens pilosaBeggar-ticksStevens and Tang (1985)Soerhovia diffusaSpiderlingSen (1976)Brausica nigraBlack mustardMuller (1969)Bromus japonicusJapanese bromeRice (1964)Camelina alyssumFlax weedGrummer and Beyer (1960)Camelina sitivaLargesced falseflaxGrummer and Beyer (1960)Candera maculosaSpotted knapweedFletcher and Renney (1963)Cenchrus pifforusSandburSen (1976)Centaurea maculosaSpotted knapweedFletcher and Renney (1963)Centaurea maculosaSpotted knapweedFletcher and Renney (1963)Centaurea maculosaCommon lambsquartersCausat histleCheoropodium albumCommon	Allium vineale	Wild garlic	Osvald (1950)
Amaranthus retrof/lexusRedroot pigweedGressel and Holm (1964)Amaranthus spinosusSpiny amaranthVanderVeen (1935)Ambrosia cumanensis–Anaya and DelAmo (1978)Ambrosia cumanensis–Anaya and DelAmo (1978)Ambrosia trifida L.Giant ragweedLetourneau et al. (1956)Antennaria microphyllaPussytoesSelleck (1972)Artemisia absinthiumAbsinth wormwoodBode (1940)Artemisia absinthiumAbsinth wormwoodBode (1940)Artemisia valgarisMugwortMann and Barnes (1945)Sclepias syriacaCommon milkweedRasmussen and Einhellig (1975)Berteroa incanaHoary alyssumBhormik and Doll (1979)Bidens pilosaBeggar-ticksStevens and Tang (1985)Borhowia diffusaSpiderlingSen (1976)Bromus japonicusJapanese bromeRice (1964)Camelina alyssumFlax weedGrummer and Beyer (1960)Camelina alyssumFlax weedGrummer and Beyer (1960)Cannelina alyssumFlax strapweedFletcher and Renney (1963)Centaurea diffusaSpifusa Spotted knapweedFletcher and Renney (1963)Centaurea diffusaSpotted knapweedFletcher and Renney (1963)Centaurea	Amaranthus dubius	Amaranth	Altieri and Doll (1978)
Amaranthus spinosusSpiny amaranth Common ragweedVanderVeen (1935)Ambrosia artemisiifoliaCommon ragweedJackson and Willemsen (1976)Ambrosia psilostachyaWestern ragweedNeill and Rice (1971)Ambrosia rifida L.Giant ragweedLetourneau et al. (1956)Antennaria microphyllaPussytoesSelleck (1972)Arremisia awlgarisMugwortMan and Barnes (1945)Asclepias syriacaCommon milkweedRasmussen and Einhellig (1975)Avena fatuaWild oatTinnin and Muller (1971)Berteroa incanaHoary alyssumBhowmik and Doll (1979)Bidens pilosaBeggar-ticksStevens and Tang (1985)Boerhovia diffusaSpiderlingSen (1976)Bromus japonicusJapanese bromeRice (1964)Calluna vulgaris—Salas and Vieitez (1972)Cantelina alyssumFlax weedGrummer and Beyer (1960)Calluna vulgaris—SandburCenchrus biflorusSandburSen (1976)Cenchrus biflorusSandburSen (1976)Cenchrus biflorusSandburSen (1976)Centaurea diffusaDiffuse knapweedFletcher and Renney (1963)Centaurea repensRussian knapweedFletcher and Renney (1963)Centaurea repensCamada thistleStachon and Zimdahl (1980)Chenopodium albumCommo lambsquartersCaussanel and Kunesch (1971)Cirisium discolorTall thistileLetourneau et al. (1976)Cirisium discolorTall thistileLetourneau et al. (1976) <td>Amaranthus retroflexus</td> <td>Redroot pigweed</td> <td>Gressel and Holm (1964)</td>	Amaranthus retroflexus	Redroot pigweed	Gressel and Holm (1964)
Ambrosia artemisiifolia Common ragweed Jackson and Willemsen (1976) Ambrosia cumanensis — Anaya and DelAmo (1978) Ambrosia triffda L. Giant ragweed Neill and Rice (1971) Ambrosia triffda L. Giant ragweed Letourneau et al. (1956) Antennaria microphylla Pussytoes Selleck (1972) Artemisia absinthium Absinth wormwood Bode (1940) Artemisia vulgaris Mugwort Mann and Barnes (1945) Saclepias syriaca Common milkweed Rasmussen and Einhellig (1975) Wena fatua Wild oat Tinnin and Muller (1971) Barteroa incana Hoary alyssum Bhowmik and Doll (1979) Bidens pilosa Beggar-ticks Stevens and Tang (1985) Boerhowia diffusa Spiderling Sen (1976) Bromus japonicus Japanese brome Rice (1964) Calluna vulgaris — Salas and Vieitez (1972) Camelina sativa Largeseed falseflax Grummer and Beyer (1960) Canelina sativa Largeseed falseflax Grummer and Reney (1963) Cenchrus pauciflorus Field sandbur Rice (1964) Cenchrus pauciflorus Sa	Amaranthus spinosus	Spiny amaranth	VanderVeen (1935)
Ambrosia cumanensis—Anaya and DelAmo (1978)Ambrosia psilostachyaWestern ragweedNeill and Rice (1971)Ambrosia rifida L.Giant ragweedLetourneau et al. (1956)Amtennaria microphyllaPussytoesSelleck (1972)Artemisia absinthiumAbsinth wormwoodBode (1940)Artemisia absinthiumAbsinth wormwoodBode (1940)Artemisia vulgarisMugwortMann and Barnes (1945)Scelpias syriacaCommon milkweedRasmussen and Einhellig (1975)Bidens pilosaBeggar-ticksStevens and Tang (1985)Boerhowia diffusaSpiderlingSen (1976)Bromus japonicusJapanese bromeRice (1964)Calluna vulgaris—Salas and Vieitez (1972)Camelina alyssumFlax weedGrummer and Beyer (1960)Calluna vulgaris—Pandya (1975)Canelina alysumFlax weedGrummer and Beyer (1960)Calluna vulgaris—Pandya (1975)Canelina alysumFlax weedFletcher and Renney (1963)Cenchrus biflorusSandburSen (1976)Cenchrus pauciflorusField sandburRice (1964)Centaurea maculosaSpotted knapweedFletcher and Renney (1963)Centaurea maculosaSpotted knapweedFletcher and Renney (1963)Centaurea maculosaSpotted knapweedFletcher and Renney (1963)Centaurea diffusaDiffuse knapweedFletcher and Renney (1963)Centaurea maculosaSpotted knapweedFletcher and Renney (1963)Centaurea dif	Ambrosia artemisiifolia	Common ragweed	Jackson and Willemsen (1976)
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Artemisia absinthiumAbsinth wormwoodBode (1940)Artemisia vulgarisMugwortMann and Barnes (1945)Saclepias syriacaCommon milkweedRasmussen and Einhellig (1975)Avena fatuaWild oatTinnin and Muller (1971)Bidens pilosaBeggar-ticksStevens and Tang (1985)Boerhovia diffusaSpiderlingSen (1976)Bronus japonicusJapanese bromeRice (1964)Bromus tectorumDowny bromeRice (1964)Bronus iaponicusJapanese bromeRice (1964)Canlelina alyssumFlax weedGrummer and Beyer (1960)Canelina alyssumFlax weedGrummer and Beyer (1960)Canelina sativaLargeseed falseflaxGrummer and Beyer (1960)Canelina sativaLargeseed falseflaxGrummer and Reyer (1960)Canelina sativaDiffuse knapweedFletcher and Renney (1963)Cenchrus biflorusSandburSen (1976)Cenchrus pauciflorusField sandburRice (1964)Centaurea maculosaSpotted knapweedFletcher and Renney (1963)Centaurea repensRussian knapweedFletcher and Renney (1963)Chrinulis lovatus—Bhandari and Sen (1971)Cirsulm discolorTall thistileLatoon and Zimdahl (1980)Cirsulus lovatus—Sen (1976)Cirsulus lovatus—Sen (1976)Cirsulus lovatus—Bhandari and Sen (1971)Cirsulus alusts—Bhandari and Sen (1971)Cirsulus alusts—Sen (1976)Cirsu	Antennaria microphylla	Pussytoes	Selleck (1972)
Artemisia vulgarisMugwortMann and Barnes (1945)Asclepias syriacaCommon milkweedRasmussen and Einhellig (1975)Avena fatuaWild oatTinnin and Muller (1971)Berteroa incanaHoary alyssumBhowmik and Doll (1979)Bidens pilosaBeggar-ticksStevens and Tang (1985)Boerhovia diffusaSpiderlingSen (1976)Brassica nigraBlack mustardMuller (1969)Bromus japonicusJapanese bromeRice (1964)Bromus tectorumDowny bromeRice (1964)Camelina alyssumFlax weedGrummer and Beyer (1960)Camelina sativaLargeseed falseflaxGrummer and Beyer (1960)Canelina sativaLargeseed falseflaxGrummer and Beyer (1960)Cenchrus pauci/lorusField sandburSen (1976)Cenchrus pauci/lorusField sandburRice (1964)Centaurea diffusaDiffuse knapweedFletcher and Renney (1963)Centaurea repensRussian knapweedFletcher and Renney (1963)Changodium albumCommon lambsquartersCausael and Kunesch (1979)Cirsium discolorTall thistileLetourneau et al. (1956)Cirullis colocynthis—Sen (1976)Cirullis luvatus—Sen (1976)Cyperus esculentusYellow nutsedgeTames et al. (1973)Cyperus rotundusPurple nutsedgeTames et al. (1971)Cirullis luvatus—Sen (1976)Cirullis luvatus—Sen (1976)Cirullis luvatus—Sen (1976) <td< td=""><td>Artemisia absinthium</td><td>Absinth wormwood</td><td>Bode (1940)</td></td<>	Artemisia absinthium	Absinth wormwood	Bode (1940)
Asclepias syriacaCommon milkweedRasmussen and Einhellig (1975)Avena fatuaWild oatTinnin and Muller (1971)Berteroa incanaHoary alyssumBhowmik and Doll (1979)Bidens pilosaBeggar-ticksStevens and Tang (1985)Boerhovia diffusaSpiderlingSen (1976)Brassica nigraBlack mustardMuller (1969)Bromus japonicusJapanese bromeRice (1964)Bromus japonicusJapanese bromeRice (1964)Calluna vulgaris—Salas and Vieitez (1972)Camelina alyssumFlax weedGrummer and Beyer (1960)Camelina sativaLargeseed falseflaxGrummer and Beyer (1960)Candelina sativaLargeseed falseflaxGrummer and Beyer (1960)Cenchrus biflorusSandburSen (1976)Cenchrus pauciflorusField sandburRice (1964)Cenchrus pauciflorusSandburRice (1964)Centaurea diffusaDiffuse knapweedFletcher and Renney (1963)Centaurea maculosaSpotted knapweedFletcher and Renney (1963)Centaurea repensRussian knapweedFletcher and Renney (1963)Cirsium discolorTall thistileLetourneau et al. (1979)Cirsium discolorTall thistileLetourneau et al. (1970)Ciruulis lavatus—Bhandari and Sen (1971)Ciruunis callosus—Sen (1976)Cyperus rotundusYellow nutsedgeTames et al. (1973)Cyperus rotundusPurple nutsedgeFriedman and Horowitz (1971)Daboecia polifolia </td <td>Artemisia vulgaris</td> <td>Mugwort</td> <td>Mann and Barnes (1945)</td>	Artemisia vulgaris	Mugwort	Mann and Barnes (1945)
Awena fatuaWild oatTinnin and Muller (1971)Berteroa incanaHoary alyssumBhowmik and Doll (1979)Bidens pilosaBeggar-ticksStevens and Tang (1985)Boerhovia diffusaSpiderlingSen (1976)Brassica nigraBlack mustardMuller (1969)Bromus japonicusJapanese bromeRice (1964)Bromus tectorumDowny bromeRice (1964)Calluna vulgaris—Salas and Vieitez (1972)Camelina alyssumFlax weedGrummer and Beyer (1960)Camelina sativaLargeseed falseflaxGrummer and Beyer (1960)Canelina sativaLargeseed falseflaxGrummer and Beyer (1960)Cenchrus biflorusSandburSen (1976)Cenchrus pauciflorusField sandburRice (1964)Centaurea diffusaDiffuse knapweedFletcher and Renney (1963)Centaurea repensRussian knapweedFletcher and Renney (1963)Chenopodium albumCommon lambsquartersCaussanel and Kunesch (1979)Cirsium discolorTall thistileLetourneau et al. (1956)Cirulis lavatus—Bhandari and Sen (1971)Cirulis lavatus—Sen (1976)Cucumis callosus—Sen (1973)Cyperus rotundusPurple nutsedgeTames et al. (1973)Cyperus rotundusPurple nutsedgeFriedman and Horowitz (1971)Digera arvenis—Salas and Vieitez (1972)Digera arvenis—Salas and Vieitez (1972)Digera arvenis—Salas and Vieitez (1972)	Asclepias syriaca	Common milkweed	Rasmussen and Einhellig (1975)
Berteroa incanaHoary alyssumBhowmik and Doll (1979)Bidens pilosaBeggar-ticksStevens and Tang (1985)Boerhovia diffusaSpiderlingSen (1976)Brossica nigraBlack mustardMuller (1969)Bromus japonicusJapanese bromeRice (1964)Bromus japonicusJapanese bromeRice (1964)Bromus japonicusJapanese bromeRice (1964)Bromus tectorumDowny bromeRice (1964)Calluna vulgaris—Salas and Vieitez (1972)Cumelina alyssumFlax weedGrummer and Beyer (1960)Camelina sativaLargeseed falseflaxGrummer and Beyer (1960)Cenchrus biflorusSandburSen (1976)Cenchrus pauciflorusField sandburRice (1964)Centaurea diffusaDiffuse knapweedFletcher and Renney (1963)Centaurea maculosaSpotted knapweedFletcher and Renney (1963)Chenopodium albumCommon lambsquartersCausanel and Kunesch (1979)Cirsium discolorTall thistileLetourneau et al. (1980)Cirrullis lovatus—Sen (1976)Cirrullis lovatus—Sen (1976)Cyperus sculentusYellow nutsedgeTames et al. (1971)Curumis callosus—Sen (1976)Cyperus rotundusPurple nutsedgeFriedman and Horowitz (1971)Digitaria sanguinalisLarge crabgrassVander Veen (1935)Cyperus rotundusPurple nutsedgeFriedman and Horowitz (1971)Digera arvenis—Salas and Vieitez (1972)	Avena fatua	Wild oat	Tinnin and Muller (1971)
Bidens pilosaBeggar-ticksStevens and Tang (1985)Boerhovia diffusaSpiderlingSen (1976)Brassica nigraBlack mustardMuller (1969)Bromus japonicusJapanese bromeRice (1964)Bromus japonicusJapanese bromeRice (1964)Bromus tectorumDowny bromeRice (1964)Calluna vulgaris—Salas and Vieitez (1972)Camelina alyssumFlax weedGrummer and Beyer (1960)Camelina sativaLargeseed falseflaxGrummer and Beyer (1960)Celosia argentea—Pandya (1975)Cenchrus biflorusSandburSen (1976)Cenchrus pauciflorusField sandburRice (1964)Centaurea diffusaDiffuse knapweedFletcher and Renney (1963)Centaurea maculosaSpotted knapweedFletcher and Renney (1963)Chenopodium albumCommon lambsquartersCausanel and Kunesch (1979)Cirsium discolorTall thistileLetourneau et al. (1980)Cirsullis lovatus—Sen (1976)Ciruulis lovatus—Bhandari and Sen (1971)Ciruulis callosus—Sen (1976)Cyperus rotundusPurple nutsedgeTames et al. (1973)Cyperus rotundusPurple nutsedgeFriedman and Horowitz (1971)DiffuralangerassVander Veen (1935)Cyperus rotundusPurple nutsedgeFriedman and Horowitz (1971)Dipirai asinguinalisLarge crabgrassParenti and Rice (1969)Cipera arvenis—Salas and Vieitez (1972) <td< td=""><td>Berteroa incana</td><td>Hoary alyssum</td><td>Bhowmik and Doll (1979)</td></td<>	Berteroa incana	Hoary alyssum	Bhowmik and Doll (1979)
Boerhowia diffusaSpiderlingSen (1976)Brassica nigraBlack mustardMuller (1969)Bromus japonicusJapanese bromeRice (1964)Bromus tectorumDowny bromeRice (1964)Calluna vulgaris—Salas and Vieitez (1972)Cumelina alyssumFlax weedGrummer and Beyer (1960)Canelina sativaLargeseed falseflaxGrummer and Beyer (1960)Canelina sativaLargeseed falseflaxGrummer and Beyer (1960)Censia argentea—Pandya (1975)Cenchrus biflorusField sandburRice (1964)Centaurea diffusaDiffuse knapweedFletcher and Renney (1963)Centaurea raculosaSpotted knapweedFletcher and Renney (1963)Centaurea repensRussian knapweedFletcher and Renney (1963)Chenopodium albumCommon lambsquartersCaussanel and Kunesch (1979)Cirsium discolorTall thistileLetourneau et al. (1980)Cirsium discolorTall thistileLetourneau et al. (1956)Cirtullis luvatus—Sen (1976)Cynodon dactylonBermudagrassVanderVeen (1935)Cyperus esculentusYellow nutsedgeTames et al. (1973)Cyperus rotundus—Salas and Vieitez (1972)Digera arvenis—Salas and Vieitez (1972) <td>Bidens pilosa</td> <td>Beggar-ticks</td> <td>Stevens and Tang (1985)</td>	Bidens pilosa	Beggar-ticks	Stevens and Tang (1985)
Brassica nigraBlack mustardMuller (1969)Bromus japonicusJapanese bromeRice (1964)Bromus tectorumDowny bromeRice (1964)Calluna vulgaris—Salas and Vieitez (1972)Cumelina alyssumFlax weedGrummer and Beyer (1960)Camelina sativaLargeseed falseflaxGrummer and Beyer (1960)Celosia argentea—Pandya (1975)Cenchrus biflorusSandburSen (1976)Centaurea diffusaDiffuse knapweedFletcher and Renney (1963)Centaurea diffusaDiffuse knapweedFletcher and Renney (1963)Centaurea maculosaSpotted knapweedFletcher and Renney (1963)Centaurea repensRussian knapweedFletcher and Renney (1963)Chenopodium albumCommon lambsquartersCaussanel and Kunesch (1979)Cirsium discolorTall thistileLetourneau et al. (1960)Cirullis colocynthis—Bhandari and Sen (1971)Ciruulis culosus—Sen (1976)Cymodon dactylonBermudagrassVanderVeen (1935)Cyperus esculentusYellow nutsedgeTames et al. (1973)Cyperus rotundusPurple nutsedgeFriedman and Horowitz (1971)Digitaria sanguinalisLarge crabgrassGressel and Holm (1964)Circine indicaGoosegrassAltieri and Doll (1978)Circine indicaGoosegrassAltieri and Doll (1978)Circine indicaGoosegrassAltieri and Doll (1977)	Boerhovia diffusa	Spiderling	Sen (1976)
Bromus japonicusJapanese bromeRice (1964)Bromus tectorumDowny bromeRice (1964)Calluna vulgaris—Salas and Vieitez (1972)Cumelina alyssumFlax weedGrummer and Beyer (1960)Camelina sativaLargeseed falseflaxGrummer and Beyer (1960)Canelina sativaLargeseed falseflaxGrummer and Beyer (1960)Canelina sativaLargeseed falseflaxGrummer and Beyer (1960)Celosia argentea—Pandya (1975)Cenchrus biflorusSandburSen (1976)Cenchrus pauciflorusField sandburRice (1964)Centaurea diffusaDiffuse knapweedFletcher and Renney (1963)Centaurea maculosaSpotted knapweedFletcher and Renney (1963)Centaurea repensRussian knapweedFletcher and Renney (1963)Chenopodium albumCommon lambsquartersCaussanel and Kunesch (1979)Cirsium arvenseCanada thistleStachon and Zimdahl (1980)Cirrullis colocynthis—Bhandari and Sen (1971)Cirrullis lavatus—Sen (1976)Cyperus esculentusYellow nutsedgeTames et al. (1973)Cyperus rotundusPurple nutsedgeFriedman and Horowitz (1971)Objera arvenis—Salas and Vieitez (1972)Digituria sanguinalisLarge crabgrassParenti and Rice (1969)CarcopariaBarnyardgrassGressel and Holm (1964)Elcusine indicaGoosegrassAltieri and Doll (1978)Ericu scopariaHeathBallester et al. (1977)<	Brussica nigra	Black mustard	Muller (1969)
Bromus tectorumDowny bromeRice (1964)Calluna vulgaris—Salas and Vieitez (1972)Cumelina alyssumFlax weedGrummer and Beyer (1960)Camelina sativaLargeseed falseflaxGrummer and Beyer (1960)Canelina sativaLargeseed falseflaxGrummer and Beyer (1960)Canelina sativaLargeseed falseflaxGrummer and Beyer (1960)Cenchrus biflorusSandburSen (1975)Cenchrus pauciflorusField sandburRice (1964)Centaurea diffusaDiffuse knapweedFletcher and Renney (1963)Centaurea maculosaSpotted knapweedFletcher and Renney (1963)Centaurea repensRussian knapweedFletcher and Renney (1963)Chenopodium albumCommon lambsquartersCausanel and Kunesch (1979)Cirsium arvenseCanada thistleStachon and Zimdahl (1980)Cirsium discolorTall thistileLetourneau et al. (1976)Ciruulis lavatus—Bhandari and Sen (1971)Ciruulis colocynthis—Sen (1976)Cyperus esculentusYellow nutsedgeTames et al. (1973)Cyperus rotundusPurple nutsedgeFriedman and Horowitz (1971)Daboecia polifolia—Salas and Vieitez (1972)Digituria sanguinalisLarge crabgrassParenti and Rice (1969)Echinochloa crus-galliBarnyardgrassGressel and Holm (1964)Echinochloa crus-galliGoosegrassAltieri and Doll (1978)Ericu scopariaHeathBallester et al. (1977)	Bromus japonicus	Japanese brome	Rice (1964)
Calluna vulgaris—Salas and Vieitez (1972)Cunelina alyssumFlax weedGrummer and Beyer (1960)Cunelina sativaLargeseed falseflaxGrummer and Beyer (1960)Celosia argentea—Pandya (1975)Cenchrus biflorusSandburSen (1976)Cenchrus pauciflorusField sandburRice (1964)Centaurea diffusaDiffuse knapweedFletcher and Renney (1963)Centaurea maculosaSpotted knapweedFletcher and Renney (1963)Centaurea repensRussian knapweedFletcher and Renney (1963)Chenopodium albumCommon lambsquartersCaussanel and Kunesch (1979)Cirsium arvenseCanada thistleStachon and Zimdahl (1980)Cirsium discolorTall thistileLetourneau et al. (1956)Cirtullis colocynthis—Bhandari and Sen (1971)Cirtullis lavatus—Sen (1976)Cyperus esculentusYellow nutsedgeTames et al. (1973)Cyperus rotundusPurple nutsedgeFriedman and Horowitz (1971)Digitaria sanguinalisLarge crabgrassParenti and Rice (1969)Chinochloa crus-galliBarnyardgrassParenti and Rice (1969)Chinochloa crus-galliBarnyardgrassAltieri and Doll (1978)Erica scopariaHeathBallester et al. (1977)	Bromus tectorum	Downy brome	Rice (1964)
Cumelina alyssumFlax weedGrummer and Beyer (1960)Cumelina sativaLargeseed falseflaxGrummer and Beyer (1960)Celosia argentea—Pandya (1975)Cenchrus biflorusSandburSen (1976)Cenchrus pauciflorusField sandburRice (1964)Centaurea diffusaDiffuse knapweedFletcher and Renney (1963)Centaurea diffusaDiffuse knapweedFletcher and Renney (1963)Centaurea repensRussian knapweedFletcher and Renney (1963)Centaurea repensRussian knapweedFletcher and Renney (1963)Chenopodium albumCommon lambsquartersCaussanel and Kunesch (1979)Cirsium discolorTall thistileLetourneau et al. (1980)Cirsium discolorTall thistileLetourneau et al. (1971)Cirtullis lavatus—Bhandari and Sen (1972)Cucumis callosus—Sen (1976)Cyperus esculentusYellow nutsedgeTames et al. (1973)Cyperus rotundusPurple nutsedgeFriedman and Horowitz (1971)Daboecia polifolia—Salas and Vieitez (1972)Digitaria sanguinalisLarge crabgrassParenti and Rice (1969)Echinochloa crus-galliBarnyardgrassGressel and Holm (1964)Elcusine indicaGoosegrassAltieri and Doll (1978)Ericu scopariaHeathBallester et al. (1977)	Calluna vulgaris	_	Salas and Vieitez (1972)
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Digera arvenis—Sarma (1974)Digitaria sanguinalisLarge crabgrassParenti and Rice (1969)Echinochloa crus-galliBarnyardgrassGressel and Holm (1964)Eleusine indicaGoosegrassAltieri and Doll (1978)Ericu scopariaHeathBallester et al. (1977)	Daboecia polifolia	-	Salas and Vieitez (1972)
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Eleusine indica Goosegrass Altieri and Doll (1978) Erica scoparia Heath Ballester et al. (1977)	Echinochloa crus-gulli	Barnyardgrass	Gressel and Holm (1964)
Erica scoparia Heath Ballester et al. (1977)	Eleusine indica	Goosegrass	Altieri and Doll (1978)
	Erica scoparia	Heath	Ballester et al. (1977)

Table	A.6.	Cont	inued.
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Scientific Name	Common Name	First Reference"
Euphorbia corollata	Flowering spurge	Rice (1964)
Euphorbia esula	Leafy spurge	Letourneau and Heggeness (1957)
Euphorbia supina	Prostrate spurge	Brown (1968)
Galium mollugo	Smooth bedstraw	Kohmmedahl (1965)
Helianthus annuus	Sunflower	Rice (1974)
Helianthus mollis		Anderson et al. (1978)
Hemarthria altissima	Bigalta limpograss	Tang and Young (1982)
Holcus mollis	Velvetgrass	Mann and Barnes (1947)
Imperata cylindrica	Alang-alang	Eussen (1978)
Indigofera cordifolia	Wild indigo	Sen (1976)
Iva xanthifolia	Marshelder	Letourneau et al. (1956)
Kochia scoparia	Kochi a	Wali and Iverson (1978)
Lactuca scariola	Prickly lettuce	Rice (1964)
Lepidium virginicum	Virginia pepperweed	Bieber and Hoveland (1968)
Leptochloa filiformis	Red sprangletop	Altieri and Doll (1978)
Lolium multiforum	Italian ryegrass	Naqvi and Muller (1975)
L <u>vchnis alba</u>	White cockle	Bhowmik and Doll (1979)
Matricaria inodora	Mayweed	Mann and Barnes (1945)
Nepeta cataria	Catnip	Letourneau et al. (1956)
Ocnothera biennis	Evening primrose	Bieber and Hoveland (1968)
Panicum dichotomiflorum	Fall panicum	Bhowmik and Doll (1979)
Parthenium hysterophorus	Ragweed parthenium	Sarma et al. (1976)
Plantago purshii	Wooly plantain	Rice (1964)
Poa pratensis	Bluegrass	Alderman and Middleton (1925)
Polygonum aviculare	Prostrate knotweed	Al Saadawi and Rice (1982)
Polygonum orientale	Princesfeather	Datta and Chatterjee (1978)
Polygonum pensylvanicum	Pennsylvania smartweed	Letourneau et al. (1956)
Polygonum persicaria	Ladysthumb	Martin and Rademacher (1960)
Portulaca ol eracea	Common purslane	Letourneau et al. (1956)
Rumex crispus	Dock	Einhellig and Rasmussen (1975)
Saccharum spontaneum	Wild cane	Amritphale and Mall (1978)
Salsolu kali	Russian thistle	Lodhi (1979)
Salvadora oleoides		Mohnat and Soni (1976)
Schinus molle	California peppertree	Anaya and Gomez-Pompa (1971)
Setaria fab eri	Giant foxtail	Schreiber and Williams (1967)
Setaria glauca	Yellow foxtail	Gressel and Hoim (1964)
Setaria viridis	Green foxtail	Rice (1964)
Solunum surattense	-	Sharma and Sen (1971)
Solidago sp.	Goldenrod	Letourneau et al. (1956)
Sorghum halepense	Johnsongrass	Abdul-Wahab and Rice (1967)
Stellaria media (L.)	Common chickweed	Mann and Barnes (1950)
Tugetes patula	Wild marigold	Altieri and Doll (1978)
Trichodesma amplexicaule	-	Sen (1976)
Xanthium pensylvanicum	Common cocklebur	Rice (1964)

"Several other reports may also be available. The reference cited is the earliest report of which we are aware.

Source: Putnam, A. R., and L. A. Weston. 1986. Adverse impacts of allelopathy in agricultural systems. In: Putnam and Tang (eds.), p 43-56.

Allalopathic	Class of	
Species	Chemical Produced	Affected Species
Trees		
Sugar maple	Phenolics	Yellow birch
Hackberry	Coumarins	Herbs, grasses
Eucalyptus	Phenolics,	Shrubs, herbs,
	terpenes	grasses
Walnut	Quinone (juglone)	Trees, shrubs, herbs
Juniper	Phenolics	Grasses
Sycamore	Courmarins	Herbs, grasses
Black cherry	Cyanogenic	Red maple
•	glycosides	
Oaks	Courmarins.	Herbs, grasses
	other phenolics	
Sassafras	Terpenoids	Elm, maple
Poplar	Phenolics	Shrub mycorrhizae
Shrubs		
Laurel	Phenolics	Black spruce
Nanzanita	Courmarins,	Herbs, grasses
	other phenolics	-
Bearberry	Phenolics	Pine, spruce
Sumac	Phenolics,	Douglas-fir
	terpenoids	-
Rhododendron	Phenolics	Douglas-fir
Elderberry	Phenolics	Douglas-fir
Lyonia	Phenolics	Slash pine
Other		_
Aster	Phenolics, terpenoids	Sugar maple, black cherry
Goldenrod	Phenolics, terpenoids	Sugar maple, black cherry
New York fern	Phenolics	Black cherry
Bracken fern	Phenolics	Douglas-fir
Fescue	Phenolics	Sweetgum
Shorthusk grass	Phenolics	Black cherry
Clubmoss	Phenolics	Black cherry
Reindeer lichen	Phenolics	Jack pine and white spruce mycorrhizae
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Table A.7.--Allelopathic Plants in Forestry.

Source: Fisher, R. F. 1987. Allelopathy: a potential cause of regeneration failure. Journal of Forestry. June: 346-8, 50.

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