Allelopathy

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Preface

No general monograph on the subject of allelopathy has been published previously in the English language, and none in any language since Grodzinsky's in 1965, in Russian. His book has not been translated and has had limited distribution outside the USSR. Moreover, much of the research that has established the field of allelopathy has been published since that time. The wide acceptance by ecologists of allelopathy as an important ecological phenomenon has occurred only within the past ten years. Thus, there appears to be a need for a general reference source in this field, both for researchers in the discipline and as an overview for those who desire to learn something about the subject.

Most significant contributions in the field, available at the time of writing, have been discussed; but no attempt has been made to include all publications that are in some way related to allelopathy. In fact, I have deliberately refrained from discussing the antibiotics involved primarily in medicine and most of the research concerned with biochemical interactions involved in plant diseases. My primary goal has been to discuss the broad ecological roles of allelopathy.

I have used the term allelopathy in the broad sense of Molisch (1937) to include biochemical interactions among plants of all levels of complexity, including microorganisms. Any restriction of this use does not make practical sense, as a perusal of this monograph will confirm. All levels of interaction are inextricably interwoven in ecological phenomena.

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Introduction

I. MEANING AND ORIGIN OF TERM ALLELOPATHY

Several recent investigators have used the term allelopathy to refer to the deleterious effect that one higher plant has on another through the production of chemical retardants that escape into the environment (Martin and Rademacher, 1960a; Muller, 1966). Molisch (1937) coined the term to refer to biochemical interactions between all types of plants including microorganisms. His discussion indicated that he meant the term to cover both detrimental and beneficial reciprocal biochemical interactions. However, the term was derived from two Greek words meaning mutual harm.

I feel that the current use of the term, allelopathy, should include any direct or indirect harmful effect by one plant (including microorganisms) on another through the production of chemical compounds that escape into the environment. That is the way I will use the term throughout this book.

The salient point concerning allelopathy is that its effect depends upon a chemical compound being added to the environment by an allelopathic agent. Allelopathy is thus separated from competition involving the removal or reduction of some factor from the environment that is required by some other plant sharing the habitat. The factors that may be reduced by competition include water, minerals, food, and light.

Unfortunately, many biologists either consider allelopathy to be a part of competition or, worse, are completely unaware of the phenomenon of allelopathy. Virtually none of the papers I have read, which purported to demonstrate some aspect of competition, has in any way eliminated allelopathy as a possible cause of the observed results.

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I agree with the suggestion of Muller (1969) that the term interference should be used to refer to the overall deleterious effects of one plant on another, thus encompassing both allelopathy and competition.

II. SUGGESTED TERMINOLOGY FOR CHEMICAL INTERACTIONS BETWEEN PLANTS OF DIFFERENT LEVELS OF COMPLEXITY

Grümmer (1955) suggested that special terms be adopted for the chemical inhibitors involved in allelopathy based on the type of plant producing the inhibitor and the type of plant affected. He recommended the commonly used term antibiotic for a chemical inhibitor produced by a microorganism and effective against a microorganism. He recommended Waksman's suggested term phytoncide for an inhibitor produced by a higher plant and effective against a microorganism. He suggested Gaumann's term marasmins for compounds produced by microorganisms and harmful to higher plants, and he coined the term kolines for chemical inhibitors produced by higher plants and effective against higher plants.

The antibiotics have been investigated chiefly in connection with the treatment of human ailments, and such investigations are not in the scope of the present ecological treatment of allelopathy. A small amount of work has been done on antibiotics, which is directly related to basic ecology, and this will be discussed elsewhere.

Marasmins are very important in the field of plant pathology and thus are obviously of great ecological significance. These compounds have been widely discussed in many papers and texts, so I will discuss them only rather briefly in future chapters. Most of the ecological work that has been done in the area of allelopathy has been concerned with phytoncides and kolines, and these will be considered in detail in the following chapters.

When a specific allelopathic substance is considered, it may have a sharply limited scope of action such that it is not effective against higher plants if it is an antibiotic. On the other hand, it may act like the antibiotic, patulin, which exhibits a marked toxicity for higher plants also (Grümmer, 1955). Additionally, there are many kolines that inhibit growth of microorganisms and many phytoncides that inhibit growth of higher plants (Floyd and Rice, 1967; W. H. Muller, 1965; Nagy et al., 1964; Rice, 1965a). There are no doubt marasmins that inhibit microorganisms also.

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Historical Account of
Research on Allelopathy

I. HIGHER PLANTS VERSUS HIGHER PLANTS

DeCandolle (1832) was apparently one of the earliest scientists to suggest the possibility that some plants may excrete something from their roots which is injurious to other plants. He observed, for example, that thistles (*Cirsium*) in fields injure oats, euphorbe (*Euphorbia*) and *Scabiosa* injure flax, and rye plants (*Lolium*) injure wheat. He also described experiments of M. Macaire in which it was found that beans (*Phaseolus*) languish and die in water containing material previously exuded by roots of other individuals of the same species, whereas wheat flourishes in water charged with exudations from legumes. DeCandolle suggested that such excretions of roots could conceivably explain the exhaustion of soil by certain plants and thus the need for crop rotation.

DeCandolle's views were apparently given little credence by his contemporaries because it was almost 50 years before a similar suggestion appeared in the literature. Stickney and Hoy (1881) observed that vegetation under black walnut, *Juglans nigra*, is very sparse compared with that under most other commonly used shade trees. They pointed out also that no crop will grow under or very near it. Stickney stated that there is a question as to whether this is caused by water dripping from the tree, or by the tree being a gross feeder, thereby exhausting the soil. Hoy claimed, however, that the main reason vegetation does not thrive under these trees is the poisonous character of the drip. He said that the juice of the leaf is poisonous, and a solution made from it will keep off flies when applied to a horse.

Livingston (1905) presented convincing evidence that the failure of nonbog plants to grow in peat bogs is due to deleterious chemical substances, and that these substances account for the xerophytic habit of the plants that grow there.

Schreiner and his associates published a series of papers starting in 1907 in which they presented evidence that exhaustion of soil by single-cropping is due to addition of growth inhibitors to the soil by certain crop plants (Schreiner and Reed, 1907a,b, 1908; Schreiner and Shorey, 1909; Schreiner and Sullivan, 1909; Schreiner and Lathrop, 1911). Schreiner and Reed (1907b) demonstrated clearly that roots of seedlings of wheat (*Triticum*), oats (*Avena*), and certain other crop plants exude materials into the growing medium that elicit chemotropic responses by the roots of wheat and oat seedlings. Schreiner and Reed (1908) developed a technique that is still used for determining possible allelopathic effects of compounds obtained from the soil or from plants. They were able to show with this technique that many compounds previously identified from various plants were inhibitory to the growth and transpiration of wheat seedlings. Schreiner and Sullivan (1909) extracted an unidentified substance from soil fatigued by the growth of cowpeas, *Vigna catjang*, and found that the substance strongly inhibited the growth of cowpeas. Moreover, the soil from which the inhibitor was extracted was no longer inhibitory to the growth of cowpeas.

Cowles (1911) suggested that plant-produced toxins may be very important as causative agents in plant succession.

Pickering (1917, 1919) demonstrated that the leachate from trays containing certain species of grasses was inhibitory to the growth of apple seedlings. He designed his experiment such that mineral deficiencies, root interaction, shading, water deficiency, and oxygen exclusion were eliminated as possible causes of inhibition.

Magnus (1920) reported that the leaf sap of *Phacelia* and *Pelargonium* is inhibitory to the germination of some seeds, and Oppenheimer (1922) demonstrated that the tomato fruit (*Lycopersicum*) contains a strong inhibitor of seed germination.

Cook (1921) described the characteristic wilting of potato, *Solanum tuberosum*, and tomato, *Lycopersicum esculentum*, plants grown near *Juglans nigra*, black walnut. He also described the injurious effect of walnut on apple trees. These observations supported those of Stickney and Hoy (1881), and subsequently Massey (1925) did a careful study of the inhibitory effects of black walnut on alfalfa and tomato plants. In both cases, he found that the test plants wilted and died whenever their roots came in close contact with the walnut roots. This
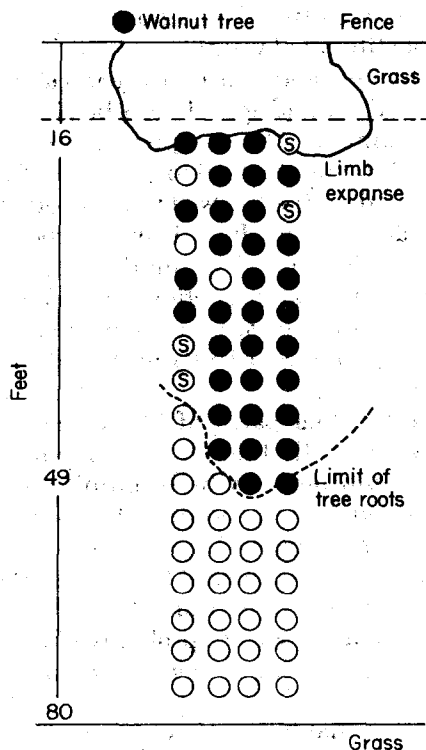
Fig. 1. Diagram showing conditions of tomato plants 8 weeks after setting plants in the immediate vicinity of a black walnut tree. Each circle indicates position in which a plant was set. Open circles indicate plants that remained healthy. Circles with S in them represent plants that died soon after transplanting. Closed circles indicate plants that wilted and died. (From Massey, 1925.)

effect was so definite that he could trace the extent of the walnut roots without removing soil just by observing the development of wilt in test plants (Fig. 1). There was no specific relationship between the region of greatest concentration of walnut roots and the wilting of tomatoes, which would be expected if the trouble were due to lowering of soil moisture. Apparently there is little or no poisoning of the soil, since the roots of the affected plants must be in close contact with those of the walnut. When several pieces of bark from walnut roots were placed in a water culture of tomato plants, the plants wilted and their roots browned within 48 hours. Addition of bark from walnut roots to soil in which tomato plants were growing caused the plants to

grow poorly. Massey suggested that juglone or some similar substance may be the toxic constituent of walnut.

Davis (1928) extracted and purified the toxic substance from the hulls and roots of walnut and found it to be identical to juglone, 5-hydroxy-α-naphthaquinone. The compound proved to be a powerful toxin when injected into the stems of tomato and alfalfa plants.

Elmer (1932) found that ripe fruits of four varieties of apples—Winesap, Stayman, Jonathan, and Ben Davis—produced volatile substances that inhibited the normal sprout development of germinating potatoes. When nongerminated sections of potato tubers were exposed to the volatile substances, bud dominance was overcome. He found also that ripe Kieffer pear fruits inhibited growth of sprouts of germinating potatoes.

Waks (1936) reported that parks of black locust, *Robinia pseudoacacia*, are nearly void of all other vegetation, and bark and wood of black locust contain substances which inhibit the growth of barley.

Molisch (1937) coined the term allelopathy, as previously indicated, and he performed a great many experiments with ripe apple fruits which confirmed and greatly extended the results of Elmer (1932).

Loehwing (1937) reviewed earlier literature on plant-produced toxins and concluded that they were probably of no great significance. In my opinion, however, he failed to give any satisfactory reasons for arriving at this conclusion.

Bode (1940) reported that foliar excretions of *Artemisia absinthium* inhibited the growth of seedlings of *Foeniculum vulgare* and other species within approximately 1 m of the *Artemisia* plants. According to Bode, the leaves of this species have glandular hairs that excrete ethereal oils and the inhibitor absinthiin. This is formed especially during dry, hot weather and appears as numerous droplets on the surface of the hairs. When it rains, these droplets are washed away and spread on the neighboring plants. Funke (1943) confirmed and extended Bode's results with *Artemisia absinthium*. He measured the effects of a hedge of this species on a large number of test species planted near it and found that all were affected. No effect was noted in the same test species planted near a hedge of *Atriplex hortensis*. Funke found that fresh or pulverized leaves of *A. absinthium* dug into the soil retarded the germination of *Pisum sativum* seeds and permanently lowered the percent germination of *Phaseolus multiflorus* seed planted in the soil. Growth of *Phaseolus* was permanently retarded also by the *Artemisia* leaves. Subsequently, seed germination and seedling growth of numerous other species were found to be

severely inhibited in soil in which *Artemisia* leaves were incorporated.

Benedict (1941) studied the reasons for the natural thinning of smooth brome, *Bromus inermis,* and he found that when oven-dried roots of smooth brome were placed in soil with seeds of that species, a significant reduction in the subsequent dry weight of the seedlings resulted. He obtained similar results by adding a leachate from an old culture of smooth brome to seedlings of the species. He thus established the production of a toxic substance by smooth brome roots.

Went (1942) investigated the relationship between certain shrubs and annual plants in a desert area in California. He reported that certain annuals were rarely associated with some shrubs unless the shrubs were dead; some annuals were chiefly associated with certain shrubs; and others showed no definite affiliations. He found that annuals were rarely associated with *Encelia farinosa* unless the shrub was dead. Went suggested that the observed relationships might be due to substances produced by living roots of the shrubs. Subsequently, Gray and Bonner (1948a,b) reported that the leaves of *Encelia farinosa* produce a substance that causes pronounced inhibition in growth of many other plants. They identified the compound as 3-acetyl-6-methoxybenzaldehyde and demonstrated that it is toxic to many plants, but not to *Encelia farinosa.* This inhibitor is produced primarily in the leaves and is released when the leaves fall to the ground and decompose. Evidence indicated that this inhibitor is relatively persistent in the soil.

Kuhn *et al.* (1943) reported that mountain ash, *Sorbus aucuparia,* produces parasorbic acid, an unsaturated lactone, which inhibits germination of *Lepidium* seeds in a dilution of 1:1000 and allows only 10–80% germination at 1:10,000.

Bonner and Galston (1944) observed that the edge rows in guayule, *Parthenium argentatum,* plantings at Salinas, California had much larger plants than the center rows and that the differences could not be eliminated by heavy watering and mineral application. Additionally, roots of adjacent plants did not intermingle but grew in entirely separate areas, and seedlings of guayule plants virtually never grew under larger guayule plants. On the other hand, such seedlings were commonly found growing under other kinds of shrubs. Experiments were designed to determine if guayule produces a growth inhibitor. Initial experiments indicated that leachates from pots of 1-year-old guayule plants were very inhibitory to guayule seedlings but not to tomato seedlings. In another type of experiment performed in sand

culture, guayule seedlings were planted in sand adjacent to a 1-year-old guayule plant. In addition, other guayule seedlings were planted in fresh sand in a glass jar, and the jar was placed in an excavation in the sand under the older guayule plant so that the shading effect on all seedlings was the same. Thus, the seedlings in the glass jar were not subjected to any possible inhibiting material that might be present in the sand around the older plant. Seedlings growing under the guayule plant had a high mortality rate and grew slowly if not contained in glass jars, whereas those grown under the same conditions, but in a separate glass jar, had good growth and a lower mortality. Results of this experiment supported those of the initial one, indicating that roots of guayule plants excrete a toxin.

Subsequent experiments with nutrient solutions and distilled water leachates of roots of guayule plants enabled Bonner and Galston to identify the toxin as *trans*-cinnamic acid. This compound is highly toxic to guayule seedlings, with significant growth reduction resulting from as little as 1 mg/liter of culture solution. Guayule seedlings were found to be at least 100 times as sensitive to cinnamic acid as tomato seedlings, which explains why tomato seedlings were not affected by the leachates of the guayule plants in the initial experiments.

In later work, Bonner (1946) found that cinnamic acid is toxic to the growth of guayule plants in soil also. Incorporation of 10 mg of cinnamic acid in 1500 gm of soil, making a concentration of less than 1 part in 100,000, significantly depressed the growth of the plants over a period of 6 weeks. He found that this toxin is unstable in the soil, however, and decreases with time. It does not disappear in sterilized soil, so obviously it is decomposed by microorganisms. Apparently it has to be added to the soil continuously to be effective as a koline, as has since been demonstrated in numerous instances with other kolines.

McCalla and Duley (1948) reported that soaking corn grains for 24 hours in an extract of sweet clover markedly inhibited subsequent germination and growth. An extract made with 1 gm sweet clover tops (cut when 18–24 inches high) in 5 ml of distilled water reduced the percentage germination of corn from 95% in the control to 33% after soaking 24 hours in the extract. The subsequent top growth of the corn seedlings after 3 days was reduced from 2.8 cm in the control to 0.3 cm in the test, and the root growth was reduced from 6.4 cm in the control to 0.8 cm in the test.

In subsequent work, McCalla and Duley (1949) found in greenhouse studies that mulching of soil from the Agronomy Farm at Lincoln, Nebraska with wheat straw at the rate of 2 to 4 tons per acre