Allelopathy: Can It Be Managed to Benefit Horticulture?

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The term allelopathy was introduced by Molisch (22) in 1937, and refers to all biochemical interactions (stimulatory and inhibitory) among plants, including microorganisms. The fact that the term is literally translated as "mutual harm or suffering" has probably led to other interpretations and confusion. Several scientists have suggested narrowing the definition to include only higher plants and harmful interactions. Rice (38) defined allelopathy in his first edition to include only harmful effects, but he recently opted to restate Molisch's premise in his 2nd edition (39). Molisch's broad definition of allelopathy is probably appropriate because considerable research has indicated that involvement of microorganisms and lower plants in phytotoxin production. Also, natural compounds that inhibit growth at certain concentrations often enhance growth at lower concentrations.

Allelopathy comprises an important mechanism of plant interference and is mediated through the addition of chemicals to the plant environment. In contrast, the other major mechanism of plant interference, competition or allelospoly, is a subtractive process that involves removal of resources, e.g., water, minerals, or light energy. The 2 interference mechanisms have been virtually impossible to separate in the field, but both are well-documented in laboratory experiments. Ecologists and weed scientists alike often have ignored allelopathy as a possible mechanism in their so-called "competition studies".

Impacts of allelopathy on horticulture

The potential impacts of allelopathy on agriculture have been reviewed extensively during the past 2 decades (2, 21, 28, 32, 35, 44). Emphasis has been placed on the detrimental influences of plants or their residues that may provide reduced crop growth or productivity. In particular, problems with certain crop rotations, toxicity of surface residues in reduced tillage systems, autotoxicity and replanting problems, and strong interference by certain weed species are frequently mentioned.

There are numerous examples of allelopathy in horticulture. Pickering (29) provided evidence as early as 1917 that orchard sods interfere with apple trees by release of toxins as well as by competition. Krylov (11) reported that potatoes interplanted in apple orchards produced toxins that inhibited apple tree photosynthesis and growth. Tukey (44) reviewed the impacts of budding and grafting trees and indicated that these biochemical interactions (often inhibitory) could be considered as allelopathic responses. Molisch's (22) pioneering work with ethylene from pome fruits showed the potential for both growth promotion and inhibition with the same compound.

An important horticultural problem that apparently involves allelopathy is the so-called replant syndrome. Replant problems are complex and often involve a buildup of pests (e.g., nematodes or diseases), but soil toxins also are implicated in the difficulty of reestablishing many perennial horticultural crops, including asparagus (10, 47), apple (4), peach (27, 30), citrus (5), and a number of ornamentals (25, 44).

Allelopathy may cause great economic losses in horticulture through strong growth interferences imposed by a number of annual and perennial weeds. Numerous weed species have been shown to have allelopathic potential (37, 39). Ahlgren and Aamodt (1) suggested as early as 1939 that quackgrass [*Agropyron repens* (L.) Beauv.] interfered with crop growth by producing toxins. Several workers have since confirmed that idea and in some instances have isolated toxic chemicals from the rhizomes or from decaying residues (7, 19, 24, 43). Recent work in our laboratory indicates living quackgrass or its residues can seriously reduce the N-fixing potential of several legumes (45). We suspect the toxins alter root growth in a manner that prevents infection by *Rhizobium* spp., since nodulation fails in the presence of ample bacteria.

Exploiting allelopathy as a weed control strategy

Weeds such as quackgrass, yellow nutsedge (*Cyperus esculentus* L.), or certain mustards [e.g., *Brassica nigra* (L.) Koch] can dominate agricultural sites (37). It was this observation that prompted W. Duke and me in 1973 to explore the possibility of achieving similar dominance of crops over weeds using allelopathic mechanisms. Our initial idea was to find allelopathic characteristics within the germplasm of crops, after which this might be genetically incorporated into cultivars (31). More recently, several other approaches, including the use of allelopathic rotational crops or intercrops, have evolved (32). The main objective of this paper is to outline the progress of these efforts from our group and others.

We observed great differences in the ability of allelopathic crops to alter the growth of both dicotyledon and monocotyledon weed indicators in the initial screening of the USDA collection of cucumber accessions (31). Some of the latter actually stimulated weed growth, while a few severely inhibited both germination and seedling growth. One apparently allelopathic accession, PI 169391, subsequently was studied intensively in greenhouse and field experiments (16–18). Field tests consistently showed superior weed suppression with PI 169391 (as compared to commercially available cultivars), but the level of weed suppression was unacceptable on some soil types and under certain environmental conditions (16). We attributed poor activity to high water solubility of inhibitors released from the seeds and seedlings within the first few days of growth (17, 18). Those assays would not have detected cucumbers, which could have expressed allelopathy at later stages of growth. Work of Ells (personal communication), Gaidamak (8), and Lockerman and Putnam (18) all suggest allelopathic potential in older cucumber plants.

Research into the allelopathic potential of crop germplasm has been quite limited. Only limited screening of oats (*Avena* spp.) (6), soybean [*Glycine max* (L.) Merr.] (20, 40), and sunflower (*Helianthus annuus* L.) (12) collections has been completed in addition to this cucumber work. Considerable differences were found among accessions and cultivars in these collections. Much more research needs to be done in this area, and certainly plant geneticists should become involved. It could also be beneficial to look at total interference ability of plants at later growth stages, in addition to allelopathic potential in younger plants.

It is surprising there has been so little effort in screening turfgrasses for allelopathic potential. Recent work in the northwestern United States indicates that certain perennial ryegrasses (*Lolium* spp.) have great potential for suppressing weeds in orchard floors (23). Whether this suppression is primarily due to allelopathic attributes has not been determined. In any event, the use of allelopathic grasses for weed control in lawns, golf courses, orchard floors, etc., could be substantial.

Other ways that allelopathy might be used for weed control are to manipulate allelopathic crops or their residues either sequentially or as intercrops in annual and perennial cropping systems. Several cereal grains in particular have strong interference ability and appear to be allelopathic. For decades, growers have used barley (*Hordeum vulgare* L.) and rye (*Secale cereale* L.) as "smother crops.". Overland (26) indicated at least a portion of barley's suppressive effect

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can be attributed to allelopathy. Recent work in this laboratory confirms that allelopathy plays an important role in both rye (3) and sorghum (13, 14, 53) interference: whereas research in North Carolina confirms allelopathy in rye and wheat residues (15, 41). Guenzi and McCalla (9) previously reported the presence of phytotoxins in the residues of a variety of cereal grains.

There was renewed interest in the 1970s in the development of reduced tillage systems for a number of crops, including vegetables. No-tillage systems in particular lend themselves to management of surface resideus.

Research was initiated in 1976 to select suitable plants whose residues might provide effective weed suppression in a variety of horticultural cropping systems (34). Both fall- and spring-planted grasses were evaluated for weed-suppressing ability after desiccation by freezing or contact herbicides. Populations of common purslane (*Portulaca oleracea* L.) and smooth crabgrass (*Digitaria ischaemum* Schreb) were reduced 70% and 98%, respectively, by residues of sorghum (33). Total weed biomass was also consistently reduced with residues of barley, oats, wheat (*Triticum aestivum* L.), and rye. In general, larger seeded vegetables (particularly legumes) grew normally or were sometimes stimulated in the cover crop residues, whereas several species of smaller-seeded vegetables (carrots, onions, etc.) were severely injured (33). The use of a nontoxic control mulch allowed separation of the physical and chemical aspects of the residues (3, 33). Greenhouse experiments with 2 soils confirmed both weed-suppressing and crop-stimulating effects of the sorghum residues. Water extracts of sorghum herbage were toxic to several weed indicators in sterile assays, indicating that at least a portion of the toxins were released directly by the plants (13, 14). Recent work with rye also indicates release of toxic compounds from its residues (3, 41).

There are several methods by which the cover crops could be managed in horticultural systems. Cover crops for cool-season vegetables (e.g., peas or cole crops), may be planted in the autumn and killed with contact herbicides in the spring, at which time the vegetables are seeded or transplanted with as little soil disturbance as possible. Sorghums have also been sown in late summer and allowed to freeze, eliminating the need for a contact herbicide in the spring. Tillage or any incorporation of the residues into the soil greatly reduces weed control (33). Spring-planted, cool-season grasses may be used prior to warm-season vegetables. When the grasses are desiccated, this technique parallels the "stale seedbed" approach with the addition of a smother crop.

Autumn-planted cover crops, that overwinter and do not compete for resources with the crop during critical growth periods, have been used in perennial cropping systems (orchards, strawberry, and asparagus plantings) (34, 36). The crops were desiccated between 1 to 10 May and usually reached a height of about 0.5 m. Rye has provided the best results in this system, probably because it produces more biomass and toxins prior to desiccation. Residues of rye are generally more toxic to a variety of annual dicotyledonous weeds, moderately toxic to annual grasses, and have little or no effect on perennial weeds (3). Weed control in these systems lasts from 30 to 75 days and is dependent on soil and weather conditions. Weed control persists longer when rainfall occurs soon after the crops are desiccated, followed by relatively dry conditions.

Apple, tart cherry, and asparagus plants have all shown slight increases in growth after 4 years of maintenance in cover-crop systems as compared to clean cultivation or to repeated herbicide use where no surface residues have accumulated. We expect the water conservation aspects of the residue are important in this regard, but certainly several other factors cannot be eliminated. Yields of strawberries maintained with overwintered cover crops were similar or slightly lower than those maintained conventionally.

Management of no-tillage systems with cover crops does provide some interesting problems. Shifts in weed species distribution were expected, based on other long-term studies with fruits and agronomic crops. We have observed drastic changes in weed species after only 2 to 3 years of no-tillage. Adapted grasses and a few perennial species soon predominate, which may require changes in herbicide programs and perhaps even occasional tillage.

Another major problem we have encountered with vegetables is difficulty in achieving adequate stands. This appears to be a mechanical problem that will require and construction of better no-till planters for these crops. There is both lack of precise distribution of seed and failure to close the furrow adequately. Good stands will, however, give yields equal or superior to those in conventional tillage.

Recently, experiments have been conducted with management systems for vegetable production that employ both allelopathic cover crops prior to planting and sequential intercropping to suppress weeds between rows. Both sweet corn and tomatoes have performed surprisingly well in these experiments where early intercrops of broccoli and peas or perennially intercropped white clover reduced weed populations up to 90%. Sweet corn yields were reduced 18% to 33%, but the pea and broccoli intercropped systems produced land equivalent ratios (LER) to double that obtained with sweet corn monoculture. Tomato yields were reduced up to 40%, but several tomato–intercrop combinations do provide higher LERs.

Other possible benefits of allelochemicals in horticulture

Major research emphasis has been on the reduction of weeds. However, management of horticultural systems with rotational crops or interplants could provide many other benefits. The obvious benefits of mulches are conservation of soil and water. Perhaps less obvious may be their impact on a number of other organisms in the ecosystem. For example, the residues of certain crops are known to suppress certain root diseases (39). It has been proposed that plants suppressive to a number of pests (nematodes, arthropods, vertebrates, etc.) could be selected (46). Conversely, plants could be found that are compatible with or hosts for symbionts (N-fixers, mycorrhizae) and natural predators of important pests. More resources should certainly be expended on these efforts.

Research on allelochemicals (i.e., higher plant and microbial products) could lead to a new generation of pesticides and plant growth-regulating chemicals. Several of the major chemical companies are actively pursuing this idea and some promising leads have already developed. For example, herbicides with glyphosate-like activity have already been isolated from *Streptomyces* cultures (35). A cineole derivative is now being developed as a herbicide. Certain plant compounds may find use as precursors or intermediates in the synthesis of other chemicals.

The primary responsibility for putting much of this technology into a profitable production system will undoubtedly fall upon the horticulturist. A cooperative effort of scientists from several disciplines will be required to realize many of the opportunities previously discussed. Why not take a weed scientist, entomologist, plant pathologist, nematologist, microbiologist, or soil scientist (or even better, all 6) to lunch soon and discuss a cooperative project. It could be one of the most enjoyable and rewarding ventures of your career.

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Predicting Effects of Modified Cropping Systems: Forestry Examples

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Small conifers often must coexist with the components of early plant succession for prolonged periods of time in forest regeneration. Forest regeneration and the management of perennial horticultural crops are similar in this respect, since individual "crop" plants in both instances usually occur in close proximity to each other or associated species. Association of the crop with its neighbors may be detrimental in both situations (10, 15), but other interactions also are possible (8). Thus it is necessary for forest managers and horticulturists to recognize the physical, physiological, and environmental components that influence the outcome of plant-to-plant associations. It also is necessary for land managers (foresters, horticulturists, etc). to understand the consequences of their actions, since short-term impacts on vegetation can have long-term influences on environmental resource availability, subsequent vegetation, and the populations of other organisms. Long-term impacts of management are not exclusive to forest regeneration, but the need for prediction may be most obvious there because of the relative longevity of forest communities in comparison to most of those in agriculture.

Many studies have been conducted that explore the relative aggressiveness of brush and herbaceous species with respect to conifer seedlings (10). These studies are useful since they effectively assess the costs (biological or economical) of mixed plant associations on tree yield. In general, a sigmoidal relationship exists between tree