UF UNIVERSITY of FLORIDA
IFAS Extension

HS944

Allelopathy: How Plants Suppress Other Plants[1]

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What Is Allelopathy?

Allelopathy refers to the beneficial or harmful effects of one plant on another plant, both crop and weed species, from the release of biochemicals, known as allelochemicals, from plant parts by leaching, root exudation, volatilization, residue decomposition, and other processes in both natural and agricultural systems. Allelochemicals are a subset of secondary metabolites not required for metabolism (growth and development) of the allelopathic organism. Allelochemicals with negative allelopathic effects are an important part of plant defense against herbivory (i.e., animals eating plants as their primary food) (Fraenkel 1959; Stamp 2003).

The term *allelopathy* is from the Greek-derived compounds *allelo* and *pathy* (meaning "mutual harm" or "suffering") and was first used in 1937 by Austrian scientist Hans Molisch in the book *Der Einfluss einer Pflanze auf die andere - Allelopathie* (*The Effect of Plants on Each Other*) (Willis 2010). First widely studied in forestry systems, allelopathy can affect many aspects of plant ecology, including occurrence, growth, plant succession, the structure of plant communities, dominance, diversity, and plant productivity. Initially, many of the forestry species evaluated had negative allelopathic effects on food and fodder crops, but in the 1980s research was begun to identify species that had beneficial, neutral, or selective effects on companion crop plants (Table 1). Early research grew out of observations of poor regeneration of forest species, crop damage, yield reductions, replant problems for tree crops, occurrence of weed-free zones, and other related changes in vegetation patterns. Our purpose here is to introduce the concept of allelopathy, to cite specific examples, and to mention potential applications as an alternative weed management strategy.

Nature of Allelopathy

Commonly cited effects of allelopathy include reduced seed germination and seedling growth. Like synthetic herbicides, there is no common mode of action or physiological target site for all allelochemicals. However, known sites of action for some allelochemicals include cell division, pollen germination, nutrient uptake, photosynthesis, and specific enzyme function. For example, one study that examined the effect of an allelochemical known in velvetbean, 3-(3',4'-dihydroxyphenyl)-l-alanine (l-DOPA), indicated that the inhibition by this compound is due to adverse effects on amino acid metabolism and iron concentration equilibrium.

Allelopathic inhibition is complex and can involve the interaction of different classes of chemicals, such as phenolic compounds, flavonoids, terpenoids, alkaloids, steroids, carbohydrates, and amino acids, with mixtures of different compounds sometimes having a greater allelopathic effect than individual compounds alone. Furthermore, physiological and environmental stresses, pests and diseases, solar radiation, herbicides, and less than optimal nutrient, moisture, and temperature levels can also affect allelopathic weed suppression. Different plant parts, including flowers, leaves, leaf litter and leaf mulch, stems, bark, roots, soil, and soil leachates and their derived compounds, can have

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[1] This document is HS944, one of a series of the Horticultural Sciences Department, Florida Cooperative Extension Service, Institute of Food and Agricultural Sciences, University of Florida. Original publication date July 2003. Revised March 2013. Visit the EDIS website at http://edis.ifas.ufl.edu.

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allelopathic activity that varies over a growing season. Allelopathic chemicals or allelochemicals can also persist in soil, affecting both neighboring plants as well as those planted in succession. Although derived from plants, allelochemicals may be more biodegradable than traditional herbicides, but allelochemicals may also have undesirable effects on non-target species, necessitating ecological studies before widespread use.

Selective activity of tree allelochemicals on crops and other plants has also been reported. For example, *Leucaena leucocephala*, the miracle tree promoted for revegetation, soil and water conservation, and livestock nutrition in India, contains a toxic, non-protein amino acid in its leaves that inhibits the growth of other trees but not its own seedlings. *Leucaena* species have also been shown to reduce the yield of wheat but increase the yield of rice. Leachates of the chaste tree or box elder can retard the growth of pangolagrass but stimulate growth of bluestem, another pasture grass. Many invasive plants may have allelopathy as a feature for their ecological success. One study in China found that 25 out of 33 highly noxious weeds screened had significant allelopathic potential.

Time, environmental conditions, and plant tissue all factor into variations in allelochemical concentrations in the producer plant. Foliar and leaf litter leachates of *Eucalyptus* species, for example, are more toxic than bark leachates to some food crops. The allelopathic potential of mile-a-minute vine (*Ipomoea cairica*) is significantly greater at higher environmental temperatures. One study indicated that soil biota reduced the allelopathic potential of sticky snakeroot (*Ageratina adenophora*). Red fescue infected by a fungal endophyte produced more allelochemicals than plants that were not infected.

Research Strategies and Potential Applications

The basic approach used in allelopathic research for agricultural crops has been to screen both crop plants and natural vegetation for their capacity to suppress weeds. To demonstrate allelopathy, plant origin, production, and identification of allelochemicals must be established as well as persistence in the environment over time in concentrations sufficient to affect plant species. In the laboratory, plant extracts and leachates are commonly screened for their effects on seed germination, with further isolation and identification of allelochemicals from greenhouse tests and field soil confirming laboratory results. Interactions among allelopathic plants, host crops, and other non-target organisms must also be considered. Furthermore, allelochemistry may provide basic structures or templates for developing new synthetic herbicides. Studies have elucidated specific allelochemicals involved in weed suppression, including benzoxanoids in rye; diterpenoid momilactones in rice; tabanone in cogongrass; alkaloids and flavonoids in fescue; anthratectone and naphthotectone in teak (*Tectona grandis*); abscisic acid beta-d-glucopyranosyl ester in red pine; cyanamide in hairy vetch; and a cyclopropene fatty acid in hazel sterculia (*Sterculia foetida*).

Incorporation of allelopathic traits from wild or cultivated plants into crop plants through traditional breeding or genetic engineering methods could also enhance the biosynthesis and release of allelochemicals. Genetic basis of allelopathy has now been demonstrated in winter wheat and rice. Specific cultivars with increased allelopathic potential are known in both these crops.

An allelopathic crop can potentially be used to control weeds by planting a variety with allelopathic qualities, either as a smother crop, in a rotational sequence, or when left as a residue or mulch, especially in low-till systems, to control subsequent weed growth. For example, in one study, rye mulch had suppressive effects on pigweed and common purslane, but had no effects on velvetleaf and common lambsquarters. A fall cover crop of forage radish had weed suppression effects on the following season's crop. In a multiseason field study, when applied as a soil amendment, mustard seed meal derived from white mustard (*Sinapis alba*) was effective for weed suppression in organic sweet onion, but crop injury was also significant.

Alternatively, application of allelopathic compounds before, along with, or after synthetic herbicides could increase the overall effect of both materials, thereby reducing application rates of synthetic herbicides. Some attempts have been reported on application of aqueous extracts of allelopathic plants on crops for weed suppression. In one study, an extract of brassica (*Brassica napus*), sorghum, and sunflower was used on rain-fed wheat to successfully reduce weed pressure. When an allelopathic plant water extract was tank-mixed with atrazine, a significant degree of weed control was achieved in wheat with a reduced dose of herbicide. Sunflower residues with a preplant herbicide (Treflan®) enhanced weed suppression in broad bean.

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Table 1. Examples of allelopathy from published research

Allelopathic plant	Impact
Rows of black walnut interplanted with corn in an alley cropping system	Reduced corn yield attributed to production of juglone, an allelopathic compound from black walnut, found 4.25 m (~14 ft) from trees
Rows of Leucaena interplanted with crops in an alley cropping system	Reduced the yield of wheat and turmeric but increased the yield of maize and rice
Lantana, a perennial woody weed pest in Florida citrus	Lantana roots and shoots incorporated into soil reduced germination and growth of milkweed vine, another weed
Sour orange, a widely used citrus rootstock in the past, now avoided because of susceptibility to citrus tristeza virus	Leaf extracts and volatile compounds inhibited seed germination and root growth of pigweed, bermudagrass, and lambsquarters
Red maple, swamp chestnut oak, sweet bay, and red cedar	Wood extracts inhibited lettuce seed as much as or more than black walnut extracts
Eucalyptus and neem trees	A spatial allelopathic relationship if wheat was grown within 5 m (~16.5 ft)
Chaste tree or box elder	Leachates retarded the growth of pangolagrass, a pasture grass, but stimulated the growth of bluestem, another grass species
Mango	Dried mango leaf powder completely inhibited sprouting of purple nutsedge tubers.
Tree of heaven	Ailanthone, isolated from the tree of heaven, has been reported to possess non-selective postemergence herbicidal activity similar to glyphosate and paraquat
Rye, fescue, and wheat	Allelopathic suppression of weeds when used as cover crops or when crop residues are retained as mulch
Broccoli	Broccoli residue interferes with growth of other cruciferous crops that follow
Jungle rice	Inhibition of rice crop
Forage radish	Cover crop residue suppression of weeds in the season following the cover crop
Jerusalem artichoke	Residual effects on weed species
Sunflower and buckwheat	Cover crop residues reduced weed pressure in fava bean crop
Tifton burclover	Growth inhibition in wheat and autotoxicity in burclover
Sunn hemp	Growth inhibition of smooth pigweed and lettuce and inhibition of vegetable seed germination
Desert horsepurslane (*Trianthema portulacastrum*)	Growth promotion of slender amaranth (*Amaranthus viridis*)
Rhazya stricta	Growth inhibition of corn
Rough cocklebur (*Xanthium strumarium*)	Growth inhibition of mungbean
Garlic mustard	Inhibition of arbuscular mycorrhizal fungi colonizing on sugar maple
Barbados nut (*Jatropha curcas*)	Extracts of leaves and roots inhibited corn and tobacco
Chicory	Inhibition of *Echinochloa crusgalli* and *Amaranthus retroflexus*
Swallow-worts	Invasive species in northeastern United States and southeastern Canada; inhibited several weed species
Vogel's tephrosia (*Tephrosia vogelii*)	Growth inhibition of corn and three narrow-leaf weed species
Green spurge	Inhibition of chickpea
Crabgrass	Inhibition of corn and sunflower but no inhibition of triticale when dry crabgrass residue was incorporated into soil
Silver wattle (*Acacia dealbata*)	Inhibition of native understory species in northwest Spain
Sticky snakeroot (*Ageratina adenophora*)	Volatiles were inhibitory to plants in non-native ranges but not inhibitory to plants in the native range
Santa Maria feverfew (*Parthenium hysterophorus*)	Aqueous extracts had inhibitory effects on cereal crops
Teak wood	Leaf extracts inhibited jungle rice and sedge, but not cultivated rice
Rabbitfoot grass	Leaf extracts and mulch inhibited wheat