



Allelopathy: How plants suppress other plants

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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) published in German (Willis, 2010).

Definition and Concept : According to Ferguson and Rathinasabapathi, “allelopathy refers to the beneficial or harmful effects of one plant on another plant, both crop and weed species, by the release of chemicals from plant parts by leaching, root exudation, volatilization, residue decomposition and other processes in both natural and agricultural systems.”

First, some definitions that relate to allelopathy.

- **Allelochemical**—for the purposes of this article, a toxic chemical produced by a plant
- **Phytochemical**—a chemical compound that occurs naturally in a plant
- **Toxicity** – the negative effect of a substance on a plant
- **Synthetic herbicide**—herbicides formed through a chemical process or chemical synthesis

According to Colquhoun, effective demonstration of allelopathy on plant growth and development and its reliable application in agricultural pest management have been minimal. The use of allelopathic cover crops such as rye has resulted in the greatest application of allelopathy in agriculture.

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.

Allelopathy is a biological phenomenon by which an organism produces one or more biochemicals that influence the growth, survival, and reproduction of other organisms. These biochemicals are known as allelochemicals and can have beneficial (positive allelopathy) or detrimental (negative allelopathy) effects on the target organisms. Allelochemicals are a subset of

secondary metabolites, which are not required for metabolism (*i.e.* growth, development and reproduction) of the allelopathic organism (Stamp, 2003). Allelochemicals with negative allelopathic effects are an important part of plant defense against herbivory (Stamp, 2003 and Fraenkel, 1959).

Allelopathy is characteristic of certain plants, algae, bacteria, coral, and fungi. Allelopathic interactions are an important factor in determining species distribution and abundance within plant communities, and are also thought to be important in the success of many invasive plants. For specific examples, see Spotted Knapweed (*Centaurea maculosa*), Garlic Mustard (*Alliaria petiolata*), *Casuarina/Allocasuarina* spp, and Nutsedge.

The process by which a plant acquires more of the available resources (such as nutrients, water or light) from the environment without any chemical action on the surrounding plants is called resource competition. This process is not negative allelopathy, although both processes can act together to enhance the survival rate of the plant species.



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.

Table 1 : Examples of allelopathy from published research

Allelopathic plant	Impact
Rice (<i>Oryza sativa</i>)	Rice allelopathy depends on variety and origin. Japonica rice is more allelopathic than Indica and Japonica-Indica hybrid.
Rows of black walnut inter planted with corn in an alley cropping system	Black walnut (<i>Juglans nigra</i>) produces (found 4.25 m (~14 ft) from trees) the allelochemical <i>juglone</i> and reduced yield attributed apple, Black berry, corn, potato and tomatoes while other not at all.
The leaf litter and root exudates of some <i>Eucalyptus</i> species of tree	The leaf litter and root exudates of some <i>Eucalyptus</i> species of tree (Sasikumar <i>et al.</i> , 2001).
Rows of Leucaena inter planted with crop plants in an alley cropping system	Reduced the yield of wheat and turmeric but increased the yield of maize and rice
<i>Chromolaena odorata</i> (<i>Eupatorium odoratum</i>) and <i>Lantana camara</i> , a perennial woody weed	Sheeja (1993) reported the allelopathic interaction of the weeds <i>Chromolaena odorata</i> (<i>Eupatorium odoratum</i>) and <i>Lantana camara</i> on selected major crops. 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, bermuda grass, and lambs quarters
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 <i>Neem</i> trees	A spatial allelopathic relationship if wheat was grown within 5 m (~16.5 ft)
Mango	Dried mango leaf powder completely inhibited sprouting of purple nut sedge tubers.
Tree of heaven	The tree of heaven, <i>Ailanthus altissima</i> , produces allelochemicals in its roots that inhibit the growth of many plants. Ailanthone, isolated from the tree of heaven, has been reported to possess non-selective post emergence herbicidal activity similar to glyphosate and paraquat
Rye 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
Sunflower and buckwheat	Cover crop residues reduced weed pressure in faba bean crop
Tifton burclover	Growth inhibition in wheat and autotoxicity in burclover
Sunhemp	Growth inhibition of smooth pigweed and lettuce and inhibition of vegetable seed germination
Desert horsepurslane (<i>Trianthema portulacastrum</i>)	Growth promotion of slender amaranthus (<i>Amaranthus viridis</i>)
<i>Rhazya stricta</i>	Growth inhibition of corn
Rough cocklebur (<i>Xanthium strumarium</i>)	Growth inhibition of mungbean
Garlic mustard	Inhibition of arbuscular mycorrhizal fungi colonizing on sugar maple
Barbados nut (<i>Jatropha curcas</i>)	Extracts of leaves and roots inhibited corn and tobacco
Chicory	Inhibition of <i>Echinochloa crusgalli</i> and <i>Amaranthus retroflexus</i>
Swallow-worts	Invasive species in northeastern United States and southeastern Canada; inhibited several 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 (<i>Acacia dealbata</i>)	Inhibition of native understory species
Santa Maria feverfew (<i>Parthenium hysterophorus</i>)	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

History : The term allelopathy from the Greek-derived compounds *allelo-* and *-pathy* (meaning “mutual harm” or “suffering”), was first used in 1937 by the Austrian professor Hans Molisch in the book *Der Einfluss einer Pflanze auf die andere - Allelopathie* (The Effect of Plants on Each Other) published in German (Willis, 2007). He used the term to describe biochemical interactions that inhibit the growth of neighboring plants, by another plant (Roger *et al.*, 2006). In 1971, Whittaker and Feeny published a study in the journal *Science*, which defined allelochemicals as all chemical interactions among organisms (Willis, 2007). In 1984, Elroy Leon Rice in his monograph on allelopathy enlarged the definition to include all direct positive or negative effects of a plant on another plant or on micro-organisms by the liberation of biochemicals into the natural environment (Rice, 1984). Over the next ten years, the term was used by other researchers to describe broader chemical interactions between organisms, and by 1996 the International Allelopathy Society (IAS) defined allelopathy as “Any process involving secondary metabolites produced by plants, algae, bacteria and fungi that influences the growth and development of agriculture and biological systems” (Roger *et al.*, 2006). In more recent times, plant researchers have begun to switch back to the original definition of substances that are produced by one plant that inhibit another plant (Willis, 2007). Confusing the issue more, zoologists have borrowed the term to describe chemical interactions between invertebrates like corals and sponges (Willis, 2007).

Long before the term allelopathy was used, people observed the negative effects that one plant could have on another. Theophrastus, who lived around 300 BC noticed the inhibitory effects of pigweed on alfalfa. In China around the first century AD, the author of *Shennong Ben Cao Jing* described 267 plants that had pesticidal abilities, including those with allelopathic effects (Chang-Hung, 2006). In 1832, the Swiss botanist De Candolle suggested that crop plant exudates were responsible for an agriculture problem called soil sickness.

Allelopathy is not universally accepted among ecologists and many have argued that its effects cannot be distinguished from the competition which results when two (or more) organisms attempt to use the same limited resource, to the detriment of one or both. Allelopathy is a direct negative effect on one organism resulting from the input of substances into the environment by another. In the 1970s, great effort went into distinguishing competitive and allelopathic effects by some researchers, while in the

1990s others argued that the effects were often interdependent and could not readily be distinguished (Willis, 2007).

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 velvet bean, 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 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; anthrathectone 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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