BIOCHEMICAL INTERACTIONS AMONG PLANTS: ALLELOPATHY AS ECOSYSTEM REGULATOR

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Summary

Plants often release metabolites that might be beneficial or detrimental to the growth of receptor plants in managed or natural ecosystems. This phenomenon was termed *allelopathy*. The more volatile compounds, such as terpenoids, are released from plants in drought areas. On the other hand, water-borne phytotoxins, such as phenolics, flavonoids, or alkaloids, are released from plants in humid zone areas (see Table 1). The naturally occurring allelopathic compounds play important roles in regulating plant biodiversity, dominance, succession and climax of natural vegetation, as well as in the productivity of agroecosystems. However, the synthetic agrochemicals, such as herbicides, fungicides, nematocides, or other pesticides, may cause imbalance of soil microorganisms, nutrient deficiency, and change of soil physicochemical properties, resulting in decrease of crop productivity. The application of allelopathic substances into agricultural practice may reduce the use of the agrochemicals and reduce the environmental hazard. A unique example of a pasture-forest inter-cropping system could be used as a model for weed control in forest management. After the deforestation of coniferous or hardwood forests, a pasture grass, kikuyu grass (*Pennisetum clandestinum*), was transplanted onto the land. The grass was quickly established within six months. Significant suppression of weed growth by the kikuyu grass was found. The growth of coniferous or hardwood plants, however, was not suppressed but stimulated. Thus, allelopathic research in the twenty-first century has become particularly important as far as sustainable agriculture is concerned. Future allelopathic research is recommended to focus on the following tasks: 1) to understand more fully the role of allelopathy in nature and agro-ecosystem, 2) to survey potential allelopathic compounds in plants or microorganisms, 3) to develop new techniques for isolating allelopathic chemicals in plants and soils, 4) to understand the mode of action of allelopathic chemicals, 5) to enhance allelopathic properties in agronomic plants, 6) to use biotechnology to transfer allelopathic chemicals from one plant to another, and 7) to establish practical methods for allelopathic plants in the field.

1. Introduction

Extinction of species and reduction of biodiversity is primarily attributable to the impact of human activities. However, perhaps a small amount of plant species extinction is due to natural selection, involving mechanism of plant interactions, such as competition and allelopathy. Through evolutionary processes, both competition and allelopathy play more important roles in regulating the species diversity of a plant community. Molisch (1937) studied the effect of ethylene upon plant growth and coined a word "*Allelopathy*" from two Greek words "allelo" and "pathy" meaning "mutual harm", but he at that time described allelopathy as both beneficial and harmful biochemical interaction between organisms. The allelopathic compounds are secondary plant metabolites, including a variety of compounds, which are released from plants into the environment by means of four ecological processes: volatilization, leaching, decomposition of plant residues in soil, and root exudation (see Figure1).

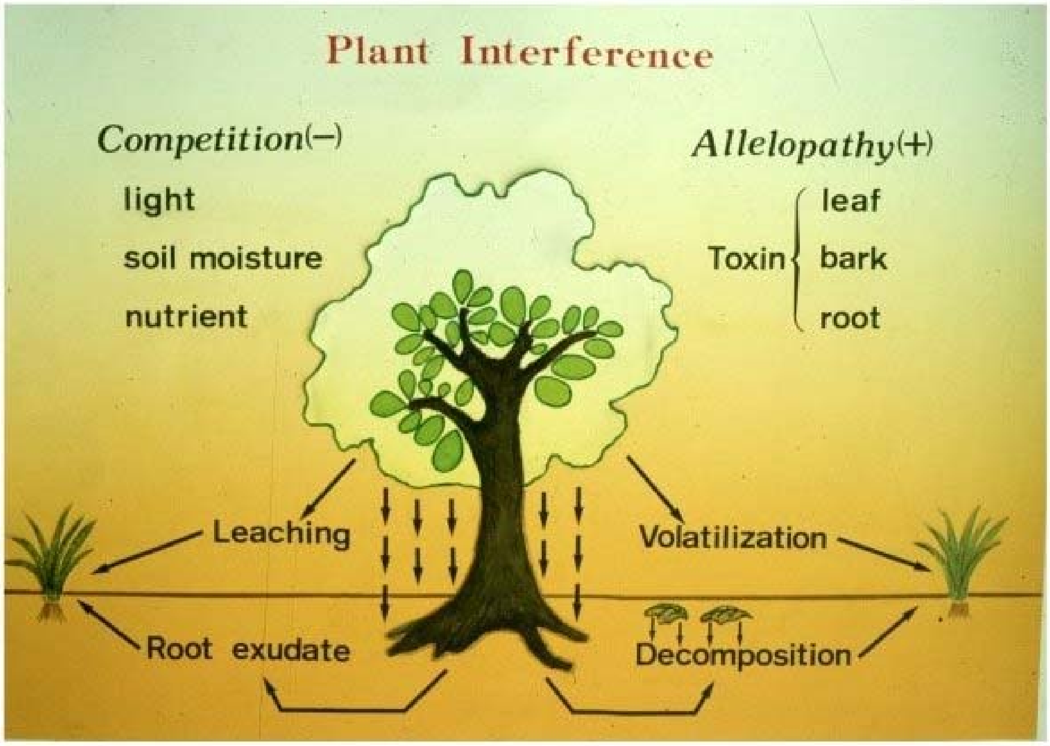

Figure 1. A diagram showing the mechanisms of plant interference, involving both competition and allelopathy. Competition (-) is defined as a plant depletes a necessary factor from the environment resulting in the suppression of growth of other plant sharing the same habitat. While, allelopathy (+) is defined as a plant releases a toxic compound (s) from plant, resulting in a detrimental effect upon the other plants sharing the same habitat.

Muller (1966) defined allelopathy as the process whereby a plant releases toxic compounds into the environment, resulting in a detrimental effect upon neighboring plants sharing the same habitat. "*Autointoxication*", another phase of allelopathy, is defined as a process in which chemicals produced by a plant or its decomposing residues in soil suppress its own growth, resulting in the decline of plant productivity in natural vegetation or an agroecosystem. Whittaker and Feeny (1971) coined *Allelochemics* and stated that "allelochemics are chemical agents that are of major significance in adaptation of the species and organisms in communities". Evolving from *allelochemics*, Chou and Waller (1983) used "*Allelochemicals*" to describe all biochemical interactions between organisms.

In the early twentieth century, allelopathy research was focused on agricultural productivity. Until the late 1960s, Muller was the first to introduce allelopathy into the field of plant ecology. In 1966 he described a unique pattern of herb exclusion by adjacent chaparral vegetation, *Salvia leucophylla* which releases toxic monoterpenoids that suppress the growth of many nearby herbaceous plants (see Table 1), resulting in the formation of bare areas of inhibition and areas of normal growth (see Figure 2). Muller and his students studied allelopathy of several chaparral shrubs and concluded that allelopathy plays a significant role in the dominance and the fire cycle phenomenon of the California chaparral. In addition, allelopathic patterns have been found to be widespread in natural and agricultural ecosystems from boreal forests to tropical rain-forest trees and from humid to desert vegetations.

	Compounds	**Representing plants**
Phenolic compounds	Caffeic acid	*Helianthus annuus*
	Chlorogenic acid	*Helianthus annuus*
	p-Coumaric acid	Many grass species and ferns
	3,4-Dihydroxybenzoic acid	*Delonix regia*
	3,4-Dihydroxybenzaldehyde	*Delonix regia*
	3,4-Dihydroxycinnamic acid	*Delonix regia*
	3,4-Dimethoxyacetophenone	*Asparagus officinalis*
	3,5-Dinitrobenzoic acid	*Delonix regia*
	Ferulic acid	Many grass species and ferns
	Fusaric acid	*Fusarium oxysporum*
	Gallic acid	*Celtis laevvigata*
	Gentisic acid	*Celtis laevigata*
	p-Hydroxybenzoic acid	Many grasses, *Miscanthus* species
	o-Hydroxyphenylacetic acid	*Oryzasativa*, many grass species
	p-Hydroxybenzaldehyde	*Sorghum bicola*
	Hydroquinone	*Arctostaphylos glandulosa* var. *zacaensis*
	Isochlorogenic acid	*Helianthus annuus*
	Phloroglucinol	*Pluchea lanceolata*
	Medicagenic acid	*Medicago* spp.
	Neochlorogenic acid	*Helianthus annuus*
	Polyacetylenic methyester	*Solidago altissimaa*
	Quercetin	*Salsola kali*
	Scopoletin	*Celtis laevigata*
	Scoploline	*Celtis laevigata*
	Syringic acid	Many grass species and ferns
	Vanillic acid	Manygrass species and ferns
Alkaloids	L-Azetidine3-carboxylic acid	*Delonix regia*
	Caffeine	*Coffea Arabica*
	6,6’-Dihydroxythiobinupharidine	*Nuphar lutea*
	Nupharolutine	*Nupha lutea*
	Mimosine	*Leucaena leucocephala*
	Pyridine-3,4-diol	*Leucaena leucocephala*
	Paraxanthine	*Coffea arabica*
	Theobromine	*Coffea arabica*
	Theophylline	*Coffea arabica*
Terpenoid	Abscisic acid	*Festuca* species, *Macaranga tanarius*
	Pinene	*Salvia leucophylla*
	ß-pinene	*Salvia leucophylla*
	Champhor	*Salvia leucophylla*
	Cineole	*Salvia leucophylla*
	SoyasaponinI	Mungbean

Table 1. Allelopathic compounds found in plants.

Figure 2. A unique pattern of herb exclusion by a California chaparral species, *Salvia leucophylla*, exhibiting a bare zone of 1 to 2 meter wide close to the shrub (A), an inhibition zone about 3 to 4 meters wide (B) next to the bare zone, and a normal growth of herbaceous plants beyond the inhibition zone. The photo was taken by Prof. C. H. Muller and used with courtesy.

Natural product chemists and biochemists studied the structure, biosynthesis, and natural distribution of secondary plant metabolites, but less attention was focused on function of the compounds. The metabolites are often stored in vacuoles or intercellular spaces when they are not being used. However, the compounds may be freely released to the cells or to the surface of leaves for defense, attraction, or as chemical signals. Even more, such compounds act as messengers in plant-insect interaction, and have an important role in the mechanisms of plant adaptation and insect co-evolution. Since then, secondary metabolites have no longer been regarded as metabolic wastes and the role of allelopathy in physiological, biochemical, and ecological functions has been increasingly understood.

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Bibliography

Al Saadawi, I. S., Rice, E. L., and Karns, T. K. B. (1983). Allelopathic effects of *Polygonum aviculare* L.III Isolation, characterization, and biological activities of phytotoxins other than phenols. Journal of Chemical Ecology 9, 761-774.

Anaya, A. L. (1999). Allelopathy as a tool in the management of biotic resources in agroecosystems. Critical Reviews in Plant Sciences 18, 697-739. [This critical review provides information concerning allelopathy in relation to the productivity of crops and natural plant resources used in conventional agriculture, in particular, in Mexico and other part of the world.]

Carballeira, A., Carral, E., and Reigosa, M. J. (1988). Asymmetric small-scale distribution and allelopathy: Interaction between *Rumex obtusifolius* L. and meadow species. Journal of Chemical Ecology 14, 1775-1780.

Chou, C. H. (1999). Roles of allelopathy in plant biodiversity and sustainable agriculture. Critical Reviews in Plant Sciences 18, 609-636. [This review provides information concerning the roles of allelopathy in regulating plant biodiversity in dominant vegetation, succession mechanism of plant communities, formation of climax vegetation in natural ecosystems and causes of productivity decline of a crop after a continuing monocultuire. The article also emphasizes frontier research of allelopathy in the twenty-first century].

Chou, C. H., and Waller, G. R. Eds. (1983). Allelochemicals and Pheromones. Institute of Botany, Academia Sinica Monograph Series No. 5, Taipei, Taiwan.

Einhellig, F. A. (1995). Mechanism of action of allelochemicals in allelopathy. In: Allelopathy: Organisms, Processes, and Application. pp.96-116. Inderjit, Dakshini, K. M. M., and Einhellig, F. A. Eds., ACS Symposium Series 582. American Chemical Society, Washington, D.C.

Elakovich, S. D. and Yang, J. (1996). Structures and allelopathic effects of *Nuphar* alkaloids: nupharolutin and 6,6'-dihydroxythiobinupharidine. Journal of Chemical Ecology 22, 2209-2219.

Gilmore, A. R. (1985). Allelopathic effects of giant foxtail on germination and radicle elongation of loblolly pine seed. Journal of Chemical Ecology 11, 583-592.

Gliessman, S. R., and Muller, C. H. (1978). The allelopathic mechanisms of dominance in bracken (Pteridium aquilinum) in southern California. Journal of Chemical Ecology 4, 337-362.

Hegazy, A. K., Mansour, K. S., and Abdel-Hady, N. F. (1990). Allelopathic and autotoxic effects of Anastatica hierochuntica L. Journal of Chemical Ecology 16, 2183-2193.

Heisey, R. M. (1990). Evidence for allelopathy by tree-of-heaven (Ailanthus altissima). Journal of Chemical Ecology 16, 2039-2055.

Lee, T. H. and Chou, C. H. (2000). Flavonoid aglycones and indole alkaloids from the roots of *Acacia confusa*. Journal of the Chinese Chemical Society 47, 1287-1290.

Lodhi, M. A. K. (1975). Allelopathic effects of hackberry in a bottomland forest community. Journal of Chemical Ecology 1, 171-182.

Numata, M. (1982). Weed-ecological approaches to allelopathy. In: Biology and Ecology of Weeds, pp. 169-173. Holzner,W., and Numata, M., Eds., Dr. Junk, W., Publ., The Hague.

Macias, F. A. (1995). Allelopathy in the search for natural herbicide models. In:Allelopathy, Organism, Processes, and Application. pp.310-329. Inderjit, Dakshini, K. M. M., and Einhellig, F. A., Eds., American Chemical Society Symposium Series 582. American Chemical Society, Washington, DC.

Molisch, H. (1937). Der Einfluss einer Pflanze auf die andere-Allelopathie. Fischer, Jena.

Muller, C. H. (1966). The role of chemical inhibition (allelopathy) in vegetational composition. Bulletin Torrey Botanical Club 93, 332 - 351.

Peters, E. J. and Lun, K. T. (1985). Allelopathy in tall fescue. In: The Chemistry of Allelopathy. pp.273-283. Thompson, A. C., Ed., American Chemical Society Symposium Series 268. American Chemical Society, Washington, DC.

Putnam, A. R., and Duke, W. B. (1974). Biological suppression of weeds: evidence for allelopathy in accession of cucumber. Science 185, 370-372.

Rice, E. L. (1984). “Allelopathy”, 2nd ed. Academic Press, New York and London.

Rice, E. L. (1995). Biological Control of Weeds and Plant Diseases. Univ. of Oklahoma Press, Norman and London.

Whittaker, R.H., and Feeny, P.P. (1971). Allelochemics: chemical interactions between species. Science 171, 757-770.