Scientific Papers. Series A. Agronomy, Vol. LXI, No. 1, 2018
ISSN 2285-5785; ISSN CD-ROM 2285-5793; ISSN Online 2285-5807; ISSN-L 2285-5785

ALLELOPATHY AND ALLELOCHEMICAL INTERACTIONS AMONG PLANTS

Ramona COTRUȚ

Research Center for the Study of Quality Food Products, 59 Marasti Blvd, District 1, 011464, Bucharest, Romania

Corresponding author email: ramona_cotrut@yahoo.com

Abstract

Allelopathy determines the dynamics of plant species in different environments. Plants can release chemicals into the environment that suppress the growth and establishment of other plants in their vicinity, a process known as 'allelopathy'. Chemicals with allelopathic functions have other ecological roles, such as plant defence, nutrient chelation and regulation of soil biota in ways that affect decomposition and soil fertility. In this review we explore allelopathy in the context of environmental characteristics that control the production and release of allelochemicals in both natural and agricultural systems. This study highlights the current understanding of how evolution might affect the intensity and importance of allelopathic interactions. Understanding this biological phenomenon could help to understand the environmental changes caused by allelochemicals and summarizes the knowledge about the mechanisms of action of these compounds.

***Key words**: allelochemicals, allelopathy, evolution, plant secondary metabolites.*

INTRODUCTION

Plants can release chemicals into the environment that suppress the growth and establishment of other plants in their vicinity, a process known as '*allelopathy*'.

Allelopathy is a biological phenomenon where a plant inhibits the growth of another plant. By releasing the allelochemical substances, some plants can greatly affect the development of other plants, either in good or bad way through leaching, decaying etc. Essentially, plant allelepathy is used as a means of survival in nature, reducing competition from nearby plants.

Allelopathy can be considered as a form of communication between plants. Chemicals with allelopathic functions have other ecological roles, such as plant defence, nutrient chelation and regulation of soil biota in ways that affect decomposition and soil fertility (Bais et al., 2004; Weir et al., 2004; Yoneya, Takabayashi, 2014).

Plants synthesize a multitude of compounds through secondary metabolism.

The production of these compounds depends on the existence of precursor molecules and the activation of specialized genes. Activation of genes required for allelochemical biosynthesis is often dependent on environmental stimulants (Croteau et al., 2000).

Allelopathy was first defined by Hans Molisch in 1937 as its reciprocity or the mutuality of the sufferings or the effects of a plant on the other, and about sixty years later a much more detailed and complete definition has been established by the International Society of Allegiance, according to which allelopathy means any process involving secondary metabolites produced by plants, algae, bacteria and mushrooms that influence the growth and development of agricultural and biological systems (Cheng, Cheng, 2015).

In this review we explore allelopathy in the context of environmental characteristics that control the production and release of allelochemicals in both natural and agricultural systems. This study highlights the current understanding of how evolution might affect the intensity and importance of allelopathic interactions. Understanding this biological phenomenon could help to understand the environmental changes caused by allelochemicals and summarizes the knowledge about the mechanisms of action of these compounds.

PLANT DEFENCE AND THE ROLE OF ALLELOCHEMICALS

Plant cannot move away from the potential threats or towards beneficial entities. During the course of evolution, plants have developed both physical and chemical mechanisms of defence from pests and pathogens (Bernards, 2010). Traditionally resource competition has been considered as the single most important factor that influences the patterning of plant communities (Niklas, Hammond, 2013).

However recent research has described allelopathy as an important aspect of plant defence that impacts plant community diversity (Fernandez et al., 2013). In this process plants release secondary metabolites that are considered to interact with the surrounding environment by inhibiting the germination or growth of neighboring plants (Ben, Jordan, Osborn, 2006; Fernandez, 2016).

The majority of the allelochemicals in the plant kingdom are found in vascular plants, but also in ancient terrestrial nonvascular plants such as mosses or liverworts, has increased over the years.

Therefore, allelochemicals can play an important role in plant succession through their release by pioneer plants (Bryophytes) which contribute substantially to the accumulation of above ground biomass, particularly in cold temperate biomes including boreal forests and peatlands (Chiapusio et al. 2013; Michel et al., 2011).

Allelochemicals are non-nutritive substances produced as plant secondary metabolites or decomposition products of microbes. Examples of allelochemicals that predominate in plants are alkaloids, phenols, terpenoids, glycosides but also acid cinnamic, benzoic acid, flavonoids and others.

Allelochemicals consist of various chemical families and are classified into the following 14 categories based on chemical similarity (Rice, 1974): water-soluble organic acids, straight-chain alcohols, aliphatic aldehydes, and ketones; simple unsaturated lactones; long-chain fatty acids and polyacetylenes; benzoquinone, anthraquinone and complex quinones; simple phenols, benzoic acid and its derivatives; cinnamic acid and its derivatives; coumarin; flavonoids; tannins; terpenoids and steroids; amino acids and peptides; alkaloids and cyanohydrins; sulphide and glucosinolates; and purines and nucleosides. Plant growth regulators, including salicylic acid, gibberellic acid and ethylene, are also considered to be allelochemicals (Cheng, Cheng, 2015).

ALLELOCHEMICAL MODE OF ACTION

Allelochemicals actively released by plants or passively produced during the decomposition process of both above and below-ground plant residues affect abiotic and biotic processes in the ecosystem and thereby influence the invasion process (Inderjit, 1996; Uddin et al., 2012; Uddin et al., 2014b).

Most of these substances are initially found to be inactive. Subsequent transformations (hydrolysis, oxidoreduction, methylation and demethylation) generate new products with distinct allelopathic properties.

Different parts of plants can have these allelopathic properties, from foliage and flowers to roots, shell, soil and mulch. Most of the allelopathic plants retain their protective chemicals in their leaves, especially during autumn. As the leaves fall and decompose, these toxins can affect the nearby plants. Some plants also release toxins through their roots, which are then absorbed by other plants and trees (Figure 1).

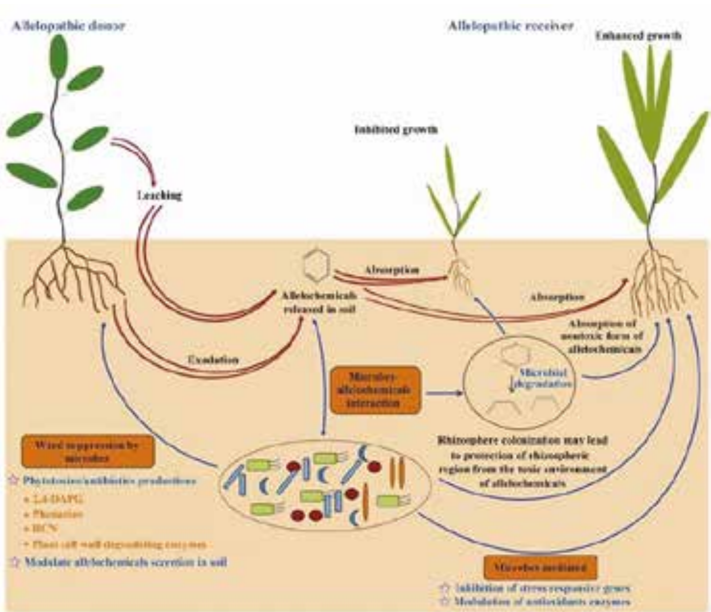

Figure 1. A schematic diagram showing the toxins released through their roots, the interaction of allelopathic donor-receiver species (Barazani, Friedman, 1999; Bais et al., 2006; Mishra et al., 2013; Cheng, Cheng, 2015)

Common plants with allelopathic properties include: *Prunus laurocerasus*, *Arctostaphylos uva-ursi*, *Rhus* spp., *Rhododendron* spp., *Sambucus* spp., *Forsythia* spp., *Solidago* spp., some species of fern, and some species of *Secale* spp., *Festuca arundinacea, Poa pratensis, Centaurea maculosa, Alliaria petiolate, Casuarina* spp. *and Allocasuarina* spp.

In the allelopathic woody species, trees are excellent examples of allelopathy in plants. For example, many trees use allelopathy to protect their space by using roots to draw more water out of the soil so that other plants cannot thrive. Some use their allelochemical substances to inhibit germination or prevent the development of nearby plant life. Most allelopathic trees release these chemicals through their leaves, which are toxic once absorbed by other plants.

Juglans nigra is a prime example of this. In addition to its leaves, the walnuts store allelopathic properties in buds, endocarp and roots. The chemical responsible for its toxicity, called juglone, remains in the soil around the tree. Other trees that are known to exhibit allelopathic tendencies are maple, pine and eucalyptus. Root-root and root-microbe communication can either be positive (epiphytes, mycorrhizal, fungi, nitrogen-fixing bacteria) or negative to the plant (parasitic plants, parasitic bacteria, fungi and insects) (Walker et al., 2003).

In natural systems, roots are in continual communication and quickly recognize and prevent the presence of invading roots. The known effects of compounds on processes related to growth and development of plants suggest for many hormonal substances such as auxin, gibberellic acids, ethylene, jasmonic acid and salicylic acid, that the compounds should have activity. Allelopathic compounds could interact by inhibiting synthesis, accumulation or utilization of energy rich compounds such as fatty acids or triacylglycerols (Seigler, 2006).

The *Sorghum* genus includes plants whose roots remove sorgolone, a poisonous substance that blocks the respiration and photosynthesis of the plants that come into contact with.

Among grain crops, poppy seeds germinate only in the presence of wheat, while rye has the gift of preventing the germination of certain types of weeds.

Common wormwood inhibits the growth of plants such as lovage, caraway, basil, lemon balm or common sage.

PLANT ALLELOPATHY IN AGRICULTURE

Allelopathy as a natural ecological phenomenon it has been known and used in agriculture since ancient times (Zeng, 2008, 2014). The purposes of research on allelopathy include the application of the observed allelopathic effects to agricultural production, reduction of the input of chemical pesticides and consequent environmental pollution and provision of effective methods for the sustainable development of agricultural production and ecological systems (Macias et al., 2003; Li et al., 2010; Han et al., 2013; Jabran et al., 2015). The suitable application of allelopathy toward the improvement of crop productivity and environmental protection through environmentally friendly control of weeds, insect pests, crop diseases, conservation of nitrogen in crop lands and the synthesis of novel agrochemicals based on allelochemicals has attracted much attention from scientists engaged in allelopathic research.

In agriculture the use of allelopathic crops is currently being realized, as components of crop rotations, crop mixtures or intercropping, as cover crops or as green manure (Cheng, Cheng, 2015).

Aiming for an ecological, sustainable and successful agriculture is also by making crop rotations, crop mixtures, intercropping, which has little harmful impact on environment conditions and maintains soil productivity over a long period of time maintaining the soil fertility, keeping the pest under control and reducing soil sickness problem.

Crop rotations - maintains and even improves the soil fertility, prevents the buildup of pest and soil sickness as compared to monoculture (Arnon, 1972) provides sustainability to agriculture by reducing the requirement of chemical nitrogenous fertilizers and thereby decreasing environmental pollution by substituting them with biologically fixed nitrogen of legumes (Narwal et al., 2000).

Crop mixtures or intercropping it is more productive in term of land use (Willey, 1979).

In soils with poor fertility, the cultivation of cereals with legumes improves both total yields and reduces the nitrogen requirement of cereal component. Besides, the legume biomass may be used as mulch/green manure. Both the crop rotations and intercropping systems or crop mixtures through inclusion of legumes maintains or improves soil fertility (Reigosa et al., 2006).

Biomass - soil fertility management in ecological sustainable agriculture gives much reliance on the use of biomass (crop residues and other organic wastes) to maintain the status of organic matter in the soil and to meet the nutrients requirement of the crops. The crop residues release allelochemicals through volatiles, leaching and during microbial decomposition (Reigosa et al., 2006). The production of allelochemicals in soil affects germination, growth and yield of crops depending on plant residue type, amount and depth of placement and length of decomposing period. The allelochemicals may either be inhibitory or stimulatory to the succeeding crops (Rice, 1984; Waller, 1987; Narwal et al., 2000).

Weed management - Several types of allelopathic plants can be intercropped with other crops to suppress weeds, crop cultivars with allelopathic potentials can be grown to suppress weeds under field conditions.

Several studies were elaborated on the significance of allelopathy for weed management. Rye, sorghum, rice, sunflower, rape seed and wheat have been documented as important allelopathic crops. These crops express their allelopathic potential by releasing allelochemicals which not only suppress weeds, but also promote underground microbial activities (Jabran et al., 2015).

Natural herbicides

Many plants make allelochemicals that deter competitors. Allelopathic chemicals interfere with growth of nearby plants. Among the plant products as herbicides - juglone, is an allelochemical produced by black walnut (*Juglans nigra*), isolated from walnut tree has been found effective against redroot pigweed (*Amaranthus retroflexus)*, velvetleaf (*Abutilon theophrasti)* and barnyard grass (*Echinochloa crus-galli*) (Shettel, Abalke, 1983; Spelce, Muselman, 1981; Weston et al., 1987).

Another allelochemical - sorgoleone is produced in *Sorghum bicolor* root hairs and exuded as oily drops; it accumulates in the soil and acts as a pre-emergence herbicide affecting photosintesis in very young seedlings.

Narwal et al., 2000, has exemplify some other important plant products having promising herbicidal activity: Dhurrin (*Sorghum*); gallic acid (spurge); Phlorizin (apple root); trimethylxanthene (coffee) and cinch (eucalyptus). The commercialization and marketing of “Herbiacae” the herbicide from microbial natural product bialaphos in Japan (Hatzios, 1987) has opened up a new era in weed management. Other microbial phytotoxins found to suppress weed growth include anisomycin, tentoxin, biopoloroxin, herbimycin etc.

CONCLUSIONS

This review study on allelopathy role plant interference, exploring the allelopathy in the context of environmental characteristics that control the production and release of allelochemicals in both natural and agricultural systems, clearly demonstrated that allelochemicals play an integral part in synergistic plants interactions. Allelopathy can be considered as a form of communication between plants. Plants are affected by each other positively and negatively. Nutrient sharing and suppression of parasitism and stress cues are the positive effect examples, while for the negative allelopathic effect is the invasive species that can suppress all others. Allelochemicals can suppress plant growth directly or indirectly. *Alliaria petiolate* (garlic mustard) it is one invasive plant example that indirectly suppress growth plant through the inhibition of their mycorrhizal fungal symbionts. Also, from fescue plants roots (*Festuca* spp.) there is *m*-tyrosine which is a non-protein amino acid that inhibits plant growth directly (Bertin et al., 2007).

Nevertheless, over the years the number of reports indicating the improvement in crop production due to allelopathic interactions had increased. The use of allelopathic crops can be achieved as components of crop rotations, crop mixtures or intercropping, weed management, etc. The use of allelopathy for controlling weeds could be either through directly utilizing natural allelopathic interactions, particularly of crop plants or by using allelochemicals as natural herbicides. For a sustainable agriculture allelopathy has achieved great success in weed management. Utilization of water extracts of allelopathic crop combined with reduced doses of herbicides can be a promising strategy for sustainable weed management and environment health (Amb, Ahluwalia, 2016).

Allelopathy determines the dynamics of plant species interaction in different environments influencing the agroecosystem. Because of these interactions, allelopathy is a complex phenomenon with limited field repeatability (Trezzi et al., 2016).

Incorporating allelopathy into natural and agricultural management systems may reduce the use of herbicides. The structure of allelochemicals can be used as an analogue for the synthesis of new pesticides which will be less harmfull for the environment as compared to synthetic agrochemicals.

REFERENCES

Amb M.K., Ahluwalia A.S., 2016. Allelopathy: Potential Role to Achieve New Milestones in Rice Cultivation, Rice Science, Volume 23, Issue 4, pp. 165-183.

Arnon I., 1972. Crop Production in Dry regions. Vol. I. Background and Principles. London: Leonard Hill. pp. 458-478.

Bais H.P., Park S.W., Weir T.L., Callaway R.M., Vivanco J.M., 2004. How plants communicate using the underground information superhighway. Trends Plant Sci. 9: 26-32.

Bais H.P., Weir T.L., Perry L.G., Gilroy S., Vivanco J.M., 2006. The role of root exudates in rhizosphere interactions with plants and other organisms. Annu. Rev. Plant Biol. 57, 233-266.

Bernards M. A., 2010. Plant natural products: a primer. Canadian Journal of Zoology, 88 (7), 601-614.

Barazani O., Friedman J., 1999. Allelopathic bacteria. In Inderjit K, Dakshini MM, Foy CL (eds) Principles and Practices in Plant Ecology. Allelochemical Interactions, pp. 149-163. CRC Press. Boca Raton.

Bertin C., Weston L.A., Huang T., Jander G., Owens T., Meinwald J., Shroeder F.C., 2007. Grass roots chemistry: meta-Tyrosine, an herbicidal non protein aminoacid. Proc. Natl. Acad. Sci. USA 104:16964-16969.

Cheng F., Cheng Z., 2015. Research Progress on the use of Plant Allelopathy in Agriculture and the Physiological and Ecological Mechanisms of Allelopathy. Front. Plant Sci. 6:1020.

Chiapusio G., Jassey V.E.J., Hussain M.I., Binet P., 2013. Evidences of bryophyte allelochemical interaction: the case of Sphagnum. In Cheema Z.A., Farooq M., Wahid A. (Eds.), Allelophaty: Current trends and future applications (pp. 39-54). Springer Science and Business media.

Croteau R., Kutchan T.M., Lewis N.G., 2000. Natural products (secondary metabolites). In: Buchanan B, Gruissem W., Joneas R., editors. Biochemistry and molecular biology of plants. Rockville: American Society of Plant Biologists; pp. 1250-1268.

Fernandez C., Santonja M., Gros R., Monnier Y., Chomel M., Baldy V., 2013. Allelochemicals of *Pinus halepensis* as drivers of biodiversity in Mediterranean open mosaic habitats during the colonization stage of secondary succession. J. Chem. Ecol. 39, 298–311.

Fernandez C., Monnier Y., Santonja M., Gallet C., Weston L.A., Prévosto B., Saunier A., Baldy V., Bousquet-Mélou A., 2016. The Impact of Competition and Allelopathy on the Trade-Off between Plant Defense and Growth in Two Contrasting Tree Species. Front. Plant Sci. 7:594.

Field B., Jordan F., Osbourn A., 2006. First encounters-deployment of defence-related natural products by plants. New Phytol. 172, 193-207.

Han X., Cheng Z.H., Meng H.W., Yang X.L., Ahmad I., 2013. Allelopathic effect of decomposed garlic (*Allium sativum* L.) stalk on lettuce (*L. sativa* var. *crispa* L.). Pak. J. Bot. 45, 225-233.

Hatzios K.K., 1987. Biotechnology applications in weed management: Now and in the future. Advances in Agronomy 41: 325-375.

Inderjit, 1996. Plant phenolics in allelopathy. The Botanical Review 62: 186-202.

Jabran K., Mahajan G., Sardana V., Chauhan B.S., 2015. Allelopathy for weed control in agricultural systems. Crop.Prot. 72, 57-65.

Li Z.H., Wang Q., Ruan X., Pan C.D., Jiang D.A., 2010. Phenolics and plant allelopathy. Molecules 15, 8933-8952.

Macias F.A., Marin D., Oliveros-Bastidas A., Varela R.M., Simonet A.M., Carrera C., 2003. Allelopathy as a new strategy for sustainable ecosystems development. Biol. Sci. Space 17, 18-23.

Michel P., Burritt D.J., Lee W.G., 2011. Bryophytes display allelopathic interactions with tree species in native forest ecosystems. Oikos, 120 (8), 1272-1280.

Mishra S., Upadhyay R.S., Nautiyal C.S., 2013. Un ravelling the beneficial role of microbial contributors in reducing the allelopathic effects of weeds. Appl. Microbiol. Biotechnol. 97, 5659-5668.

Narwal S.S., 2000. Weed management in rice: wheat rotation by allelopathy. Crit. Rev. Plant Sci. 19, 249-266.

Narwal S.S., 2006. Allelopathy in ecological sustainable Agriculture, In Manuel J. Reigosa, Nuria Pedrol, Luís González (eds.), Allelopathy: A Physiological Process with Ecological Implications, 537-564.

Niklas K.J., Hammond S.T., 2013. Biophysical effects on plant competition and coexistence. Functional Ecology, 27 (4), 854-864.

Rice E.L., 1974. Allelophathy. New York: Academic Press.

Rice E.L., 1984. Allelopathy. 2nd Ed. New York: Academic Press.

Seigler D.S., 2006. Basic pathways for the origin of Allelopathic compounds. In Manuel J. Reigosa, Nuria Pedrol, Luís González (eds.), Allelopathy: A Physiological Process with Ecological Implications, 11-61.

Shettel N.L., Balke N.E., 1983. Plant growth response to several allelopathic chemicals. Weed Science 31: 293-298.

Spelce D.L., Muselman L.J., 1981. *Orobanche minor* germination with strigol. Compounds. Zeitschrift Pflanzen physiologie 104: 281-283.

Trezzi M.M., Vidal R.A., Balbinot A.A. Jr., Bittencourt H. von H., Filho A.P.S.S., 2016. Allelopathy:driving mechanisms governing its activity in agriculture, Journal of Plant Interactions, 11: 1, 53-60.

Uddin M.N., Caridi D., Robinson R., 2012. Phytotoxic evaluation of *Phragmites australis*: an investigation of aqueous extracts of different organs. Marine and Freshwater Research 63: 777-787.

Uddin, M.N., Robinson R.W., Caridi D., Harun M.A.Y., 2014b. Suppression of native *Melaleuca ericifolia* by the invasive *Phragmites australis* through allelopathic root exudates. American Journal of Botany 101: 479-487.

Waller G.R., 1987. Allelochemicals, Role in Agriculture and Forestry. ACS Symposium Series No. 330. Washington, D.C: American Chemical Society.

Walker T.S., Bais H.P., Grotewold E., Vivanco J.M., 2003. Root Exudation and Rhizosphere Biology, Plant Physiology, Vol. 132, pp. 44-51.

Weir T.L., Park S.W., Vivanco J.M., 2004. Biochemical and physiological mechanisms mediated by allelochemicals. Curr Opin Plant Biol. 7: 472–479.

Weston L.A., Burke B.A., Putnam A.R., 1987. Isolation, characterization and activity of phytotoxic compounds from quackgrass (*Agropyron repens* L. Beauv). Journal of Chemical Ecology 13: 304-431.

Willey R.W., 1979. Intercropping - Its importance and research needs. Field crops Abstracts 32: 1-10, 73-85.

Yoneya K., Takabayashi J., 2014. Plant-plant communication mediated by airborne signals: ecological and plant physiological perspectives. Plant Biotechnol. 31: 409-416.

Zeng R., 2008. Allelopathy in Chinese ancient and modern agriculture. In Allelopathy in Sustainable Agriculture and Forestry, eds. R. Zeng, A. Mallikand S. Luo, New York: Springer New York Press, 39–59.

Zeng R.S., 2014. Allelopathy-the solution is indirect. J. Chem. Ecol. 40, 515-516.