

Ecological aspects of allelopathy

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Abstract

Plants, one of the biotic factors of the ecosystem, release a number of chemical compounds that can change environmental factors as well as they are affected by environmental changes. These compounds, called allelochemicals, most of which are secondary metabolites, are produced as a sub-branch of their primary metabolic pathways. Besides the direct effect of allelochemicals on growth and development of other plants, they are released from decomposed plant residues and cause indirect allelopathic effects by changing the activity of microorganisms in the environment. It also has indirect environmental impacts on soil bioavailability by preventing microbial symbiosis activities in the soil, preventing nitrogen fixation, nutrient uptake and changing nutrients in the soil. It can affect the plant species and variety in the environment and cause significant changes in natural vegetation and plant communities in the long term. Over time, plant succession occurs, which is defined as the dominant species replacing other species. As a result, allelopathy is a complex phenomenon that causes clear changes at many subsystem levels of the ecosystem. Therefore, allelopathic interactions should be analyzed at the ecosystem level rather than at the population level and their multi-directional effects should be evaluated with a holistic approach.

Key words: allelochemical, mycorrhizae, plant biodiversity, plant succession

INTRODUCTION

All plants living in the same ecosystem are closely related and in interaction with each other. Allelopathy, which has an important role in the ecological relations of plants, is the direct or indirect effects of both cultivated plants and weeds on the germination, growth or development of the neighboring plant by secreting certain chemicals. (Rizvi et al., 1992; Willis, 2007). Due to its multifaceted effects on ecology, it is not enough to evaluate the effects of chemicals released by a plant on nearby plants from one side. In order to talk about the presence of allelopathy in the environment, first of all, the identification, isolation and release form of plants with allelopathic potential should be determined. It should be investigated how persistent allelochemicals released into the environment affect the environmental conditions and the target

plant (Inderjit, 1998). On the other hand, allelochemicals are more biodegradable than conventional herbicides but there may be concern that they may have undesirable effects on non-target species (Ferguson and Rathinasabapathi, 2003). In this context, detailed ecological studies should be carried out before the use of allelochemicals. Plant studies with allelopathic potential are mostly carried out at the agroecosystem level or are limited to laboratory trials. Whereas, investigating the mechanism of action of allelochemicals at an ecosystem level in a broad sense is not enough to understand the subject in depth. For this reason, more comprehensive studies should be done on plant biodiversity, soil microecology, plant communities and their succession. This review attempts to explain the subject matter based on the literature.

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ALLELOCHEMICALS AND THEIR ROLE IN THE ENVIRONMENT

Chemicals released from allelopathic plants are called allelochemicals and are defined as most secondary metabolites that are not required for the metabolism (growth and development) of the allelopathic organism (Rice, 1984). Some allelochemicals are known to have structural functions as lignification intermediates in cell walls (Hock and Elstner, 2004). Allelochemicals are released into the environment under favorable environmental conditions by root exudation, leakage and volatilization from aboveground parts or decomposition of plant residues (Rice, 1984). Factors such as UV, deficiency of plant nutrients, physiological stresses such as age of plant organs, water stress, temperature, humidity, environmental stresses such as pests and diseases, herbicides and the activities of microorganisms in the soil are effective in the secretion of allelochemicals (Ferguson and Rathinasabapathi, 2003; Blanco, 2007). It has been reported that allelochemicals, which often have inhibitory effects on other organisms, play an important role in plant defense against herbivores and plant pathogens (Wardle et al., 1998; Kruse et al., 2000; Stamp, 2003; Koocheki et al., 2013).

In some cases, successive plants can be affected by allelochemicals (Ferguson and Rathinasabapathi, 2003). Microbial activities in the soil are ecological factors that affect the allelopathic interaction process and can change the expression of allelochemicals (Singh, 2001). It has been demonstrated that allelochemicals released by plants can alter plant communities in the long run with their effects on vegetation, plant biodiversity, and soil ecology such as plant nutrients and mycorrhizae in soil. (Kruse et al., 2000; Sinkkonen, 2006; Koocheki et al., 2013). It has been reported that progress in the study of allelopathy should focus on its effects on different components of the soil ecosystem rather than directly investigating plant-plant chemical interactions, and that these studies will provide prospective benefit to allelopathy studies (Inderjit and Weiner, 2001).

ALLELOPATHIC INTERACTION

Allelopathy is defined as the mechanism of plant-plant, plant-microorganisms, plant-virus, plant-insect and plant-soil-plant interactions mediated by chemicals produced by plants or microorganisms released into the environment (Gniazdowska and Bogatek, 2005). There are 3 main components in allelopathy. First, the interaction material is plants. The latter are allelochemicals and chemical compounds that affect the growth and development of itself or neighboring plants. Third, the compounds secreted by the material of interaction plants have a convenient way of entry into the environment (Chengxu et al., 2011).

Allelopathic interaction; direct (narrowest meaning of allelopathy) allelopathic interaction is categorized into four classes as indirect interaction, indirect toxicity, and indirect environmental effects. Its direct effects are the most well-known definition of allelopathy, it is a plant-plant interaction. In simpler terms, one plant secretes a chemical compound, inhibiting the emergence or growth of the other plant. Indirect allelopathic effects; It is the interaction that occurs when the compound secreted from decomposed plant residues is reduced by the activation of the microorganisms in the environment or by the intervention of a living organism by promoting the secretion of different compounds and affecting

the other plant. Indirect toxicity; It is the interaction of the secreted compound affecting the soil ecosystem and causing the production of another compound different from this compound. Indirect environmental effects, on the other hand, is the situation where the chemical compound prevents the development, survival and generative development of another plant by affecting the microbial activities and nutrient availability in the soil (Inderjit and Weiner, 2001; Koocheki et al., 2013). Allelochemicals may also affect soil nutrient uptake and bioavailability by indirectly altering biotic and abiotic factors (IAS, 2015).

Allelochemicals can affect the target plant physiologically, molecularly, biochemically and ecologically. Several allelopathic compounds can be released from a plant and these compounds can act together. Among the most important allelochemicals are phenolic compounds, flavonoids, terpenes, alkaloids, steroids, carbohydrates and amino acids (Chengxu et al., 2011). The combined effect of these compounds may be greater than their effect alone. When sensitive plants are exposed to allelochemicals germination, growth and development may be affected. The most frequently reported morphological effects of allelochemicals on plants; Inhibitory and retarding effects on seed germination, coleoptile elongation, radicle shoot and root growth (Ferguson and Rathinasabapathi, 2003). When they reach the receiving plant; It can affect many functions such as plant respiration, photosynthesis, ion uptake, enzyme activity, water availability, transpiration, stomatal opening, hormone levels, cell division and differentiation, signal transduction, gene expression and structure, cell membrane and wall permeability (Reigosa et al., 1999). Its effects on photosynthesis and respiration are its most important consequence characterizing the allelopathic interaction (Gniazdowska and Bogatek, 2005). These biochemical and metabolic changes cause darkened and swollen seeds in the recipient plant, while causing various morphological changes such as shortening of roots, radicles, shoots or coleoptiles, swelling or necrosis of the root tips, curling of the roots, reduction or increase of root hairs (Bhadoria, 2011).

THE EFFECT OF ALLELOPATHY ON THE ECOSYSTEM

The study of the concept of allelopathy in terms of plant ecology such as interactions between plants, plant dominance and succession was first carried out by the American botanist Cornelius Herman Muller in the late 1960s. In his research, he observed that the soft cross-plant called *Salvia leucophylla* produces monoterpenes and thus suppresses the growth of many herbivorous plants near it, creating bare areas in the field. He claimed that this was due to the phenomena of competition and allelopathy known as the interference of plants in a habitat. Later, Whittaker and Feeny (1971) emphasized in their article titled "Allelochemistry: chemical interaction between species", that these chemicals are of great importance in the adaptation of species and in the construction of plant communities.

The effects of allelopathy on many forest trees and cultivated plants were revealed, and it was determined that allelopathic plants could have beneficial, neutral and selective effects on other plants with the researches conducted towards the end of the 20th century (Ni et al., 2012). Allelopathic effects are always expressed as inhibitory negative effects.

However, carboxylates from allelochemicals may show positive effects such as dissolving phosphate in the rhizosphere and avoiding aluminum toxicity.

It can be said that allelopathy is of fundamental importance at the ecosystem level. Allelopathy is an ecological factor that can reduce biodiversity by removing susceptible genotypes from the gene pool by selection (Lawrence et al., 1991; Hock and Elstner, 2004), change the plant population and thus community structures, and increase the ability to rebuild habitats.

It has been noted that invasive weeds, which are not specific to the region and brought to the environment by chance or by man, can cause many negative effects in the ecosystem by reducing species richness and diversity. One of the most important factors for strong invasive species to successfully dominate new habitats is their allelopathic potential. It has been reported that allelopathic compounds play an important role in the formation of nutrient dynamics, the chemical properties of the soil, availability of nutrients in the soil, microbial symbiosis, the emergence, development and distribution of plants, plant diversity, dominance and invasion, plant succession (sequential change). Accordingly, it has been reported that it affects the ecosystem by causing long-term changes in plant communities. (Lawrence et al., 1991; Wardle et al., 1998; Kruse et al., 2000; Zhang et al., 2004; Nissanka et al., 2005; Ni et al., 2012; Koocheki et al., 2013).

The effect of allelopathic compounds on agroecosystems is more important than their effect on natural ecosystems. Production and sustainability in agricultural systems are more sensitive to ecological changes. If agricultural production systems cannot adapt to ecological conditions, their productivity decreases gradually. Agroecosystems are man-made agricultural systems that contain ecological principles in which all biotic and abiotic factors play a role. In this system, allelopathy has broad effects in terms of the interaction between cultivated plant-cultivated plant, cultivated plant-weed and forest trees-weed. These interactions may have negative effects such as inhibitory effect on the recipient plant and dominance in the environment for the donor plant, damage to the subsequent crops of the remaining plant residues after the harvest of allelopathic crop plants. If allelopathic plants can be managed properly in agricultural systems, they can be used to improve soil structure and fight weeds that cause yield losses in cultivated plants. (Kohli et al., 2006). Theophrastus observed in 300 BC that some legume plant species in agricultural lands increased the productivity of the field where they were present and on the other hand, chickpea plant caused negative effects on the iron thorn (*Tribulus terrestris*) weed. It is one of the first examples that use allelopathy in agricultural systems to control weeds (Amb and Ahluwalia, 2016). Research on the correct management and use of allelopathy in agroecosystems has become widespread in recent years (Verdeguer Sancho et al., 2018). In modern agricultural systems, allelopathic plants are included in crop rotation as the second crop after the main crop, as cover crops, and in either inter-planting or co-cultivation methods. In addition, the compounds obtained from allelopathic plants can be purified or used as environmentally friendly natural herbicides and insect repellents as aqueous extracts (Singh, 2001). In the use of allelopathic chemicals in weed control, it will not be economical to use in dense volumes, the use of plant extract mixtures with low doses of synthetic herbicides is an

application method that can provide benefits in terms of environmental and economic costs.

EFFECTS ON PLANT BIODIVERSITY

Allelopathy affect many organisms including plants, bacteria, fungi and other soil microorganisms, and can alter the fauna and flora diversity of the environment. The allelopathic activity of a plant reduces the number of plant species and population size by reducing the competitiveness of other plants in the environment, thus significantly altering plant and/or microbial biodiversity (Koocheki et al., 2013).

There are many examples of allelopathic plants that reduce or change biodiversity. *Lantana camara* L. is a powerful allelopathic plant, which is rapidly spreading in about 60 countries around the world, taking the top place in the list of most harmful weeds. This plant, which was first introduced as a hedge plant, was later revealed to be an invasive species, and its negative effects on the ecosystem were revealed by invading many areas. Some of these damages are; loss of biodiversity, plant succession (relocation of plants), interference with forest regeneration, promoting soil erosion, hosting disease-carrying vectors, toxic effects to animals and promoting the possibility of fire (Bhakat and Maiti, 2012).

Bitter vine (*Mikania micrantha* Kunth) is a perennial invasive plant with widespread distribution in Southeast Asia and Australia. The bitter vine has been called the plant killer because it rots the crop and forest trees around. It has been reported that bitter vine has a negative effect on the plants around it and under its canopy, and its rapid spread is due to the allelochemicals they secrete into its surroundings (Chengxu et al., 2011).

After the destruction of oak forests, kikuyu grass (*Pennisetum clandestinum* Hochst. ex Chiov.) rapidly adapts to the environment and significantly suppresses weed growth, which is expressed as the role of allelopathic plants on plant biodiversity (Chou, 1999). Studies have reported that allelopathy rather than resource competition has an effect on the reduction of natural species diversity in eucalyptus tree (*Eucalyptus urophylla* S.T.Blake) plantations (Quin et al., 2018) and common mugwort (*Artemisia vulgaris* L.) which is an allelopathic invasive species and that is very difficult to control also reduces biodiversity. (Foy, 2001).

In a study conducted on that the pyrrolizidine alkaloids in the roots of the tall fescue (*Festuca arundinacea* Schreb.) affect neighboring plants allelopathically, it was determined that the concentrations of these compounds were higher in the tall fescue infected with endophytes. It has been noted that this plant causes a negative interaction in competition with the red clover plant (*Trifolium pratense* L.) and that allelochemicals can be important in reducing species diversity. (Malinowski et al., 1999).

In plant populations with allelopathic plants, sensitive plants may exit the gene pool. Tree of heaven (*Ailanthus altissima* (Mill.) Swingle) is among the top 25 most harmful invasive plants and poses a threat to plant health and biodiversity in the UK (Kruse et al., 2000). Lawrence et al. (1991) revealed that allelochemicals released from *A. altissima* are responsible for changing the genetic pool of susceptible neighboring plant species. Both the near (<1 m) and distant (> 10 m) populations of purpletop tridens (*Tridens flavus* (L.) Hitchc.) were inhibited by *Ailanthus* toxins, whereas in the farther distant population only susceptible species were

inhibited. Thus, susceptible genotypes in the nearby plant population were excluded from the gene pool due to allelochemicals.

Nissanka et al. (2005), in their study to reveal the allelopathic effects of the Caribbean pine (*Pinus caribaea* Moralet) on vegetation regeneration and soil biodiversity, it was determined that the allelochemicals released by the Caribbean pine have significant effects on the diversity of flower and fauna species. It has been observed that the total number of plant species, species and family diversity under the canopies of trees in *Pinus* forests are less than natural and semi-natural forests. As a result, examining the effects of allelopathy on biological diversity provides understanding of many ecological events such as succession and plant invasion.

EFFECTS ON MICROBIAL ACTIVITIES IN SOIL

Allelochemicals cause qualitative and quantitative changes in soil content and affect the availability of nutrients depending on many factors such as climatic conditions and the presence of other plant species nearby (Inderjit, 1998; Kruse et al., 2000). However, the effect of soil microorganisms changing the environment chemicals in which they thrive is more important than the effect it creates on soil nutrients (Inderjit and Weiner, 2001). It has been reported that phenolic acids have significant effects on the nutrient cycle in the soil, cause toxicity by inhibiting the oxidation of NH_4^+ to NO_3^- (Rice, 1984) and can change the availability of nutrients in the soil by forming complexes with nutrients (Appel, 1993).

One of the indirect effects caused by the accumulation of allelochemicals in the soil is its effect on other plant species by inhibiting microbial symbiosis such as mycorrhiza and nitrogen fixing bacteria. Mycorrhizae provide easy absorption of water and nutrients in the soil, control of plant pathogens and drought tolerance, and the flow of organic matter from the plant to the soil. The advantage of mycorrhizae to the plant in the soil ecosystem is to benefit more effectively from the nutrients in the soil, and the advantage provided by the plant to mycorrhiza is that it provides a living environment and an attachment surface (Grove et al., 2012). However, soil microfloral density measured as mycorrhizal spore numbers and fungal population is relatively low in *Pinus* soils compared to natural forests. Allelochemicals contained in *Pinus* root exudates can inhibit mycorrhizal relationships and other mycorrhizal associations such as vesicular-arbuscular mycorrhiza (VAM) of neighboring plant species, reducing floral and faunal species diversity. Worm and non-parasitic nematode populations in the soil have also decreased under the *Pinus* forests. The fact that the microbial activity is four times higher in the natural forest than in the *Pinus* forest indicates that there is higher biodiversity in the soil under the natural forest cover (Nissanka et al., 2005).

Grove et al. (2012) reported that the allelochemicals released from the allelopathic bush scotch broom (*Cytisus scoparius* (L.) Link) had a direct inhibitory effect on the growth of seedlings of Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco), a local tree species, and indirectly a decrease in the density of ectomycorrhizal fungi in the soil. Scotch broom residues added to the forest soil in this area reduced the EMF abundance in the soil. According to these results, they reported that ecologically, allelopathy causes immediate and long-term permanent effects on natural plants and degradation of microbial communities or transformation.

In a study in which the effect of aqueous extracts of blueberry (*Empetrum nigrum* L.) on Scotch pine (*Pinus sylvestris* L.) seedlings was observed in laboratory and greenhouse experiments. It was reported that the N (nitrogen) uptake of the saplings decreased and this was due to the inhibition of the N uptake ability of mycorrhizae (Nilsson et al. 1993). In soil samples taken from areas from close (<1 m) and distant (> 1 m) black spruce (*Picea mariana* (Mill.) B.S.P.) to sheep laurel (*Kalmia angustifolia* L.), which is an allelopathic shrub, ectomycorrhizal community structure, degree of mycorrhizal infection and found differences in N, P, K, Ca and Mg concentrations by leaf analysis. It was determined that the nitrogen (N) and phosphorus (P) amounts were significantly lower in the seedlings close to sheep laurel compared to the far-growing seedlings, and the mycorrhizal infection rate in the soil was lower (Yamasaki et al., 1998).

Free or symbiotic bacteria in the ecosystem are also affected by allelochemicals and consequently denitrification, ammonia or bacterial pathologies may disappear or decrease in density. (Rizvi et al., 1992). It has been reported that compounds released from both living and herbicide-killed plant materials of quackgrass (*Agropyron repens* L.) inhibit the formation (nodulation) of nitrogen-fixing nodes in legume species (Weston and Putnam, 1985).

In a study conducted on pastures in New Zealand, it was observed that the allelochemicals secreted from musk thistle (*Carduus nutans* L.) suppress the white clover (*Trifolium repens* L.), which are intense in the environment, and create bare areas in the environment. They found that the success of the decomposed materials of the musk thistle in inhibiting the development of white clover resulted from the negative effect of symbiotic nitrogen fixation with the reduction of nodulation in the roots (Wardle et al., 1998). Being more tolerant of a decrease in the amount of nitrogen in the soil compared to forage plants, the musk thistle has succeeded in increasing its population in the environment. With this example, it has been revealed that the allelopathic activity of a plant species can affect the symbiotic activities, causing population size and perhaps change in ecosystem function (Kruse et al., 2000).

It has been reported that rasana (*Pluchea lanceolata* (DC.) Oliv. & Hiern) plant has higher phenolic acid content compared to 10-40 m distant soils and causes growth retardation in various mass plants growing here by changing soil PH, electrical conductivity, potassium and chloride content (Inderjit, 1998). In addition, in the study conducted by adding the aqueous extracts obtained from the leaves to different soil structure, it was understood that the phenolics released from the aqueous extracts changed the chemical properties of the soil. Also their inhibition was higher in soils with sandy loam and clay loam structure. The importance of soil structure in allelopathy studies was revealed with the present study (Dakshini, 1994).

In this sense, while conducting allelopathy studies, determining the soil structure and microbial status in the soil in advance is important for the detailed consideration of the studies.

EFFECTS ON PLANT SUCCESSION

Succession is the change over time in the architecture of the plant composition, structure or vegetation in a particular region. Plant succession is an important process in newly established ecosystems after vegetation destroyed by reasons

such as intensive use in grazing, adverse effects of climate change on vegetation and fire. For many years, researchers suggested that changes in habitat and vegetation change depending on soil nutrients, but later, Cowles (1911) stated that this was caused by chemicals secreted by plants and played an important role in plant succession. Plants with allelopathic potential lead to the extinction of precursor plant species and change in the population by establishing dominance in the environment, and of course, they cause changes in the successive arrival of plants in the long term (Reigosa et al., 1999). Habitats that are particularly low in species can be changed by one or two allelopathic plants (Wardle et al., 1998).

In a study conducted in Oklahoma to investigate the role of allelopathy in succession, it was reported that in the first stage of succession, the vast majority of several plant species produce phenolic compound toxins and other species have a self-inhibiting (autoinhibition) effect in some cases. Some early weeds in the environment disappeared rapidly and replaced them by prairie threeawn (*Aristida oligantha* Michx.). It was understood that this situation was caused by the allelochemicals released from prairie threeawn inhibiting nitrogen fixation in the soil. Its ecological success in the habitat of the prairie threeawn is due to the allelochemicals it contains and also its ability to stay in nutrient-poor habitats for a long time. Over time, there has been an afterthought with native weed species, affecting the plant succession in the environment and the species community composition in the environment in the long term (Bazzaz, 1979).

CONCLUSIONS

Allelopathy is an ecological factor in the adaptation of communities and species in plant communities and has significant effects on the ecosystem. Allelochemicals are compounds produced by plants, animals, or microorganisms that do not play a fundamental role in metabolism and are often known as secondary metabolites. However, as allelochemicals affect environmental factors, environmental factors also have an effect on the release of allelochemicals. In this sense, the phenomenon of allelopathy is a complex subject that needs to be studied deeply in terms of its ecological effects. Considering both plant species and diversity and their communities and the changes they cause in plant success in the long term, it is known that this situation affects events such as the direct inhibitory of allelopathy and indirectly the availability of nutrients in the soil. Allelopathic plants can change the distribution and development of plants in natural vegetation, microbial activities in the soil, and in plant süksasyon that so lead to clear changes in the ecosystem with long-term that has been supported by many studies. The effects of allelopathic potential plants on other weeds, plants or mikroorganisms are mostly studied under laboratory conditions. Experiments in the laboratory are mostly carried out by monitoring the effects of allelopathic plants on the germination development and growth of other plant seeds. Of course, it may also be useful in terms of isolating more allelochemicals at the preliminary stage of the studies to obtain natural pesticide. But, stresses such as environmental conditions and climatic changes that are effective in the secretion of allelochemicals can be ignored. It is necessary to investigate the existence of allelopathic plants in the field conditions or their direct and indirect effects on

environmentally both soil microbial activities and plant species diversity. In addition, the indirect effect of allelochemicals on soil nutrient availability and microbial activities, especially in agricultural systems, seems to be more important than their direct effect. While the effect of allelochemicals on the ecosystem does not pose a problem in their own order in nature, their success in prevalence and dominance in the environment where invasive plants are found is mostly due to their allelopathic properties. Although it is possible to use allelopathic plants in agricultural control systems with the right management, good monitoring and follow-up of environmental interaction is important for the correct evaluation of the studies. Especially the use of allelopathic plant extracts in weed control in field conditions is an alternative method of control and their effects on the ecosystem should be evaluated in multiple ways during and after the application. Since laboratory studies take place under controlled conditions and it is known that allelopathy is a phenomenon that affects and is affected by its environment, field and pot trials should be included in the studies. In field trials, studies should be carried out by examining the effects on plant biodiversity and microbial activities in the soil from multiple perspectives.

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CONFLICT OF INTEREST

The author declare that there are no conflict of interest.

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