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Allelopathy as a Stress Management Mechanism In Plants

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Abstract

Plants face several stresses throughout their life cycle. In agricultural systems, in order to achieve higher yields, excessive usage of chemical based herbicides, pesticides, weedicides and fertilizers have become a necessity which is harming the environment and ultimately the human life. Alleopathy is a mechanism in plants in which specific compounds are produced that influence the growth and development of other living organisms as a part of defence system as well as they contribute in determining the dynamics of species distribution. The strategy has the potential to become a successful alternative for plant protection strategy.

Keywords: Allelopathy, allelochemicals, plant defence, biotic stress, abiotic stress.

1. Introduction

Plants, being the immobile organisms, have to face a variety of biotic and abiotic stresses. These adverse conditions prove as one of the major limitations in crop productivity in agriculture. Plants may face adverse environmental conditions such as heavy metal, salinity stress, mineral toxicity due to polluted soils and waters, extreme temperatures, water stress, radiations, etc. Crop plants, when come across these unfavourable conditions, have direct impact on human life. It has been established that about 45% of total agricultural land is affected by drought conditions, 19.5% is affected by excessive amounts of salt while 16% of total agricultural rice land is subjected to flash floods, and this in turn, drastically reduces the food production at the global level [1, 2, 3]. The plants specifically stressed with heavy metals, chemical pesticides, insecticides, fungicides not only have damaging effects on the plant growth, development and yields but also are a threat to animals and humans who consume these as food. Also, attack by microscopic pathogens such as fungi, bacteria, viruses, or macroscopic organisms like nematodes, insect pests, arachnids and even other plants such as weeds, leads to biotic stress in plants and thus becomes a major cause of low productivity. These biotic agents cause nutrient deprivation of plants which may ultimately lead to death [4]. Both biotic and abiotic stresses also lead to the formation of reactive

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oxygen species (ROS) such as superoxide anion, singlet oxygen, hydrogen peroxide and hydroxyl radical [5]. These ROS, at low concentrations, act as signaling molecules and regulate various signaling cascades, however, over-production of these molecules due to stresses has toxic effects in plants [6, 7].

To overcome these hazards, plants have evolved several defence strategies at cellular level as well as genomic level. At cellular level, modifications in membranes, cell walls, cell multiplication, cell cycle are involved [8]. At genomic level, expression of several genes involved in production of stress protective enzymes, transcription factors and biosynthesis of secondary metabolites gets up-regulated [9]. Out of these, production of allelochemicals is one such mechanism that plants utilize to overcome stress. It is a less explored branch of plant defence mechanisms and can become a promising strategy which is for plant protection.

2. Allelopathy as an Alternative Mechanism for Plant Protection

The term allelopathy is a combination of two Greek words 'allelon' which means 'of each other', and 'pathos' that refers to suffering [10, 11, 12]. This phenomenon is an ancient concept which was already known to Greek researchers, and these damaging effects of plants on other plants were first documented by Theophrastus (285 B.C.) and Pliny II (1 A.D.) [12]. Later, De Candolle, a popular taxonomist, in 1832 recognized this phenomenon and named it as soil sickness [13]. He established from his study that it occurred due to toxic exudates from the plants into the soil and suggested its control through crop rotation [13]. The term allelopathy, however, was first used and defined by a Molisch (1937), a plant physiologist from Austria [12, 13]. He included both beneficial and harmful biochemical interactions between plants and other micro-organisms [13]. The study of allelopathic compounds and their effects is garnering attention because the interaction of these compounds are instrumental in patterning of vegetation, growth of weeds and yields of crops [13].

Allelochemicals or allelopathic compounds can act in their original chemical form or may serve as precursors in biosynthesis of other toxic compounds. These are usually secondary metabolites out of which phenols and terpenoids exhibit maximum allelopathic properties [13]. Based on the structure and properties, the major categories of allelochemicals are shown in Figure 1. The biosynthesis of most of the metabolites generally involves shikimic acid pathway, melonic and mevalonic acid pathways and methylerythritol phosphate pathway, while isoprenoid pathway results in the synthesis of terpenoids [14]. Their biosynthesis also

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depends on the growth stage of the plant and its susceptibility to the stress it is facing [15]. The release of allelochemicals from the plant parts can occur by volatilization from aerial parts, leaching from aerial parts through rain, fog and dew, root exudates, decomposition of organic matter and leaching from the plant litter [13]. The allelochemicals, once formed aid in overcoming both biotic and environmental stresses and thus help in enhancing plant immunity and productivity.

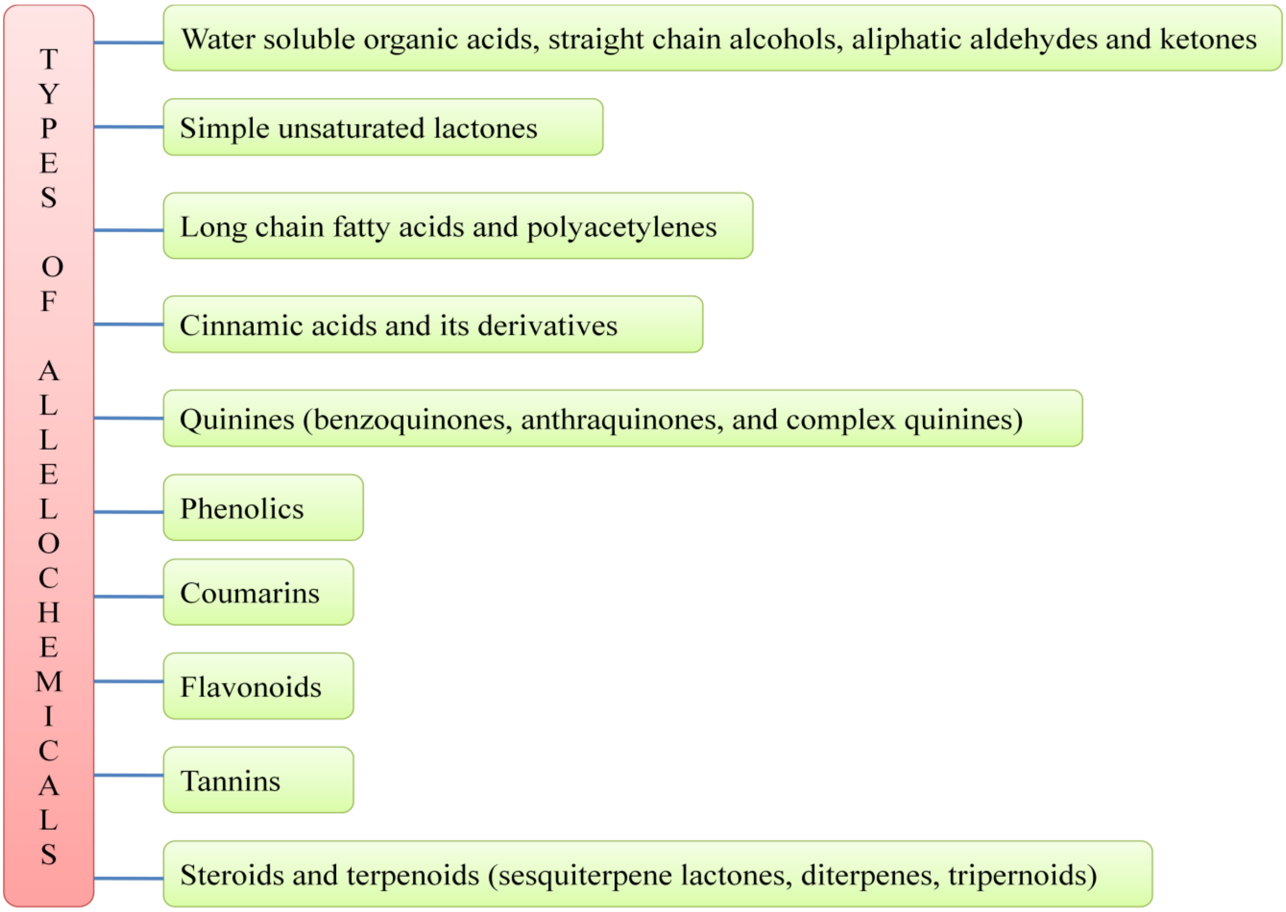

Fig. 1. Major classes of allelochemicals

a. Allelopathy in Response to Biotic Factors

The usage of allelopathic properties of plants in agriculture has been chiefly recommended as allelochemicals reduce the requirement of herbicides, chemical pesticides [16]. These chemicals protect the environment and serve the purpose of enhancing the crop yields through control of weeds without using weedicides or herbicides, checking the plant pests and diseases, maintaining nitrogen in agricultural soils and triggering the synthesis of new agrochemicals [16]. The allelochemicals cause various physiological as well as biochemical changes in pathogens and invasive plants to check their growth. The changes occurring in

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shape and ultrastructure of the cells due these chemicals cause major damage to pathogens. It has been reported that some volatile monoterpenes and compounds like eucalyptol and camphor have the ability to shorten the size of the root cells, enhance the number of vacuoles and abnormalities of the nucleus [17, 18]. It has also been revealed that allelochemicals from *Convolvulus arvensis* and *Nepeta meyeri* have the ability to change the DNA profiles as assessed by random amplification of polymorphic DNA [19, 20,]. Another biochemical called citral from lemongrass can cause alteration in mitotic microtubules in roots of *Arabidopsis* and wheat plants [21, 22]. Several allelochemicals also act by altering the proliferation rates of cells and DNA synthesis in meristematic tissues [23]. The mitotic process at G2-M checkpoint has been reported to be inhibited by 2(3H)-benzoxazolinone in lettuce plants [24]. A study on 2(3H)-benzoxazolinone and 2, 4-dihydroxy- 1,4(2H)-benzoxazin-3-one of rye reported the inhibition of root growth by disrupting the regeneration of cells of root cap in cucumber [25]. It was also observed by Cal and Mu [26] that soybean plants when treated with water extracts of the leaves of *Datura stramonium*, showed reduced elongation of primary root and lateral roots, reduction in cell division in meristematic zone and enhanced levels of chromosomal aberrations.

A rapid production of ROS in plants parts treated with allelochemicals is yet another mechanism by which the plants control the growth of other species. This leads to oxidative stress and further modification of the activities of antioxidative enzymes so as to counter the stress. The hypocotyl cuttings of *Phaseolus aureus* when treated with caffeic acid, the activities of enzymes such as proteases, peroxidases and polyphenol oxidase were observed to be altered and reduction in endogenous content of total phenolics was found [27]. An overproduction of ROS in *Acropora millepora* led to protein degradation and apoptosis due the application of allelochemicals [28]. The oxidative burst due to allelochemicals also lead to enhanced levels of lipid peroxidation in cellular membranes, that damage their intergrity. Loss of membrane integrity leads to enhanced permeability which causes leaky membranes. It was reported that essential oil from *Cymbopogon citratus* causes electrolyte leakage and lipid peroxidation in membranes of *Echinochloa crus-galli* [29]. The allelochemicals also have the ability to modify the contents of plant hormones and thus cause imbalance in overall plant growth and development. It has been established that allelochemicals of phenolic origin can change the activity of Indole acetic acid (IAA) oxidase and further disrupt the reaction of peroxidase with IAA or bound gibberellic acid [30]. In barnyard grass, enhanced activity of IAA oxidase was observe after the treatment with aqueous extract from rice which led to decreased seedling growth due to reduced IAA levels [31]. Several allelochemicals have been reported to act adversely on respiratory system of the cell in which electron transfer, oxidative phosphorylation, activity of ATP enzymes, intake of oxygen and CO_2 generation are affected [16]. Similarly another vital process in plants is photosynthesis, which is negatively affected by allelochemicals which have the damaging effects on biosynthetic machinery of plant pigments or stimulation of pigment degradation process [16].

b. Allelopathy in Response to Abiotic Factors

Abiotic stress in plants can induce the production of allelochemicals that in turn influences the vegetation pattern of an area [33]. Environmental factors like light, ultraviolet (UV) radiations, temperature, soil quality, water status or nutrient content play a key role their accumulation [32]. The abiotic factors can affect the allelopathic properties of a plants in three manners, firstly the production of allelochemicals through gene expression, secondly the bioavailability of these compounds and lastly the effects on the target species [33]. It has been hypothesized through studies that UV radiations, nutrient scarcity in soils/media, infections, stimulate the activity of phenylalanine ammonia-lyase (PAL) which is the first step in the biosynthetic pathway of phenolic compounds [33]. Similarly, cinnamic acid, occurring in many allelopathic plants, acts as a precursor of many phenylpropanoids and in target species causes lipid peroxidation of cellular membranes and reduces the H-ATPase activity in roots [34]. Production of allelochemicals in a particular plant is also influenced by interaction with the plants growing in its vicinity [35]. A study on rice plants showed that when they were planted alongside *Echinochloa crus-galli*, seven times higher accumulation of momilactone B was observed as compared to plants grown alone [36].

The process of transference of alleochemicals determines their bioavailability in the soils. The transference chiefly includes adsorption and leaching of the compounds and their degradation [33]. The bioavailability of these allelochemicals is governed by several factors such as nature of soil, its pH, biological activity in it, organic matter content and availability of water [33]. Therefore, if the soil conditions are unfavourable, the allelochemicals will not be available to the target species despite being present in the adequate amounts [33]. The degradation of allelopathic compounds in soils is also a crucial factor that determines their efficacay. The compounds with shorter half lives degrade early and thus have lesser effect while those with longer half lives are more efficient on target plants [33]. Thus, overall effect and fate of allelochemicals depends on environmental variables, allelopathic plants and the

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target plant [33]. Therefore, allelochemicals produced by plants can cause major environmental changes with respect to the community level, species inclusion and exclusion at the level of ecosystem [27, 33].

3. Concluding Remarks

Studies have indicated the ability of allelopathy as a significant factor in influencing the ecosystems and their roles in agriculture. Exploring the complexity of production, action, interaction and degradation of allelochemicals will help to successfully these compounds in field in weed management and pest management strategies. This will provide a cost effective and sustainable approach and reduce our dependency on chemical herbicides, weedicides and pesticides.

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