

Review

Plant Allelopathy in Response to Biotic and Abiotic Factors

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Abstract: The allelopathy definition accepted by the International Allelopathy Society is any process or phenomenon via which organisms such as plants, microorganism, viruses, and fungi release specific metabolites, known as allelochemicals, into the environment that affect the growth and development of other surrounding plants, resulting in mutual inhibition or promotion of the organisms. Allelopathy in donor plants is either self-induced or induced by specific external biotic and abiotic factors. The external factors may determine the types and quantities of allelochemicals released into the environment by a donor plants. Biotic factors inducing allelopathy include plant competition, herbivory by animals and insects, and soil-borne pathogens. For example, competing plants produce allelochemicals in response to competing weeds. Plants may emit signaling chemicals from their roots to induce the production of protective metabolites against organisms, herbivores, or competitors. Additionally, herbivory is a selection pressure that triggers defensive measures in plants, such as the synthesis of allelochemicals in response to injury. Moreover, some leaves release volatile substances that help the plant to deter or attract herbivores or pests that attack leaves. Likewise, root compounds may be produced in response to soil-borne pathogens. Furthermore, some abiotic factors, including light, temperature, drought, CO₂, and nutrient deficiency, can also induce plants to release allelochemicals. Therefore, it is pertinent to understand this natural phenomenon in plants and how external factors lead plants to exert allelopathy to compete, defend themselves, and survive in a challenging environment.

Keywords: allelochemicals; weeds; secondary metabolites; plant competition; plant–plant interaction



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1. Introduction

The term allelopathy derived from the two Greek words “*allelon*”, meaning mutual, and “*pathos*”, meaning harm or suffering, was first used in 1937 by the Austrian professor Hans Molisch [1]. Allelopathy, according to the definition accepted by the International Allelopathy Society, is the phenomenon via which organisms such as plants, microorganism, viruses, and fungi release secondary metabolites, known as allelochemicals, into the environment to influence the growth and development of agricultural and biological systems [2]. There are two types of allelopathy: true (or direct) and functional (or indirect) allelopathy. In true allelopathy, transformation of allelochemicals in the environment happen. Perhaps, once released into the soil, allelochemicals interact with physical, chemical, and biological soil characteristics that affect their retention, transformation, and transport processes and,

consequently, their phytotoxic level [3–5]. Previously [6], allelopathy was considered only in higher plants. However, it has now also been reported in bacteria [7], fungi [8], lower plants [9], and animals [10].

Allelochemicals are mainly primary and secondary metabolites, natural products, idiolytes, dispensable metabolites, and volatile organic compounds (VOCs) [11] that are produced and released by donor plants into the environment; they play a vital role in plant–plant and even plant–animal communication [4]. Allelochemicals are primarily discharged through common volatilization [11], leaching [12], root exudates [13,14], decomposition of plant residues or litters [12], seed germination [15], and pollen pathways [16]. Allelochemicals belong to a wide range of chemical classes that include approximately 25,000 terpenoids, 21,000 alkaloids, 700 nonprotein amino acids, 2000 flavonoids, 6000 phenolic acids, 700 quinones, 1500 polyenynes, 60 cyanosides, and 100 glucosinolates [17–19]. For example, the terpenoids produced by plants affect herbivorous insects, microorganisms, and other plants, resulting in various environmental impacts [20]. Similarly, alkaloids are defensive substances synthesized by plants to cope with attack by organisms, insects, or animals, and are vital substances within the chemical defense system [21]. Moreover, another critical nitrogen allelochemical, in the form of non-protein amino acid, is present in leguminous plant seeds and seedling roots and may be released into the environment during sprouting, repressing the development of plants and microorganisms [22]. Likewise, flavonoids such as pisatin and prunetin are produced by plants. Pisatin, found in *Pisum sativum* L., is a plant defensive hormone induced by organisms, and prunetin, present in the root of pea plants, attracts *Aphanomyces euteiches* Drechs. Both can help plants to withstand infection or attack by insects and herbivores [23]. Allelopathic inhibitions are usually not caused by a single substance but by a synergistic effect of numerous allelochemicals [24], which interfere with several physiological activities [25]. Allelochemicals have different environmental effects and capacities such as antiherbivore, antibacterial, antifungal, phytotoxic, attractant, facilitator, internal regulator of growth and development, or seed germination stimulant or inhibitor [26–29]. Plant signaling molecules play an important role in various defensive mechanisms that might be one of the functions of allelopathy [30].

Allelopathy plays different roles in different ecosystems. For example, in an agricultural ecosystem, allelopathy is mainly present in the chemical interactions between crop and weed species [31] and plays a vital role in the successful invading of exotic plants into natural communities [31,32]. Similarly, it is beneficial in terms of yield improvement in agricultural production and crop rotation [33]. In addition, plant age and plant parts affect the qualitative and quantitative composition of donor plant allelochemicals [34].

Further, in microbial biological systems, microbes and actinomycetes can hinder or eradicate other microbial species, which they compete with by discharging allelochemicals. Moreover, in freshwater biological systems, a few green algae such as *Myrophyllum spicatum* L. and *Ceratophyllum demersum* L. discharge allelochemicals that influence their neighbors, hindering their development and making them better able to survive. Additionally, they can discharge polyphenolic allelochemicals to hinder the development of *Microcystis aeruginosa* Kützinger and *Matricaria spicatum* L. [35]. Furthermore, in marine biological systems, marine green algae emit allelochemicals to compete with numerous other sea-growing plants and creatures. Likewise, other aquatic plants, such as Tengou algae of the genus *Gonyaulax* (*Gonyaulax* spp.), secrete a non-protein toxin called 3-acetylcholine, which is not only autotoxic but also harmful to aquatic crustaceans [36]. In polar ecosystems, such as high mountains and glacial outcrops, lichens can suppress surrounding plants by releasing allelochemicals [37].

Allelochemicals have many unique roles in plants' defensive mechanisms against herbivores, insects, and pathogens [4]. Chemosynthesis, often seen as a natural phenomenon, is a phenotypically synthetic phenomenon that changes with natural conditions. In any case, allelopathy is ubiquitous in plants and induces or is activated by various signaling cascade reactions [30]. Plant allelopathy is self-induced or due to external factors [37].

These factors enhance the effect of allelopathy, including biotic factors and abiotic factors. Biological factors include plant competition [38], animal/insect feeding [39], and microbial poisoning [40]. Abiotic factors include light [41], shading [42], temperature [43], drought [44], CO₂, nutrient deficiency [45], and salinity [46]. Biotic and abiotic factors activate the generation of allelochemicals and modify the microenvironment in natural and controlled biological systems [38]. The high concentration of allelochemicals in plant organs could be associated with allelopathy between neighboring plant species [47]. Root response to allelochemicals in plant–plant interaction and competition have important implications for natural biological and agricultural ecosystems [48]. Further, inducing allelopathy could be a defense mechanism that permits plants to develop and breed better than they would on their own. In general, allelopathy enables plants to enhance their competitiveness and tolerance for better adaptation to the environment. Allelopathy, as induced by these different factors, is described below, according to a search we performed on the Web of Science database using the keywords “induce” + “allelopath*”.

2. Biological Factors

2.1. Plant Competition

Plants use signaling molecules to identify and recognize their neighbors and trigger allelopathic interactions to drive interspecific or intraspecific interactions. Plants may identify and react to neighboring competitors by changing the production and discharge of defensive metabolites such as allelochemicals. Previous studies showed that some plants may emit signaling chemicals such as jasmonic acid, salicylic acid, and (–)-loliolide from their roots to stimulate the generation of protective metabolites against organisms, herbivores, or competitors [38,49,50]. Plants monitor their neighbors and enhance their own resistance when they sense volatile compounds being discharged from their neighboring plants in response to leaf herbivores [51,52]. Plant competition can either increase [53] or decrease [54] the release of allelochemicals. Autotoxicity is a form of intraspecific allelopathy, in which a plant species discharges toxic chemicals that repress or delay the germination and growth of other plants of the same species. Autotoxicity occurs in natural biological systems and is considered to have biological significance in controlling plant population and density [55]. Furthermore, in terrestrial plants, autotoxicity can be used to control population density, limit inbreeding, and advance hereditary diversity, favoring the presentation of foreign genotypes [56]. Naphthoquinone levels were altogether higher in *Echium plantagineum* L., developed with intraspecific competition, with a three-fold increase in acetyl shikonin and around a 20-fold increase in isovaleryl shikonin [57].

Plant development is influenced by the root exudates of neighbors, which play a vital role in inducing allelopathic activity [48]. It has been shown that buckwheat root exudates repressed pigweed growth when both plant species were growing next to each other, and pigweed recognition by buckwheat induced changes in the buckwheat root exudation profile [24]. It is worth mentioning that root–root interactions play an important role in barnyard grass-induced production of allelochemicals in rice and weed-induced production of allelochemicals in wheat [37]. No matter the kind of barnyard grass, the root exudates induce rice to produce allelochemicals [58]. Monoculture and intercropping barnyard grass–rice system experiments showed that the proximity of competitive weeds and their root exudates can increase rice allelochemicals such as momilactones and flavone, resulting in an improvement in rice allelopathy by the chemical components in barnyard grass root exudates [48]. Moreover, the rice root exudates also expanded the allelopathic movement of barnyard grass [59]. One major phytotoxin inside the root exudates of *Sorghum bicolor* L. is sorgoleone, which was discharged in crucial amounts in the presence of a crude extract of velvet leaf root, indicating that seedlings could have increased phytotoxicity and improved allelopathic potential in the presence of other plants [60]. When a plant induces other plants to create allelochemicals, some substances such as root exudates will act as transitional information to accomplish the process.

Methyl jasmonate (MeJA) and methyl salicylate (MeSA) are compounds inducing plant defense against microbial pathogens and insect herbivores. Exogenous application of MeJA and MeSA to rice (*Oryza sativa* L.) increases phenolic and enzyme activities in response to the enhanced rice allelopathic potential [59]. Volatile methyl jasmonate can spread in the air and induce the synthesis of chemical defense substances in plants [61]. Exogenous jasmonic acid induces the synthesis of antimicrobial substances in rice leaves [62]. For example, jasmonic acid treatment could induce maize to create HDMBOA-Glc, which is a group of important defense chemicals widespread in grasses [63]. The increase in the secretion of rice chemo-sensitive substances induced by exogenous substances leads to targeted changes in inter-root microbial community structure and function, and the changes in microorganisms simultaneously promote rice chemo sensitization [64].

Rice is often affected by a major weed, barnyard grass, in paddy soil. Rice seedlings with allelopathic traits were found to be able to detect certain chemicals discharged by barnyard grass and react by creating more allelochemicals to repress barnyard grass [65]. Less consideration has been paid to the allelochemical production of crop plants in the presence of competing weeds. In reality, plants can adjust their production of secondary metabolites in response to plant competitors, or biochemical plasticity [66]. The main allelochemicals in rice are flavonoids, diterpenoid lactones, and cyclo hexenones [59,67]. Biotic and abiotic stress conditions, such as starvation and higher accompanying weed densities, may induce rice to produce allelochemicals [68]. The generation of allelochemicals in crops is known to increase when crop plants grow in the presence of competing weeds [38]. For example, the allelopathic activity of rice was increased by the existence of barnyard grass seedlings or barnyard grass root exudates [69]. Moreover, allelopathy in rice (*O. sativa*) could be chemically induced by the exogenous application of chemical compounds of barnyard grass root exudates [70], suggesting the presence of certain signaling chemicals that evoke the generation of rice allelochemicals [38]. Rice allelopathy may be primarily dependent on the secretion of momilactone B. The momilactone B production and allelopathic activity in rice seedlings may be induced by some chemical compounds in barnyard grass root exudates [69]. Allelopathic rice might identify the existence of barnyard grass through the presence of (–)-loliolide and jasmonic acid in barnyard grass root exudates, which act as signaling components, via increased generation of the allelochemicals momilactone B and triclin [38,62]. In addition to barnyard grass, a few exogenous compounds also induce allelochemicals in rice. The inhibitory impact of rice on barnyard grass may be caused by compounds generated by the root system. Rice may recognize the existence of neighboring barnyard grass by the discovery of certain allelochemicals in barnyard grass root exudates, which may trigger a signaling cascade and give rise to increase rice allelopathy by discharging momilactone B in the rhizosphere. Subsequently, rice allelopathy is probably an inducible defense component by chemical-mediated plant interactions between rice and barnyard grass [59]. Further, rice has a clear recognition effect. When rice identifies the surrounding organisms, it releases fewer allelochemicals; when it identifies the plants living around it as weeds such as barnyard grass, it releases more allelochemicals to inhibit the growth of weeds and make its own growth better. The induction of allelochemicals in rice and barnyard grass is mainly to repress other species and ensure the successful survival of one's own species.

Similarly, wheat also has an induced defense phenomenon. Many studies have shown that some wheat varieties can produce benzoxazinoids against different pests, most notably in allelopathy, influencing the germination and development of weeds in a wheat crop [71]. One report indicated that the production of DIMBOA in wheat was induced by the root exudates from the weeds [72]. Moreover, it has been reported that the concentration of DIMBOA was induced by a few weeds with root isolation [71]. When wheat was exposed to the basic oils of wild oat and crabgrass, the generation of DIMBOA was enhanced [66]. The induction defense strategy is also present in wheat. When weeds exist, wheat senses weeds through root exudates and releases allelopathic substances to suppress the growth of weeds and improve its own survival.

Similar induced defense procedures are seen in marine plants. Induced defense mechanisms in phytoplankton include altered morphology, organic chemistry, and life history characteristics [73]. Similarly, induced responses were observed in algae of freshwater and marine systems [74]. For example, the bloom-forming marine coccolithophorid *Emiliana huxleyi* Lohmann has induced chemical protection via dimethylsulfoniopropionate (DMSP) [73]. Further, some algae produce allelochemicals in response to competitors, herbivores, or pathogens. For example, zooplankton, detecting the allelopathic impacts of other oceanic plants, synthesize allelochemicals to counter the allelopathic substances of other organisms [75]. Competitors may fight back against allelopathy. Under different competitive pressures, the amount and type of allelochemicals released are also different. An increase in allelochemicals has been observed at low or medium levels of competition, with a depletion at high competition levels [54]. The growth differentiation balance hypothesis proposes that secondary metabolite generation is restricted by low resource availability [76]. Mounting evidence suggests that induced germination inhibition could be an adaptive reaction to competitive conditions, not the result of toxin exposure [77]. Like inducible herbivore protections, allelochemicals are produced only when encountering competition may enhance fitness [78]. Under experimental conditions with intraspecific competition, an increase in terpenoid emissions at low or medium competition levels (when nutrients are accessible) and a decrease in terpenoid emissions at high competition levels (low nutrient concentration) have been observed. At low levels of competition, plants release allelochemicals to suppress or kill surrounding plants so that they can obtain more nutrients; however, at high levels of competition, plants allocate energy to growth or reproductive organs so that they can grow taller and complete reproduction in the current generation as soon as possible. By perceiving the presence of surrounding plants, plants release allelochemicals to enhance their competitiveness and harm surrounding plants, enabling them to obtain more environmental resources.

2.2. Animals

Herbivory may be a selection pressure that activates defense components in plants. Numerous seaweeds and terrestrial plants induce chemical protections in reaction to herbivory [79,80]. Plants produce toxins to defend against insects; these toxins are mainly secondary substances. As a reaction to herbivory, plants can alter their phenotype to increase certain compounds or synthesize new chemicals [81–83]. The content of secondary metabolites has a great impact on the quality of edible plants [84]. When plants are attacked by herbivores, lignin and tannin are released to affect herbivores. Lignin affects the digestion and absorption of livestock, and tannin reduces the feeding rate of animals [85]. Plants release many sensory substances to protect themselves against natural enemies [86]. Inducing allelopathy can also cause a certain harm to the plant itself, while reducing the feeding of pests. Pest-induced plant volatiles also have a significant inhibitory effect on own growth (autotoxicity), which at the same time increases the cost of producing these substances [87].

Herbivore feeding enhances the chemosensory effect of rice [88]. Rice can protect itself by discharging allelochemicals and altering its growth and development against herbivorous creatures to decrease their feeding. The production of volatiles from leaves increases during attack by herbivores, which helps plants to deter herbivores [89]. Furthermore, artificial wounding may also trigger a similar effect [90,91]. For instance, mechanical damage can improve the allelopathy of lucerne and winter rye [92]. Moreover, some researchers have suggested that methyl jasmonate plays a chemosensory activity in plants, whereby mechanical damage can induce a large release of methyl jasmonate [72]. However, there are also some different conclusions, e.g., that physical damage and treatment with 2,4-D had no effect on the allelopathic potential of plant or the concentration of the major compounds present. Anthropogenic factors did not seem to induce plants to produce higher levels of allelopathic phytochemicals [72].

The phenomenon of animal-induced plant allelopathy is also applied to aquatic plants or phytoplankton [93–96]. Herbivores trigger induced protection (the generation of allelochemicals such as phlorotannin) by damaging macroalgae [73]. After animals induce plants to create more allelochemicals, plants enhance their ability to defend not only against those particular animals but also against other creatures. The zoobenthos enhances the algal suppressive effect of macrophytes by inducing a stimulation reaction in select macrophytes [97]. *M. aeruginosa* increases poison production in reaction to zooplankton as an induced defense mediated by the discharge of info chemicals from zooplankton [98,99]. *Microcystis* increases their chemical defenses, reducing zooplankton's ability to feed on them and allowing them to grow better. Aquatic plants and algae live in the water and compete. In this way, aquatic plants suppress the growth of algae, so that they can reproduce and develop better [97].

2.3. Insects

When plants are damaged by phytophagous insects, they can release some volatile secondary metabolites that are qualitatively and/or quantitatively different from healthy plants. These volatile chemicals have an important role to play in regulating the inter-relationship among plants, phytophagous insects, and their natural enemies [100]. Pest damage may induce an increase in the release of plant chemosensitive substances, which may enhance the chemosensory effect of the plant [87]. Plants stimulate various defensive mechanisms such as increasing the production of phenolics, alkaloids, terpenes, and defense proteins, which decrease further herbivory attacks [59]. The qualities and times of allelochemicals being released by the plant could not only modify the toxicity and repellent mechanisms but also influence insect feeding habits and feeding behavior [101]. When plants are attacked by insects, volatile chemical signals are released not only from the damaged parts but also from other parts of the plant system, and they continue to be released after the insects stop feeding. Evidence showed that mounting such signals can also affect neighboring intact plants; certain plants can release stress signals even when undamaged [102]. Glucosinolates are unique to cruciferous plants, and their chemical combination and discharge can be induced by insect feeding [103]. Pest-induced plant volatiles have a chemosensory effect; green leafy odorants, salicylic acid, methyl ester, and other volatiles have particularly strong chemosensory activity [87]. After insect and grazing herbivore attack, MAPK cascades are rapidly activated in plants, followed by the induction of jasmonate or ethylene signaling pathways [104–106]. *E. plantagineum* can distribute metabolic flux and nutrient assignment in reaction to environmental stresses, thus affecting pest resistance [107]. Allelopathy induced by insects is mainly a way to protect functions. The main ecological function of volatiles from *Ageratum conyzoides* L., affected by *Erysiphe cichoracearum* DC. or exposed to aphid feeding, may not be to affect neighboring plant development. Infection and aphid feeding are, in fact, more destructive to *A. conyzoides* than competition with neighboring plants [75].

Allelopathic substances released by plants when attacked by insects not only directly resist insect attacks, but also attract natural enemies of these insects, which helps plants to defend themselves against their enemies. For example, when the beet moth feeds on corn, the corn releases volatile terpene molecules into the air, triggering a chemical defense mechanism that attracts the moth's natural enemies, parasitic wasps [108]. Plants do not release as many allelochemicals when they are not under attack because releasing allelochemicals requires energy, which is instead allocated to vegetative or reproductive organs to allow them to flourish and occupy more ecological niches. However, when a plant is being eaten by insects, it will use that energy to release more allelopathic substances. These extra allelopathic substances will have a negative impact on insects, thus reducing insects' feeding on the plant and allowing the plant to grow better. Pest-induced plant volatiles also have a significant inhibitory effect on their own growth (autotoxicity), which at the same time increases the cost of producing these substances [87]. Plants that are regularly exposed to biotic stressors usually utilize constitutive strategies when producing allelochemicals to prevent and/or kill their predators. Plants that are seldom attacked rely

mainly on induced defense systems [57]. Inducing allelopathy also causes certain harm to the plant while reducing the feeding of pests, and the mechanism via which insects induce plants to create allelochemicals is unclear.

At the same time, studies of plant–insect interactions, especially in multitrophic systems, have the potential to identify insect signaling chemicals that may elicit plant defense responses [109]. When plants are assaulted by insects, neighboring intact plants can be influenced by volatile signals by triggering their own signaling systems to be repellent to approaching herbivores, foraging predators, and parasitic insects [102]. Plants are also able to activate defense mechanisms against assaulting herbivores by detecting volatile compounds, such as methacrolein and methyl jasmonate, discharged by herbivore-attacked plant cells [59]. When plants are eaten by insects, they release a signal to neighboring plants to produce allelopathic substances. This can prevent insects from feeding, which is a chemical defense activity [102].

2.4. Microorganisms

Soil microorganisms have an important impact on plant–plant allelopathic interaction [110]. Compared to feeders’ (such as insects) chemical defense induction, the chemical defense of plants against pathogens tends to be more specific and local [101]. When sensing elicitors of pathogen origin, many plants can accumulate allelochemicals around infection sites of pathogens [59]. Plants increase allelochemical production to resist the damage of pathogens. There have been some reports that arbuscular mycorrhizal fungi (AMFs) could induce the accumulation and synthesis of allelochemicals in the tissues of host plants, impacting their allelopathic potential. AMFs have an important role in enhancing different plants’ allelochemicals [111]. Other studies have demonstrated that mycorrhizal fungi produce allelochemicals, antibiotics, toxins, and root exudates to protect plant roots from diseases [112]. AMFs not only reduce plants’ allelochemical production, but also create allelochemicals to help plants resist disease.

Microorganisms induce plants to create allelochemicals that might have an important effect on the interactions between colonized plants and the environment. The phenomenon will change the soil chemical composition around a plant, thus changing the chemical ecological environment to some extent. The purpose of allelochemicals is to increase the ability of the plant to resist microorganism invasion and infection and inhibit the growth of microorganisms. Some researchers have reported that how induction by insects affects fungal chemical diversity is poorly understood [113]. Microorganism-induced plant allelochemical production is less understood compared to animal-induced allelopathy. Research on this phenomenon needs to be intense in the future. Examples of biotic factors are summarized in Table 1.

Table 1. Examples of biotic factors summary.

S.No	Factor	Target Plant	Description	Reference
1	Plant competition	Rice (<i>O. sativa</i>)	<i>Barnyard grass</i> may emit signaling chemicals such as (–)-loliolide from their roots to stimulate the generation of protective metabolites such as momilactone B and tricinin in rice against competitors. Moreover, barnyard grass–rice system experiments showed that the proximity of competitive weeds and their root exudates can increase rice allelochemicals such as momilactones and flavone, resulting in an improvement in rice allelopathy by the chemical components in barnyard grass root exudates.	[38] [48]

Table 1. Cont.

S.No	Factor	Target Plant	Description	Reference
1		<i>B. rapa</i> ssp.	Elicitor application of <i>salicylic acid</i> (SA) and <i>methyl jasmonate</i> (MJ) induces a targeted rhizosecretion of high levels of anticarcinogenic glucosinolates in the turnip organs, as well as in turnip root exudates.	[49]
		<i>E. plantagineum</i>	<i>E. plantagineum</i> is a noxious invasive weed in Australia forming monocultural stands in pastures and rangelands. It produces a naphthoquinones (NQs) which suppress competition from weeds, insects, and pathogens, and influence invasion success.	[57]
		pigweed (<i>A. retroflexus</i> L.)	Buckwheat (<i>Fagopyrum esculentum</i> Moench) root exudates repressed pigweed growth when both plant species were growing next to each other, and pigweed recognition by buckwheat induced changes in the buckwheat root exudation profile.	[24]
		<i>Sorghum</i> (<i>S. bicolor</i>)	The root exudate of sorghum includes sorgoleone, which was discharged in crucial amounts in the presence of a crude extract of velvet leaf root, indicating that seedlings could have increased phytotoxicity and improved allelopathic potential in the presence of other plants.	[60]
		<i>Wheat</i> (<i>T. aestivum</i>)	Many studies have shown that some wheat varieties can produce benzoxazinoids such as DIMBOA against different pests, most notably in allelopathy, influencing the germination and development of weeds in a wheat crop.	[71,72]
2	Animals	Nicotiana attenuate, Arabidopsis, maize, Chinese cabbage	As a reaction to herbivory, plants can alter their phenotype to increase certain compounds or synthesize new chemicals.	[81–83]
		Algae	Herbivores trigger induced protection (the generation of allelochemicals such as phlorotannin) by damaging macroalgae.	[73]
		Higher plants (Mulberry)	When plants are attacked by herbivores, lignin and tannin are released to affect herbivores. Lignin affects the digestion and absorption of livestock, and tannin reduces the feeding rate of animals.	[85]
		Rice	Herbivore feeding enhances the chemosensory effect of rice.	[88]
3	Insects	Cabbage leaves, maize seedlings, <i>N. attenuata</i> system, tomato	When plants are damaged by phytophagous insects, they can release some volatile secondary metabolites have an important role to play in regulating the interrelationship between plants, phytophagous insects, and their natural enemies.	[100]
		<i>Arabidopsis thaliana</i> L., Brassica vegetables (<i>Brassica napus</i> L., <i>B. rapa</i> , and <i>B. juncea</i>)	Glucosinolates are unique to cruciferous plants, and their chemical combination and discharge can be induced by insect feeding.	[103]

Table 1. Cont.

S.No	Factor	Target Plant	Description	Reference
3		<i>A. conyzoides</i>	The main ecological function of volatiles from <i>A. conyzoides</i> affected by <i>E. cichoracearum</i> DC. or exposed to aphid feeding may not be to affect neighboring plant development.	[75]
			Infection and aphid feeding are, in fact, more destructive to <i>A. conyzoides</i> than competition with neighboring plants	
		Maize	When the beet moth feeds on corn, the corn releases volatile terpene molecules into the air, triggering a chemical defense mechanism that attracts the moth's natural enemies, parasitic wasps.	[108]
		<i>A. thaliana</i>	Studies of plant–insect interactions, especially in multitrophic systems, have the potential to identify insect signaling chemicals that may elicit plant defense responses.	[109]
4	Microorganisms	tomato (<i>S. lycopersicum</i>)	Jasmonic acid (JA)- and salicylic acid (SA)-regulated defensive pathways in tomato beneficial root endophytes (<i>Trichoderma</i> spp.) induced resistance to the root knot nematode <i>Meloidogyne incognita</i> .	[50]
		<i>E. plantagineum</i>	When sensing elicitors of pathogen origin, many plants can accumulate allelochemicals around infection sites of pathogens.	[59]
		<i>Solanum nigrum</i> , <i>Digitaria sanguinalis</i> , <i>Ipomoea purpurea</i>	Arbuscular mycorrhizal fungi (AMFs) could induce the accumulation and synthesis of allelochemicals in the tissues of host plants, impacting their allelopathic potential. AMFs have an important role in enhancing different plants' allelochemicals.	[111]

3. Abiotic Factors

Abiotic factors such as light, nutrient, and water deficiency may improve the allelopathic potential of plants [114]. The types and quantities of allelochemicals synthesized by plants and released to the environment are regulated by abiotic and biotic factors [75]. It is worth mentioning that secondary metabolites with phytotoxic activity do not always function as allelochemicals, even if they are released into the soil or air; they need to demonstrate that they can persist in the soil or air at effective concentrations for a certain period of time [115,116]. Abiotic stress can induce expression of related enzymatic genes and promote the synthesis and discharge of terpene VOCs [117,118]. Plants that develop in full sun or with adequate soil resources may prioritize the allocation of resources to development and generation instead of protective chemistry. Costs related to allelochemical production would be incurred once resources were restricted [119]. In higher plants, their VOCs are recognized as antioxidant agents to scavenge ROS and protect cell membranes and photosynthetic apparatus under stress. The generation and emission of VOCs are useful to algal cells scavenging ROS under abiotic stresses. In algae, a wide range of VOCs are discharged in aquatic ecosystems. Abiotic variables such as temperature, light, and nutrition deficiency influence their emission. VOCs can trigger the exchange of information between algae to provide protection against predators and, thus, indirectly play an allelopathic role to improve resistance to abiotic stresses [7]. These abiotic factors enhance the allelopathic activity of plants due to increased production of allelochemicals [59].

3.1. Light

Light is an important environmental factor that induces plants to create allelochemicals. In the environment, the allelochemicals released by plants will change when the

intensity and quality of light change, which will induce plants to produce allelochemicals. Shading may decrease resource availability and, therefore, decrease assignment to allelochemicals [120]. Changes in light quality can also affect the production of allelochemicals in plants [121,122]. After UV irradiation, plants release mycorolactone B. UV radiation increases the concentration of momilactone B in the shoots and roots of rice seedlings. Since mycorolactone B has antibacterial and allelopathic effects, the excretion of mycorolactone B to the rhizosphere could have a competitive benefit for root creation by locally inhibiting dirt microorganisms and inhibiting the development of competitive plant species [123]. In the case of mint, abiotic stressors such as UV radiation induce the production of mint essential oils, the main ingredients of which are monoterpenes [124]. Photoinduced allelochemicals can increase the success rate of liana substitution by making liana redistribute resources according to light differences during early forest regeneration. Understanding how allelopathic potential changes with light accessibility may help with clarifying the dynamic role of allelochemicals in plant communities [120]. The main role of light-induced allelochemicals in plants as a competitive mechanism is to make them better adapted to their environment. In contrast to light, shading also plays an important role in allelopathy. A previous study suggested that 60% plant shading in cultivated cardoons increased the sesquiterpene lactone content and phytotoxicity of its leaf extracts [42].

3.2. Temperature

Temperature may be a key factor that drives allelopathic activity. It is reported that temperature specifically impacts plant growth by possibly improving allelochemical production, which subsequently impacts the growth of related plants [25]. Rice seedlings under submergence and high-temperature conditions showed increased levels of whole phenolics and flavonoids; for example, the rice cultivar Koshihikari may produce more syringic, p-hydroxybenzoic, vanillic, sinapic, and benzoic acids, which conceivably suppress the plants' growth. Extracts and root exudates had the highest amount of total phenolic and flavonoid substances when rice seedlings were treated at 37 °C under abiotic stress. Allelopathic responses of rice seedlings depend on genotype and stress conditions, with temperature being a key factor [125]. High temperature could induce the generation of enormous amounts of ROS in algae, which benefits the oxidation of halide ions, carotenoids, and fatty acids, driving the formation of halogenated hydrocarbons, GLVs, and carotenoid degradants [41]. Climatic warming and eutrophication may lead to a shift in *Microcystis* populations toward blooms that contain a more prominent rate of toxic *Microcystis* cells and, consequently, more noteworthy concentrations of microcystin. When the temperature is over 25.8 °C, with a further increase in temperature, some toxic or nontoxic *M. aeruginosa* strains will release more allelochemicals to inhibit the growth of the green alga *Chlorella vulgaris* Beyerinck [74]. *E. plantagineum* roots exposed to the highest temperature regime appeared to show improved accumulation of naphthoquinones over time in contrast to roots created at the lowest temperature treatment. Allelochemicals such as deoxyshikonin, dimethylshikonin, and shikonin showed significantly higher concentrations over time in roots exposed to a high-temperature regime [57]. Some researchers have found that the discharge of monoterpenes from rosemary (*Rosmarinus officinalis* L.) was significantly higher in the high-temperature season than in other seasons, and its release was significantly influenced by the environment [126]. Temperature stress changed the relative water content of *Trifolium*. Allelopathy of the extract increased *Vicia faba* L. root tip cells' toxicity, with more prominent inhibition of cell mitosis, and induced a higher frequency of chromosomal aberrations and micronucleus. At high temperatures, the impact of allelopathy was more prominent than at low temperatures [127]. It has been observed that simultaneous exposure to high temperature and dry stress brought about an accumulation of allelochemicals in the roots and stimulation of secondary metabolites in the foliage of *Holcus lanatus* L. and *Alopecurus pratensis* L. [128].

The above studies clearly showed that plants release more allelopathic substances with an increase in temperature, to increase their defense capability. Further, this may prevent the activity of pathogens and feeders, or the growth of weeds.

With the current climate warming, plants may release more allelopathic substances due to the increase in overall environmental temperature; this will have an impact on the plants' ecosystem.

3.3. Drought

A dry environment may induce a vast range of allelochemicals and a sharp increase in their concentrations [129,130]. Drought stress triggers accumulation of ROS and bioaccumulation of bioactive chemicals such as terpenes, phenols, and alkaloids to facilitate defense against pathogens, insects, and weeds. Water stress (45% of field water capacity) and treatment with prohydrojasmon before sowing seemed to improve the chemosensory resistance to grass induction in a few tested wheat varieties [131]. The collection of terpenoids was recently explored within the herbaceous weed, *Tanacetum vulgare* L., which was challenged by leaf herbivory and drought stress [57]. Under water deficiency, the level of phenolic substances in *Tagetes erecta* L. was much higher than that in normal water conditions [130]. *E. plantagineum* under stress, including drought and elevated temperature, showed improved generation of shikonins, including those related to improved allelopathic or weed-suppressive activity and those acting as potent antimicrobials [57]. In other cases, *Bidens Pilosa* L., appeared to enhance phytotoxicity in periods of drought [112]. The biosynthesis of anthocyanins by *A. thaliana* improved under drought conditions, and generation was related to protection against drought stress [132]. From the above examples it is clear that, under drought stress, plants produce more allelopathic chemicals to help them better withstand drought.

3.4. Carbon Dioxide

An increase in air CO₂ concentration may increase allelochemical emissions from plants [133–137]. The monoterpene of *R. officinalis* was significantly enhanced with an increase in CO₂ concentration, particularly in the high-temperature season compared to other seasons [126]. Increasing air CO₂ levels may improve the biosynthesis and phytotoxicity of allelochemicals in *Mikania micrantha* H.B.K., one of the most obtrusive weeds in the world, which in turn might improve its potential allelopathic effect on neighboring local plants if discharged in bioactive concentrations [138]. In the future, the increase in atmospheric carbon dioxide levels may alter the strength of plant allelopathy, and the release of more allelochemicals may interfere with the regeneration and diversity of forest ecosystems.

4. Nutrient Deficiency

Nutrient deficiency is another crucial trigger for plants to induce the synthesis and discharge of allelochemicals. The main nutrient deficiencies are of nitrogen and phosphate. In rice, allelopathic activity may be increased under nutrient starvation conditions. Rice has shown strong allelopathic activity under phosphorus and nitrogen deficiency, which indicates the influence of nutrient starvation [69]. Low-phosphorus stress not only increases chemosensitive substances, but changes in chemosensitive substances can also induce an increase in relevant herbicidal microorganisms in the soil, thereby increasing the chemosensitive potential of plants [139]. The inducible phenomenon in rice was observed when the P content dropped below the optimum level in hydroponic culture [140]. In lower P conditions, the defensive enzyme activities and other physiological and biochemical indices of barnyard grass were restrained. Further analysis revealed that the activity of phenylalanine ammonia lyase and the total phenol content in root and leaf tissues increased remarkably compared with that in non-allelogenic rice [141]. Rice produces more allelochemicals in nitrogen- and phosphate-limited conditions. The main role of rice's induced allelopathy in nutrient deficiency is to enhance competitiveness with other plants. With the increase in nutrient deficiency, the allelochemicals produced by *Helianthus annuus* increased significantly.

Inhibition and enhancement of germination were observed in *Amaranthus retroflexus* L. [124]. In *A. thaliana*, P deficiency induces the expression of more than 1000 traits, of which a large number of genes are related to terpene VOCs and phenylalanine metabolism [142].

In marine ecosystems, nutrient deficiency can increase the secondary metabolites of cyanobacteria and discharge a range of VOCs [143]. In *Microcystis*, the discharge of VOCs was dramatically increased in a low-nitrogen medium [45]. *M. aeruginosa* increased the release of VOCs and β -cyclocitral when N availability was insufficient [144]. It has been reported that the production of allelochemicals was stimulated in *Alexandrium tamarense* Lebour after exposure to N-limited and P-limited conditions [145]. The decrease in P availability promotes VOC emission in cyanobacteria [146]. The allelochemicals of cyanobacteria were dramatically influenced by the nutritional status. This could be due to the expression of related synthase genes, enhancing the synthesis and discharge of VOCs under P-free conditions. Cyanobacteria will discharge numerous VOCs, which place allelopathic restraints on the development of other algae, to help cyanobacteria maintain a nutritional competitive advantage, and further decrease the diversity and structure of the algal community [143]. As shown in the above example, N and P restriction is the main factor inducing allelopathy in plants and phytoplankton. Examples of abiotic factors are summarized in Table 2.

Table 2. Examples of abiotic factors summary.

S.No	Factor	Target Plant	Description	Reference
1.	Light	<i>Cynara cardunculus</i> L.	A previous study suggested that 60% plant shading in cultivated cardoons increased the sesquiterpene lactone content and phytotoxicity of its leaf extracts.	[42]
		<i>Toxicodendron radicans</i> L., <i>Parthenocissus quinquefolia</i> L., <i>Celastrus orbiculatus</i> Thunb, <i>Lonicera japonica</i> Thunb, and <i>Vitis vulpina</i> L.	Photoinduced allelochemicals can increase the success rate of liana substitution by making liana redistribute resources according to light differences during early forest regeneration. Understanding how allelopathic potential changes with light accessibility may help with clarifying the dynamic role of allelochemicals in plant communities.	[120]
		<i>Fagus sylvatica</i> L.	Changes in light quality can also affect the production of allelochemicals in plants.	[122]
		<i>O. sativa</i>	After UV irradiation, plants release mycorolactone B. UV radiation increases the concentration of momilactone B in the shoots and roots of rice seedlings.	[123]
		<i>Mentha × piperita</i> L.	In the case of mint, abiotic stressors such as UV radiation induce the production of mint essential oils, the main ingredients of which are monoterpenes.	[124]
2.	temperature	<i>Synechococcus</i> spp.	High temperature could induce the generation of enormous amounts of ROS in algae, which benefits the oxidation of halide ions, carotenoids, and fatty acids, driving the formation of halogenated hydrocarbons, GLVs, and carotenoid degradants	[41]

Table 2. Cont.

S.No	Factor	Target Plant	Description	Reference
2.	temperature	<i>E. plantagineum</i>	<i>E. plantagineum</i> roots exposed to the highest temperature regime appeared to show improved accumulation of naphthoquinones over time in contrast to roots created for the lowest temperature treatment.	[57]
			Allelochemicals such as deoxyshikonin, dimethylshikonin, and shikonin showed significantly higher concentrations over time in roots exposed to a high-temperature regime.	
		<i>M. aeruginosa</i>	Climatic warming and eutrophication may lead to a shift in <i>Microcystis</i> populations toward blooms that contain a more prominent rate of toxic <i>Microcystis</i> cells and, consequently, more noteworthy concentrations of microcystin. When the temperature is over 25.8 °C, with a further increase in temperature, some toxic or nontoxic <i>M. aeruginosa</i> strains will release more allelochemicals to inhibit the growth of the green alga <i>Chlorella vulgaris</i> Beyerinck.	[74]
		<i>O. sativa</i>	The rice cultivar Koshihikari may produce more syringic, p-hydroxybenzoic, vanillic, sinapic, and benzoic acids, which conceivably suppress the plants' growth. Extracts and root exudates had the highest amount of total phenolic and flavonoid substances when rice seedlings were treated at 37 °C under abiotic stress.	[125]
		<i>R. officinalis</i>	Some researchers found that the discharge of monoterpenes from rosemary (<i>R. officinalis</i>) was significantly higher in the high-temperature season than in other seasons, and its release was significantly influenced by the environment.	[126]
		<i>V. faba</i>	Allelopathy of the extract increased <i>V. faba</i> root tip cells' toxicity, with more prominent inhibition of cell mitosis, and induced a higher frequency of chromosomal aberrations and micronucleus. At high temperatures, the impact of allelopathy was more prominent than at low temperatures.	[127]
3.	Drought	<i>H. lanatus</i> and <i>A. pratensis</i>	It has been observed that simultaneous exposure to high temperature and dry stress brought about an accumulation of allelochemicals in the roots and stimulation of secondary metabolites in the foliage of <i>H. lanatus</i> and <i>A. pratensis</i> .	[128]
		<i>E. plantagineum</i>	<i>E. plantagineum</i> , under stress, including drought and elevated temperature, showed improved generation of shikonins, including those related to improved allelopathic or weed-suppressive activity and those acting as potent antimicrobials.	[57]
		<i>B. pilosa</i>	<i>B. pilosa</i> appeared to enhance phytotoxicity in periods of drought.	[112]

Table 2. Cont.

S.No	Factor	Target Plant	Description	Reference
3.	Drought	<i>T. erecta</i>	Under water deficiency, the level of phenolic substances in <i>T. erecta</i> was much higher than that in normal water conditions.	[130]
		<i>P. sativum</i>	Drought stress triggers accumulation of ROS and bioaccumulation of bioactive chemicals such as terpenes, phenols, and alkaloids to facilitate defense against pathogens, insects, and weeds. Water stress (45% of field water capacity) and treatment with prohydrojasmon before sowing seem to improve the chemosensory resistance to grass induction in a few tested wheat varieties.	[131]
		<i>A. thaliana</i>	The biosynthesis of anthocyanins by <i>A. thaliana</i> improved under drought conditions, and generation was related to protection against drought stress	[132]
		<i>R. officinalis</i>	The monoterpene of <i>R. officinalis</i> was significantly enhanced with an increase in CO ₂ concentration, particularly in the high-temperature season compared to other seasons	[126]
		<i>B. napus</i>	Elevated carbon dioxide on volatile terpenoid emissions and multitrophic communication of transgenic insecticidal oilseed rape (<i>B. napus</i>).	[134]
4.	Carbon dioxide	<i>Mucuna pruriens</i> L. and <i>Arundo donax</i> L.	We found a significant enhancement of isoprene emissions per unit leaf area in <i>M. pruriens</i> under subambient CO ₂ concentrations relative to ambient controls but not for <i>A. donax</i> .	[135]
		<i>M. micrantha</i>	Increasing air CO ₂ levels may improve the biosynthesis and phytotoxicity of allelochemicals in <i>M. micrantha</i> , one of the most obtrusive weeds in the world, which in turn might improve its potential allelopathic effect on neighboring local plants if discharged in bioactive concentrations.	[138]
		<i>O. sativa</i>	The main nutrient deficiencies are of nitrogen and phosphate. In rice, allelopathic activity may be increased under nutrient starvation conditions. Rice has shown strong allelopathic activity under phosphorus and nitrogen deficiency, which indicates the influence of nutrient starvation.	[69]
5.	Nutrient deficiency	<i>O. sativa</i>	Rice produces more allelochemicals in nitrogen- and phosphate-limited conditions.	[124]
		<i>O. sativa</i>	The inducible phenomenon in rice was observed when the P content dropped below the optimum level in hydroponic culture.	[140]
		<i>O. sativa</i>	In lower P conditions, the defensive enzyme activities and other physiological and biochemical indices of barnyard grass were restrained. Further analysis revealed that the activity of phenylalanine ammonia-lyase and the total phenol content in root and leaf tissues increased remarkably compared with that in non-allelogenic rice.	[141]
		<i>O. sativa</i>		

Table 2. Cont.

S.No	Factor	Target Plant	Description	Reference
5.	Nutrient deficiency	<i>Microcystis</i> spp.	In <i>Microcystis</i> , the discharge of VOCs was dramatically increased in a low-nitrogen medium.	[45]
		<i>A. thaliana</i>	In <i>A. thaliana</i> , P deficiency induces the expression of more than 1000 traits, of which a large number of genes are related to terpene VOCs and phenylalanine metabolism.	[142]
		<i>M. aeruginosa</i>	<i>M. aeruginosa</i> increased the release of VOCs and β -cyclocitral when N availability was insufficient.	[144]
		<i>A. tamarensis</i>	It has been reported that the production of allelochemicals was stimulated in <i>A. tamarensis</i> after exposure to N-limited and P-limited conditions	[145]
6.	heavy metals	<i>O. sativa</i>	These heavy metals increase the generation and emission of momilactone B in rice. The rice allelopathic activity might be enhanced due to heavy metals, with a rise in the emission of momilactone B, which has formidable phytotoxin and allelopathic efficacy.	[147]
7.	high salinity	<i>Solieria chordalis</i> J. Agardh and <i>Gymnogongrus antarcticus</i> Skottsborg	During high salinity, <i>S. chordalis</i> and <i>G. antarcticus</i> increase the production of allelochemicals.	[148]
		<i>O. sativa</i>	Similarly, when rice cultivars are influenced by high salt, the production of salicylic acid is significantly elevated. Allelochemical production by rice is an effective defense for rice seedlings against barnyard grass.	[149]

5. Other Environmental Factors

Apart from the factors discussed above, other environmental factors such as heavy metals and high salt can induce a plant to synthesize and discharge allelochemicals. For example, FeCl_2 and CuCl_2 may enhance the allelopathic potential of rice seedlings; CuCl_2 treatment has stronger activity. These heavy metals increase the generation and emission of momilactone B in rice. The rice allelopathic activity might be enhanced due to heavy metals, with a rise in the emission of momilactone B, which has formidable phytotoxin and allelopathic efficacy [147]. During high salinity, *S. chordalis* and *G. antarcticus* increase the production of allelochemicals [148]. Similarly, when rice cultivars are influenced by high salt, the production of salicylic acid is significantly elevated. Allelochemical production by rice is an effective defense for rice seedlings against barnyard grass [149]. Changes in pH and conductivity in soil will also induce plants to create more allelochemicals, like the phenolic compound concentration [150].

Sometimes, the allelochemicals released by plants are the result of a combination of stresses. The differential accumulation of defense metabolites by *E. plantagineum* after exposure to different stressors suggests stress-dependent biosynthetic regulation, especially concerning naphthoquinone generation, which was rapidly induced following drought, intraspecific competition, and high-temperature treatment, thus positively affecting resistance or defense against herbivores, weeds, and pathogens. The extent to which allelochemical generation is affected by natural factors, subsequently affecting plant defense against pests, remains unclear. When stress is applied to plants grown under constrained resources and exposed to herbivory, plants commonly experience subsequent trade-offs. However, they can quickly reallocate resources toward the creation of inducible metabolites [57]. The amount of specific allelochemicals may be improved by one kind of stress and diminished

by another kind of stress [151]. At the same time, one may hypothesize that allelopathic impacts also include the induced release of allelopathic compounds [152]. From the previous expression, we can see that induced allelopathy is the result of not only the action of individual factors, but also the combined action of multiple factors (Figure 1).

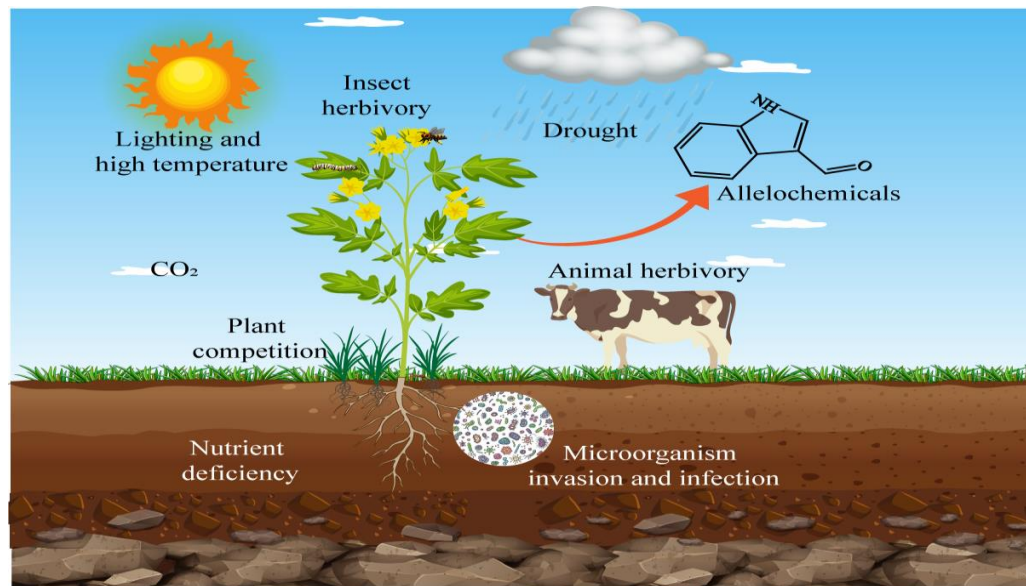


Figure 1. Stress factors that affect allelopathy.

6. Conclusions and Future Perspectives

An increase in allelopathic activity is a defense method used by plants to withstand biotic and abiotic stresses [143]. Plant allelopathy is related to environmental stresses, but not all stress factors enhance plant allelopathy. Some studies have shown that nutritional deficiency, plant competition, and herbivory can produce more allelopathic substances in crops compared to physical damage and hormone treatment. The plant senses a lack of nutrients in a scenario of plant competition around it or herbivory and manages the production of allelochemicals accordingly, to get more nutrients and maintain its own growth and development given limited nutritional resources.

The ecological significance of induced allelopathy refers to the specialized allelochemicals produced in response to certain factors. If such allelochemicals have development and utilization value, plants can be provided with specific factors to produce such allelochemicals. These discoveries provide the basis for new crop protection strategies. These are mechanisms via which a damaged plant could signal to a neighboring plant, and thus elicit a defensive response [102]. The purposes of inducing allelopathy are to increase (1) the resistance of plants to intense light, high temperature, drought, and other environmental stresses and help them resist natural enemies including animals, insects, microorganisms, and diseases, and (2) the competitiveness of plants; a plant can sense the existence of surrounding plants growing under limited resources, and release allelochemicals to have a negative impact on surrounding plants. However, the production of allelochemicals also means that a large amount of energy will be consumed. The significance of inducing allelochemicals is to allow plants to accurately regulate the distribution of their energy. When there are no plants around or when the competitiveness of surrounding plants is not too strong, plants will not release many allelochemicals. Instead, plants can use their energy for growth and development, to reproduce better. In that way, their population could occupy more niches.

For the application of induced allelopathy, research on seedlings and product development related to roots should be emphasized [48]. Under natural conditions, the impact of plant competition on allelochemical generation has been less widely studied, particularly for woody species [54]. It is noted that less research has been conducted on the mechanism

of inducing allelopathy. Now, due to climate change, high-temperature phenomena are becoming more and more serious. High temperature and CO₂ will induce plants to produce allelochemicals. After plants release allelochemicals, there will also be some changes to the environment. However, few studies have been conducted on the impact of high temperatures and CO₂ on the environment after plants produce allelochemicals. We hope that this review will stimulate integrative research projects on induced allelopathy and applied aspects of induced allelochemicals in agricultural systems.

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