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REVIEW ARTICLE

Allelopathy: an alternative tool for sustainable agriculture

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Abstract Population increase, poverty, environmental degradation, and the use of synthetic herbicides are interdependent and closely linked and hence influence global food safety and stability of world agriculture. On the one hand, varied weeds, insects, and other pests have caused a tremendous loss in agricultural crop productivity annually. On the other hand, the use of synthetic insecticides, herbicides, fungicides, and other pesticides significantly disturbed the ecology of biotic communities in agricultural and natural ecosystems. Eventually, it destroyed the ecological balance in food chains. Interestingly, natural products released by the plants (allelochemicals) are secondary metabolites involved in ecological interactions and could be an important source of alternative agrochemicals. Mainly released by the plants as an outcome of acquaintances with other plants in their vicinity, these allelochemicals can also be used as eco-friendly substitutes for synthetic herbicides and other pesticides. Despite these facts, agrochemicals are either preferred over allelochemicals or the latter are not known in the direction of their use in achieving sustainability in agriculture. Given this, considering recent reports, this paper aims to: (1) emphasize allelochemicals; (2) overview the major biochemistry of allelochemicals; (3) critically discuss the role of allelopathy (and underlying major mechanisms) in the management of noxious weeds, insect pests, and major plant pathogens; and (4) enlighten the significant aspects so far not or least explored in the current context.

Keywords Sustainability · Ecological balance · Biopesticides · Allelochemicals · Secondary metabolites

Introduction

Population explosion has caused global food insufficiency, which has become an open challenge for the global agricultural community and researchers (Cheeseman 2016; Fischer et al. 2017). Overpopulation is the ultimate dare also to the crop production sector. The farming community is under immense pressure to produce higher under limited arable land and other resources. Plant diseases, fast-growing weeds, pests, water and soil pollution, and conventional crop growing techniques leading to unfair crop nourishment are the foremost intimidation to agricultural production. Extreme climatic variations leading to ecological imbalance are another big factor to affect crop production globally (Fahad et al. 2017; Zhao et al. 2017). Because of increasing temperatures and irregular rainfall distribution, the growth of crops is severely affected, resulting in a considerable reduction in crop yields (Ali et al. 2017; Malhotra 2017). Pests are usually responsible for the destruction and reduction of crops by 10–40% through competition for light, water, minerals, space, and sunlight (weeds) and tissue dilapidation (pathogens) (Fried et al. 2017). Owing to the dependence of modern agriculture on chemical-based pesticides and inorganic nutrients, this sector has become the major source of contamination in natural ecosystems (Weldeslassie et al. 2018). Varied chemicals entering the ecosystems were rooted to speeding up the process

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of succession, approaching the climax communities abnormally and disrupting the micro-flora and fauna, and eventually resulted in the severely disturbed ecological balance of agro-ecosystems (Walker and Del 2003; Akhosi-Setaka 2009). Additionally, the natural ecosystems are also rushing towards natural deaths (Balbus et al. 2013). To maintain the quality of the environment and to protect it from synthetic inputs, it is necessary to replace them with organic ones (Lamine 2011; Geng et al. 2019).

Fortunately, some crops/plants harbour chemicals (allelopathic chemicals) widely reported to act as essential alternatives to disastrous plant-protection chemical agents and thereby help in the sustainable management of noxious weeds and eventually abridged herbicide rates (Belz 2007; Bhadoria 2011). The phenomenon of allelopathy provides ways to achieve sustainability in pesticide management. Allelopathy is a phenomenon in which one plant releases chemicals (allelochemicals) to affect the growth and survival of other plants in its vicinity. The use of allelopathic chemicals can help to discover the natural vigour of a plant species towards pest control (Cheng and Cheng 2015). Fortunately, most allelochemicals can be used as natural and green herbicides which can also substitute the disastrous chemical weedicides with organic allelopathic ones. Indeed, the allelopathic phenomenon may be used to embark upon these tribulations (Bhadoria 2011). This topic is gaining interest because of the ongoing discussion about sustainability. The phenomenon of allelopathy has got multiple definitions throughout history. Recently, the International Allelopathy Society (IAS) has somewhat modified the term as, “any process involving secondary metabolites (allelochemicals) generated by plants, microbes, viruses, and fungi that affect the growth and development of agricultural and biological systems” (Aci et al. 2022). Even though the aforementioned definitions attempted to encompass all potential physiological and morphological changes brought by allelochemicals (secondary metabolites), the consequences of allelochemicals (beneficial or harmful) are not characterized. Also, agrochemicals are either preferred over allelochemicals or the latter is not much explored in the direction of their judicious use for achieving sustainable agriculture.

In the following sections, efforts have been made to (1) overview the concept of allelopathy; (2) outline plant breeding in allelopathy (3) gives an account of allelochemicals; (4) overview the major biochemistry of allelopathy; (5) critically discuss the role of allelopathy (and underlying major mechanisms) in management of noxious weeds, insect pests, and the major plant pathogens; and also to (6) enlighten the major aspects so far not or least explored in the current context.

Allelopathy: an overview

Allelopathy is a biological phenomenon in which living organisms release chemicals by various mechanisms to interrupt the growth of other living organisms in their vicinity (Freeman and Beattie 2008; Macías et al. 2014). It is a natural supremacy of plants to guard themselves and distress the growth, metabolism, and development of nearby plants by producing natural organic compounds. It is a branch of chemical ecology, dealing with the study of the effects of chemical compounds secreted by a plant or microorganism by different methods on germination, growth, metabolism, and allocation of nearby flora and micro-fauna in agricultural or natural ecosystems (Jabran 2017). Allelopathy has prevailed since ancient times when allelopathy was in use as a prominent ecological phenomenon in crop-growing techniques (Zeng 2014). The study of allelopathy has undergone speedy advancement since the mid-1990s and has become a trendy subject in ecology, botany, environmental botany, agriculture, horticulture, agronomy, edaphology, and other related areas of research in current years (Macías et al. 2014). Allelochemicals concerned in particular with plant-microorganism and plant-plant interactions may prove to be an essential possible source for different agrochemicals for solving many tribulations resulting from unsatisfactory traditional practices and ill-treatment of synthetic herbicides (López-Ráez et al. 2012). Accordingly, through the comprehensive analysis of allelopathy, many policies for organizing ecological restoration and agricultural production concerning the use of allelopathy and allelochemicals are enhancing (Cheng and Cheng 2015). To this end, several methods have been developed to recognize and classify the efficient chemical compounds in stem, root, leaf, fruit and seed extracts, and volatile chemicals released by the plants (Li and Hu 2005; Chen et al. 2011; Macías et al. 2019).

Many conventional cover crops demonstrating allelopathic activity are important for weed management and thereby in getting rid of non-ecofriendly synthetic chemicals (herbicides) (Haramoto and Gallandt 2004; Büchi et al. 2019). Moreover, these plants could eliminate the long-chain hazardous effects in the agroecosystems, produce green or organic herbicides, and prevent disastrous phenomena like bioaccumulation and biomagnification (McGuire 2016; Liebman et al. 2018). Allelochemicals can be used as weedicides at higher concentrations and germination enhancers at lower concentrations ((Ebrahimi et al. 2016; Dhyani et al. 2017). Notably, some endemic plants in Asia are already notable by local farmers in the area as cover crops, used in agro-forestry, intercropping, hedgerow etc. (Altieri et al. 2015; Catacutan et al. 2017). These plants (typically the leguminous plants, offering protein-rich food) were found to acquire powerful allelopathic capabilities and need no synthetic pesticides and fertilizers. The use of these allelopathic cover crops could help both in environmental protection and also in solving food scarcity in rural areas. Globally, researchers have acknowledged several plant varieties acquiring powerful allelopathic intrusion intervened by root exudation of allelochemicals. The cereals like *Oryza sativa, Triticum aestivum, Hordeum vulgare,* and *Sorghum bicolor* have grabbed a lot of scientific research. Previous research paid attention to germplasm selection for best allelopathic cultivars and the classification of the found allelochemicals. Allelopathic cultivars, possessing the good potential of reducing the introduction of non-biodegradable synthetic chemicals and efficiently controlling weeds, signify the most capable use of allelopathy (Cheng and Cheng 2015). Based on this assumption, many conventional propagating techniques were prompted in wheat and rice to produce agriculturally suitable weed-censoring species with advanced allelopathic intrusion. Strong oppressive generations are in exploration. The genetics of allelopathy is explained by a molecular approach with the help of QTL mapping that linked the characters in rice (Chung et al. 2020) and sorghum (Shehzad and Okuno 2020) with several chromosomes and recommended the contribution of numerous allelochemicals. Possibly the chief chemicals which are released as root exudates have been recognized in all the plant species under analysis (Badri et al. 2013; Aci et al. 2022). These metabolites are biosynthesized and released through a discrete sequential pattern. Their exudation and biosynthesis might be provoked by several abiotic and biotic factors. Allelopathy has been suggested to engross the variable combination of allelochemicals and released secondary metabolites, controlled by the genome, growing period of an allelopathic plant, ecology, microclimatic conditions, cultivating effects, and revenue of chemical compounds in the plant rhizosphere. The classification of genetic material, concerned with the biosynthesis of some known allelochemicals, is performed by functional genomics, offering the prospect of improving the allelopathy by molecular breeding (Belz et al. 2007; Aci et al. 2022). The developmental of allelopathy of crops, plant signalling, and inductive mechanisms are also achieving attention. Future exploration must be heading for discovering techniques to conquer dormancy, amplify the decaying of weed seeds or restrain seed germination of weeds, and also to unveil the major mechanisms underlying the release of allelochemicals, differentiation and selectiveness, and mode of operation. The formation of genetically modified cultivars with the capability of weed suppression and enhanced allelopathic intervention is still a big challenge. However, conventional propagating practices or breeding methods and biotechnology must offer the techniques. Hence, despite the significant knowledge about allelopathy, built up in the scientific literature, its importance to weed science in agriculture is yet to be completely acknowledged and lacks its appliance in modern agriculture.

Plant breeding in allelopathy

Sustainability is the main aim of plant breeding on earth. The development of allelopathic crops is encompassed in sustainable agriculture. Various methods can be used to accomplish this objective depending on genetic diversity or modification. While genetic transformation creates variants with a large impact on phenotypic characteristics, natural genetic variability is employed to create many genotypic variants with little impact in the first scenario. Variability (among different species or within the same species) acts as a genetic pool from which we can choose crops with higher allelopathic potential (Mahé et al. 2022). With the joint investigation of marker genotype segregation in individuals or lines, QTL analysis (quantitative trait loci) enables the location and effect estimation of the genetic components regulating any trait (Wu et al. 2003; Asins et al. 2009). In a population resulting from a hybrid between a weed-suppressing *indica* rice line and a non-weed-suppressing *japonica* cultivar, Zhang et al. (2005) examined the genetic regulation of early vigour parameters such as seed germination, plumule length and dry weight. Each of the thirteen QTLs was shown to regulate about 5 to 10% of the variation in the early vigour constituents. Jensen et al. (2008) cited some cases in rice, carried out thorough research and developed some recombinant inbred lines (RILs) for the identification of QTLs, controlling allelopathy. Moreover, Chung et al. (2020) used high-throughput SNP genotyping to find QTLs related to allelopathic properties of rice. A species with a high allelopathic potential (Sathi) and a non-allelopathic species (Nong-an) were crossed to create 98 F8 RILs (recombinant inbred lines) for such a purpose. Plumule and radicle length inhibition was caused by two QTLs on chromosome 8 (q1TL-8 and q1SL-8) which accounted for 20 and 15% of the phenotypic variance, respectively. It is intriguing to consider that 31 genes were identified among these QTLs. At a mercantile organic rice production line in Texas, Rondo, a rice cultivar with a promising yield potential, rice blast resistance and weed-suppressing ability has been cultivated. It has got a superior weed-suppressive ability than other several commercial species (Yan and McClung 2010; Gealy and Yan 2012). In wheat, potential genes on chromosomes 1A, 2B, and 5D were identified by QTL analysis that may be useful for the breeding of allelopathic wheat. These findings might be useful for breeding wheat cultivars with allelopathic potentiality (Zuo et al. 2012). The research results indicate that it is possible to improve the allelopathic potential using marker-assisted selection (Bertholdsson and Tuvesson 2005). Improving allelopathy in association with plant breeding could result in crop cultivars with better weed suppressive potentiality.

Allelochemicals

Allelochemicals are non-nutritious vital elements mainly produced as secondary metabolites by living organisms exerting a detrimental morphological and physiological effect on other species in their vicinity (Jabran 2017). In plants, allelochemicals are mostly released as byproducts in various physiological and biochemical processes (Bhadoria 2011; Ashraf et al. 2017; Dahiya et al. 2017). The list of chief secondary metabolites acknowledged as allelochemicals include terpenoids, alkaloids, phenolics, flavonoids, jasmonates, momilactone, glucosinolates, hydroxamic acids, salicylates, brassinosteroids, amino acids, carbohydrates (Lotina-Hennsen et al. 2006; Lalremsang 2020). Most of these chemicals are known to mediate the phenomenon of allelopathy (Hussain and Reigosa 2014; Jabran 2017). Allelochemicals are an appropriate substitute for synthetic chemical herbicides, as they rarely possess toxic or residual consequences, even though the specificity and efficiency of several allelochemicals are restricted (Bhadoria 2011). They can boost or suppress seed germination, aid development, and allow the growth of crop plants with little phytotoxic remains in soil and water, easing the process of recycling and wastewater treatment (Zeng et al. 2008; Abouziena and Haggiag 2016). Allelochemicals act in a different way to put across the growth behaviour of test species, i.e. retardatory effect at a higher concentration of some species may aggravate the growth in similar or dissimilar varieties at lesser concentrations (Singh et al. 2005a; Belz et al. 2007). The concentration of these chemicals determines their activity (performance depends on concentration) (Kobayashi 2004; Farooq et al. 2020). Allelochemicals restrain seed germination and development at higher concentrations and enhance the same at their lower concentrations (Subtain et al. 2014). Thus, at higher concentrations, allelochemicals can be utilized as organic weedicides (Farooq et al. 2020), and at lower concentrations, allelochemicals may be used as growth promoters. The inhibitory function of allelochemicals was the only prior discovered dimension of allelopathy and has been well-explored for their utilization in weed management, directly or indirectly. It is a practical alternative to synthetic chemical herbicides as organic allelochemicals interdict toxic or lingering effects (Bhadoria 2011). The suppressive role is accredited to the obstruction or extermination of essential metabolic and physiological mechanisms of plants. A great deal of investigation efforts has been made to further explore the suppressive role of so many allelopathic plants for weed execution (Jamil et al. 2009; Lambers et al. 2009; Amb and Ahluwalia 2016). The allelochemicals at lower concentrations, also enhance growth and develop resistance to many abiotic and biotic stresses (Farooq et al. 2013). Application of aqueous extracts of allelopathic plants at lesser concentrations improves growth and boosts germination of many crop varieties (Cheema et al. 2012; Abbas et al. 2017; Rehman et al. 2019). Thus allelochemicals, when applied to the crops in lower amounts, can result in an economical, efficient, and professional method to improve crop productivity and to endorse the growth and development of crop species. There is variability in the concentration and activity of allelochemicals in the varied parts of the same plant, and the activity also varies along the growing seasons (Qasem and Foy 2001; Kato-Noguchi 2002; Jilani et al. 2008; Uniyal and Chhetri 2010; Gatti et al. 2010).

The allelochemicals are released into the atmosphere or rhizosphere by root exudation (Bertin et al. 2003; Weston 2003), volatilization (Bertin et al. 2003; Xie et al. 2021), leaching through soil (Bertin et al. 2003; Kobayashi 2004), residue decomposition (Singh et al. 2005a, b; Kong et al. 2006; Zohaib et al. 2016), pollen grains like maize (Roshchina 2008; Loughnan 2014) and stress conditions like droughts, high temperature, and exposure to UV radiations (Alexieva et al. 2001; Pedrol et al. 2006; Bornman et al. 2015). The release and fate of allelochemicals in the environment are shown in Fig. 1.

Based on the resemblance in the chemistry of compounds, allelochemicals are categorized into the subsequent 14 groups namely aliphatic aldehydes, straight-chain alcohols, water-soluble organic acids, benzoic acid, and its derivatives; simple unsaturated lactones; long-chain fatty acids and polyacetylenes; anthraquinone, benzoquinone, and complex quinones; simple phenols, alkaloids, and cyanohydrins; cinnamic acid and its derivatives; coumarin, flavonoids, tannins, terpenoids and steroids; amino acids and peptides; sulfide and glucosinolates; and purines and nucleosides (Rice 1974). The speedy growth of investigation skills (such as column chromatography using silica gel and Sephadex LH-20) has made the possibility to separate and classify the small compositions of allelochemicals and to perform their complex molecular analyses. The techniques like GCMS, LCMS, HPLC, etc. are used to analyze the complex organic and biochemical extracts of allelopathic plants. These analyses have provided the chemical and structural details of compounds present in the extracts.

Biochemistry of allelopathy

Allelopathic plants suppress the growth of neighbouring plants by affecting their biochemical and physiological processes. The secondary metabolites (allelochemicals) carry on various chemical reactions with other plants, which result in the suppression of their growth by affecting the plant machinery at the cellular, physiological, and biochemical

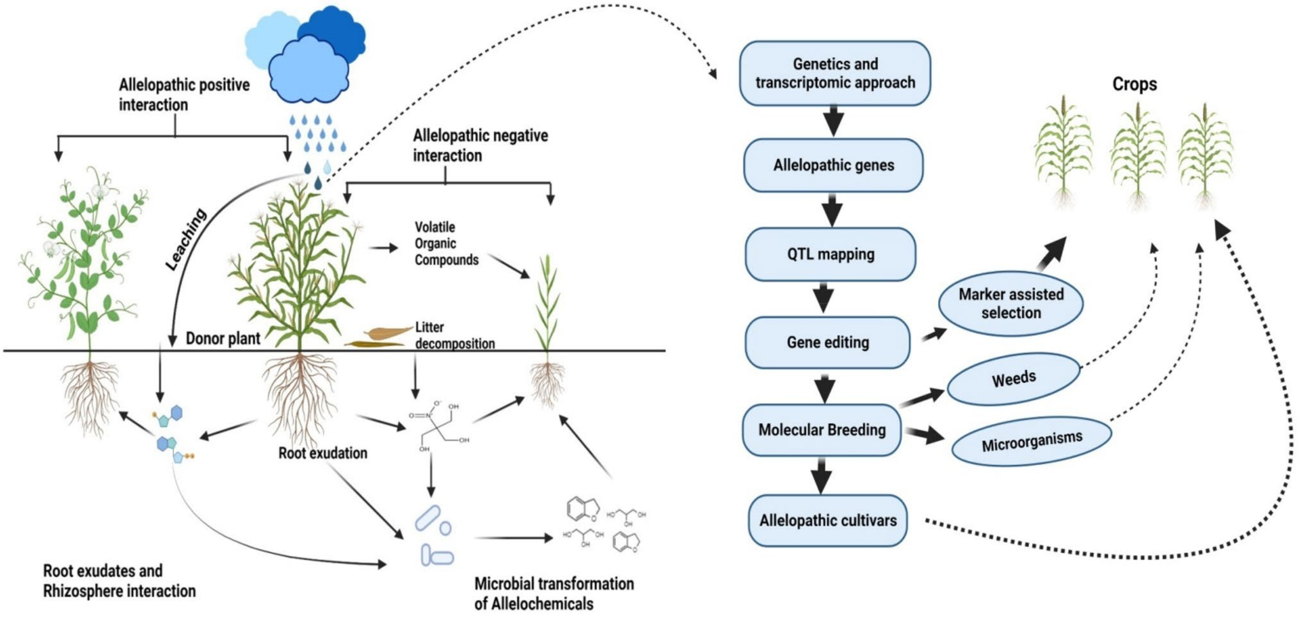

Fig. 1 Diagram showing the process of allelopathy in the biological system. The diagram depicts that Volatile Organic Compounds moderate the above-ground interactions, while below-ground interactions in the rhizosphere are mediated by root exudates and phytotoxins released by litter decomposition and leaching. Microorganisms modify, improve, or diminish the allelopathic effects by transforming the allelochemicals into different forms. With the help of the transcriptomic approach and molecular breeding, we can create new cultivars with greater allelopathic potential

levels. Below are some examples of the physiological and biochemical alterations caused by allelochemicals in plants.

Effect on photosynthesis

Allelochemicals primarily affect the circuitry used for photosynthesis in plants and hasten the breakdown of photosynthetic pigments (Rehman et al. 2019; Yuliyani et al. 2019). There are many allelochemicals which have been studied for their effect on photosynthesis in plants. But the most comprehensive study has been executed on sorgoleone, an important allelochemical released by *Sorghum bicolor* (Głąb et al. 2017). Sorgoleone and other natural allelochemicals showed a similar trend of the mechanism of action as that of synthetic chemicals. Photosynthetic enzymes were found to be degraded by allelochemicals (Cheng and Cheng 2015; Rehman et al. 2019). These allelochemicals mostly damage Photosystem II (PSII) and thereby significantly affect photosynthesis (Wang et al. 2014; Hussain and Reigosa 2017). Sorgoleone is a well-known allelotoxin and a lipophilic benzoquinone component known to inhibit PSII by restraining the photosynthetic electron transport chain (ETC) (Dayan et al. 2009). It completely inhibits the binding sites of atrazine (a synthetic chemical) and thereby stops the decline of plastoquinone B (Q_B) by disturbing the ETC linking Q_A and Q_B (Czarnota et al. 2001; Sowiński et al. 2020). There are several other allelotoxins (such as resorcinolic lipids) from the root exudates of *Sorghum bicolor* which have been reported to inhibit oxygen evolution in photosynthesis (Rimando et al. 2003). Sorgoleone is also known to induce foliar bleaching resulting from deranging the carotenoid synthesis by inhibiting hydroxyphenylpyruvate dioxygenase (HPPD) (Meazza et al. 2002). Ye et al. (2013) investigated the effect of the dried macroalga, *Gracilariatenuistipitata* on a microalga, *Phaeodactylumtricornutum* and observed a reduction in the number of active reaction centres and a blockage of the electron transport chain. Allelotoxins like o-hydroxyphenyl acetic acid, p-coumaric acid, and ferulic acid have been found to inhibit chlorophyll accumulation in *Oryza sativa* (Yang et al. 2002). The interference in photosynthesis is caused by disrupting the biochemical pathways and photosynthetic pigments (Yu et al. 2003).

Effect on cell permeability and antioxidant enzyme activity

Multiple investigations have demonstrated that allelochemicals severely reduce the activity of antioxidant enzymes and raise free radical levels, which causes increased membrane lipid peroxidation and alteration in membrane potential (Harun et al. 2014). The methanolic extracts have been proven to affect the antioxidant enzymes (including peroxidase activity, super oxidase dismutases and catalases), and to cause cell injury by malondialdehyde

(MDA) content (Ullah et al. 2015). Allelochemicals and root extracts of *Cucumis sativus* are also known to enhance the activity of root peroxidase and super oxidase dismutase, and also significantly elevate membrane peroxidation (Yu et al. 2003). On the cellular level, these phytotoxins provoke lipid peroxidation and perform the depolarization of cell membranes, thus enhancing the membrane permeability and clogging up nutrient uptake of plants (Weir et al. 2004). On the contrary, some allelochemicals were earlier known to reduce the concentration of antioxidant enzymes, like secalonic acid F ($C_{32}H_{30}O_{14}$) produced by *Aspergillus japonicus* reduced the activity of peroxidase and superoxide dismutase activity of many test plants (Zeng et al. 2001). Similarly, aqueous extracts of *Oryza sativa* significantly inhibited the activity of catalase and superoxide dismutase in barnyard grass (Lin et al. 2000). The results reflect that sometimes allelotoxins are directly involved in the production of reactive oxygen species, which ultimately enhance the activity of peroxidase and superoxide dismutase. Sometimes, allelotoxins directly inhibit oxidizing enzymes, allowing the plant to oxidative annihilation. Studies have shown that aqueous extracts and methanolic extracts of *Capparis spinosa* L. and siliquae of *Cleome arabica* L. improved the MDA levels in leaves and roots of lettuce and exhibited cytotoxic effects on root cells causing root necrosis, reduction in mitotic index (Ladhari et al. 2014). Aqueous extract of *Crysanthemum morifolium* stimulated the MDA level in the leaves of the same species (*Chrysanthemum morifolium*) by disturbing the balance of anti-oxidative enzymes and lipid peroxidation in membranes (Zhou et al. 2009) and this affected the structure and function of cell membranes, the ultimate method of allelopathy (Singh et al. 2001).

Effect on cell proliferation and DNA synthesis

Allelochemicals like camphene, alpha-pinene, beta-pinene, 1,8-cineole, and camphor impacted DNA synthesis and cell proliferation in *Brassica campestris* L. (Nishida et al. 2005). Being equal to the number of cells in mitotic phases, the mitotic index is used as a marker of cell proliferation. Allelochemicals from the ethyl acetate fraction of *Aglaia odorata* left a strong mitodepressive effect on the dividing cells of *Allium cepa*. The fraction inhibited cell division and induced cell abnormalities by manipulating the structure and functions of chromosomes and spindle fibres in the exhibited roots (Teerarak et al. 2012). The same mitodepressive effects were shown by allelochemicals, xanthosine (Charoenying et al. 2010) and cyanamide (Soltys et al. 2011). Many other studies agreed that allelochemicals interfere with mitotic division and perform morphological, cytological, and physiological changes in target plants (Singh et al. 2005b; Batish et al. 2006; Gulzar et al. 2016; Mushtaq et al. 2019). The disparity of mitosis could be because of the blocking in the G2- phase of cell division, averting the cell from entering mitotic division. The decrease in the mitotic index might be due to the inhibition of DNA synthesis and microtubule arrangement, marred nucleoprotein synthesis, and a diminished amount of ATP for providing energy for spindle elongation, chromosome movement, and microtubule inclination (Türkoğlu 2012).

Effect on respiration

Allelochemicals regulate many steps of respiration in plants, including electron transport, ATP enzyme activity, CO_2 emission, and oxidative phosphorylation (Cheng and Cheng 2015). These phytotoxins seem to affect the respiratory mechanism by interrupting various phases like oxygen uptake, preventing NADH oxidation, ATP synthesis enzyme activity, ATP creation in mitochondria, disrupting plant oxidative phosphorylation, and eventually inhibiting respiration. It has been suggested that allelochemicals are responsible for the interruption of mitochondrial respiration (Weir et al. 2004). The interruption is attributed to the inhibition of enzymatic activities of glycolysis and pentose phosphate pathway (Musculo et al. 2001). Juglone, an allelochemical from *Juglans regia* has been found to decrease H+-ATPase activity in maize and soyabean. It has been discovered that juglone may enter the mitochondria of maize and soyabean seedlings through roots, interfering with their ability to uptake oxygen (Hejl and Koster 2004a). Alpha-pinene exerts its effects through the suppression of electron transfer and decoupling of oxidative phosphorylation. The generation of ATP in the mitochondria is severely inhibited by alpha-pinene, which also lowers the transmembrane potential and hampers mitochondrial energy metabolism (Abrahim et al. 2003a). Camphor is known to carry out mitochondrial uncoupling and limonene is supposed to inhibit ATP synthase and the activity of adenine nucleotide translocase complexes (Abrahim et al. 2003b).

Effect on protein and nucleic acid synthesis

Allelopathic potential can be seen in most alkaloids. While some can stop protein production, others can inhibit DNA polymerase I and stop DNA from being translated and transcribed. Some alkaloids tightly interact with DNA and raise the temperature at which it cleaves (Inderjit et al. 1995; Wink and Latz-Bruning 1995). All phenolic acids have the possibility of disrupting DNA and RNA stability. Moreover, numerous phenols and alkaloids, including ferulic acid, cinnamic acid, and many others, can prevent the formation of proteins (Zeng et al. 2001; Li et al. 2010). Romero-Romero et al. (2002) found that the protein pattern of *Lycopersicon esculentum* (tomato), was significantly hindered by the aqueous leachates of *Sicyos deppei, Lantana camara, Sebastiania adenophora and Acacia sedillense*. While examining the gene expression pattern of the plant *Arabidopsis thaliana* L., after being exposed to the allelochemicals of *Fagopyrum esculentum* (fagomine, rutin, and gallic acid), it has been noticed that the majority of the genes that responded to the allelochemicals fit into various essential groups, including metabolism, cell rescue, resistance and pathogenicity, cellular uptake, proteins with a binding role, and proteins that demand cofactors (Golisz et al. 2008). According to Kato-Noguchi et al. (2013), allelochemicals from rice (momilactone A and B) may prevent the storage proteins—cruciferin and cruciferina from degrading, hence preventing the germination in Arabidopsis. This implies that these fundamental targets, including DNA, RNA, protein production, and associated activities, are contributing factors in the observed allelopathic phenomenon.

Effect on water and nutrient uptake

Several allelochemicals interfere with plant roots' ability to absorb nutrients or cause water stress by permanently reducing water uptake. The actions of Na^+/K^+-ATPase, which are responsible for the absorption and transport of ions at the cell membrane, can be inhibited by allelochemicals, which inhibit cellular uptake of K^+, Na^+, and other essential ions. Cinnamic acid and p-hydroxybenzoic acid, the two primary allelochemicals in cucumber root exudates severely suppressed the activity of root dehydrogenase, root combined ATPase, and nitrate reductase in cucumber, preventing the absorption of K^+, NO_3^-, and $H_2PO_4^-$ by the roots (Lv et al. 2002). Abenavoli et al. (2010), found that trans-cinnamic, p-coumaric and ferulic acids had a concentration-dependent impact on net nitrate uptake in *Zea mays* seedlings. Residues of *Helianthus annus* had a deleterious impact on plant growth, the effectiveness of assimilation, and nutrient absorption in *Brassica rapa* (de Morais et al. 2014). Another mechanism contributing to the reported plant growth inhibition by sorgoleone is the disruption of crucial plant functions like water and solute absorption, driven by proton pump across the root cell plasma membranes (Hejl and Koster 2004b). Allelochemical dosages and types are directly related to how allelochemicals affect ion uptake. For instance, a small amount of dibutyl phthalate enhances the uptake of N while lowering the uptake of P and K. Yet, a large amount of this substance prevents the absorption of N, P, and K. Similarly, tomato roots absorb N and K more readily than P when diphenylamine is present at low concentrations (Geng et al. 2009).

Effect on plant growth regulator system

Allelochemicals can change the composition of plant growth regulators or cause instabilities in a variety of phytohormones, which prevents plants from growing and developing. The majority of phenolic allelochemicals can increase IAA oxidase activity and reduce the ability of POD, bound gibberellic acid, or indole acetic acid to interact with endogenous hormone levels (Yang et al. 2005). The roots of *Solanum lycopersicum* were affected by cyanamide (1.2 mM), which upset the equilibrium of plant hormones ethylene and auxin. In barnyard grass, an aqueous extract of rice was found to drastically increase IAA oxidase activity and decrease IAA levels, affecting the plants's growth regulatory system and preventing growth parameters (Wenxiong et al. 2001).

Plant growth can be affected by phytotoxins through different methods. They can affect the plant's biochemistry, physiology, cytology, and morphology of plants, thereby directly affecting the plant's growth and development. Irrespective of relations between plant species, a firm base for the scientific foundation of the subsistence and utility of the allelopathic process should be generalized.

Role of Allelopathy in;

Weed management

Weeds are the undesired plants in the crop fields and are the most obstinate competitors of crops that compete for nutrients, water, space, and other necessities for photosynthesis, decreasing the harvest yield (Sardrood and Goltapeh 2018). Non-natural fabricated herbicides have got the capability of controlling weeds efficiently and lessen the exertion of weeding but can cause hazardous effects on the ecosystem by boosting the evolution of chemical herbicide-resistant weeds and other serious ecosystem problems like bioaccumulation (Jabran and Chauhan 2015). This has got a negative effect on the health and survival of living organisms and their environment. Since it is known that plants can self-regulate their existence, distribution, and densities in nature via allelopathic interactions, scientists have attempted to make use of those characteristics of crops and weeds in agricultural fields. Many agronomic scientists have been attracted to the utilization of allelopathy in the biological control of weeds. Many allelopathic aqueous extracts have been successfully used by many scientists to control the growth and germination of weeds in agricultural fields. Being diverse in nature, allelochemicals lack similar methods of accomplishment. It is the phytotoxicity of allelochemicals that affects the germination, growth and establishment of weeds and crops. The allelochemicals interfere with membrane permeability and integrity (Poulin et al. 2018), plant water relations (Araniti et al. 2017), cell division (Goga et al. 2017), hormone biosynthesis and transport (Li et al. 2019), mineral uptake and transport (Lupini et al. 2018), nutrient composition of the soil (Mohammadkhani and Servati 2018), stomatal oscillations (Syahri et al. 2017), photosynthesis (Bortolo et al. 2018), metabolism (Long et al. 2018), respiration (Lelong et al. 2011) and protein metabolism (Ashraf et al. 2017). Allelopathic aqueous extracts have abridged herbicide dosages by half of the recommended ones, controlling hazardous fast-growing weeds of common crops effectively. Aqueous extracts of *Sorghum bicolor, Helianthus annuus* and *Eucalyptus globulus* (Cheema et al. 2003), *Sesamum indicum, Oryza sativa* and Brassica have shown efficient consequences in regulating weed plants via diminishing herbicide doses likely half of the standard ones(Nawaz et al. 2014). Hence, allelochemicals can substitute synthetic weedicides and can help in controlling weeds to minimize weed-crop counteraction and in improving crop yield and growth. There are shreds of evidence that rhizosphere soil also possesses allelochemicals, hence playing an important role in eliminating weeds. Many experiments have been done on rhizosphere soil (root residue and leaf residue rhizosphere amended soils) and they have proved fruitful in controlling the growth of weeds. Mulching of residues also provided good results by suppressing the growth of weed plants (Mahmood et al. 2016; Naeem et al. 2015). The rhizosphere soil of *Ecliptaalba* influence the germination, escalation, and establishment of common crop plants (*Oryza sativa* and*Phaseolus aureus*) and weeds (*Cassia sophera* and *Cassia tora*) (Gulzar et al. 2014). Crude extracts of rhizosphere soil of *Saussurealappa* exhibited repression on the seeds of *S. lappa* and *Lactuca sativa* in a concentration-dependent manner (Liu et al. 2018). The infestation of soil with *Chenopodium morale and* ameliorated with it showed the inhibitory effect on seedling emergence, growth, and some physiological parameters of *Triticum aestivum, Trifolium alexandrinum, Lycopersicum esculentum, Melilotus indices and Cucumis sativus* (El-Khatib et al. 2004). These plentiful advancements of allelopathic application have varying degrees of achievements based on ecological and managing causes. However, all the approaches can play a role as organic weed-managing agents. Natural weed control using allelopathy has magnificent functions in the agricultural sector. This will work proficiently if the integration of all these methods is done in a scientifically glossed way. There is a need for biotechnological improvements and genetic modifications for improving the allelopathic potential in plants, which ultimately will help in improving their potential and competitiveness. Table 1 shows the recent reports on the role of the major allelochemicals in weed management.

Insect-pest management

Insects are the biotic agents responsible for the considerable loss of cereals, pulses, fibre crops, fruits, and vegetables. In agriculture, many chemical insecticides are used to get rid of these hazardous agents. But the chemicals used to repel these insects create serious problems in the natural ecosystems. Moreover, the insects develop resistance to these chemicals, which in turn forces the farmers to increase the doses of these chemicals, leading to an increase in the problems. Unlike chemical insecticides, allelochemicals can prove environmental-friendly in modern agriculture. Extracts from different medicinal plant species and their active components are natural sources of bioinsecticides. The effect of the aqueous extract of *Satureja montana* has an insecticidal property. The aqueous extract has shown a toxic effect with a high mortality rate of greenhouse whitefly, with a non-toxic effect on test plants—pepper seedlings (Sućur et al. 2015a). Good knowledge of allelochemicals can provide fruitful tools to eliminate the use of chemical pesticides. The aqueous extracts of *Salvia sclarea* in lower concentrations induce lipid peroxidation in black nightshade (*Solanum nigrum*) roots and a toxic effect against whitefly (*Trialeuro desvaporariorum*) with 56.6% mortality (Sućur et al. 2015b). Some medicinal plant extracts have got a variety of chemical compounds in their essential oils. The repellency of several essential oils, including those from the family Lamiaceae like *S. sclarea*, against several insect species, including the common house flies, is reported (Fakoorziba et al. 2014). The essential oils of *Pogostemoncablin, Mentha pulegium, Mentha citrata, Nepeta cataria, Thuja occidentalis, Salvia sclarea, Thymus mastichina, Origanum majorana, Origanum vulgare, Origanum compactum, Melissa officinalis,* and *Lavandula angustifolia,* applied by fumigation proved highly toxic against larvae *Spodoptera littoralis* (Pavela 2005). Essential oils of *Chenopodium ambrosioides* and *Ocimumlamiifolium* have got a larvicidal effect against *Anopheles arabiensis* and *Aedes aegypti* (Massebo et al. 2009). Pest management (management of insects) through allelochemicals could be a valuable contrivance to control injurious insects organically. Insect pest resistance of crop plants against synthetic insecticides must be abridged in this way. Table 2 shows the allelopathic works done for insect management.

Plant disease management

Plant diseases arise because of the invasion of plant pathogens or any other abiotic or biotic stress. Plant pathogens being parasitic in nature, consume the nutrients of plants

Table 1 Major reports on the allelopathic effect of some plant extracts on some weeds and crops

Plant	Test plants	Types of inhibition	References
Cassia angustifolia Vahl	*Avena fatua, Dactyloctenium aegyptium, Echinocloa colona, Phalaris minor* and *Sorghum halepense*	Germination and seedling growth characters	Hussain et al. (2007)
Oryza sativa	*Heteranthera limosa* and *Echinochloa crus-galli*	Plant growth and development through declining soil properties	Asaduzzaman et al. (2010)
Compositeae family with *Xanthium occidentale*	Barnyard grass *(Echinochloa crus-galli)*	Shoot and root dry weights	Chon and Kim (2005)
Lactuca sativa, Xanthium occidentale and *Cirsium japonicum*	*Medicago sativa*	Seedling growth	Chon et al. (2003)
Lactuca sativa (Lettuce)	*Medicago sativa* (alfalfa)	Root length and seed germination	Chon et al. (2005)
Populus deltoides, *Melia azedarach* and *Morus alba*	*Triticum aestivum*	Germination percentage, root and stem height and dry biomass while higher concentration	Majeed et al. (2017)
benjamin fig *(Ficus benjamina)*	Sunflower hybrids (Oliver, Parsun-3, SFH-80 and NKS-278)	Germination, radical and plumule length	Muhammad et al. (2018)
Salvia moorcroftiana, Verbascum thapsus and *Chenopodium album*	*Avena fatua, Euphorbia helioscopia*	Germination and growth parameters	Arafat et al. (2015)
Trema micrantha	*Raphanus sativus* L	Germination and early growth	Borella et al. (2014)
Datura metel. L	*Parthenium hysterophorus* L	Seedling growth, shoot and root biomass and biochemical parameters	Ramachandran (2016)
Parthenium hysterophorus L	*Arachis hypogaea* and *Glycine max*	Seed germination, shoot and root length	Sorecha and Bayissa (2017)
Datura stramonium L	maize (*Zea mays* L.) and sunflower (*Helianthus annuus* L.)	Density, height and fresh weight	Pacanoski et al. (2014)
Ammi majus L., *Oxalis corniculata* L., *Plantago lagopus* L, *Urtica urens* L.; *Cynodon dactylon* L., *Desmostachya bipinnata* L., *Dichanthium annulatum, Echinochloa colona* L., *Phragmites australis* and *Sorghum virgatum*	*Eruca sativa, Triticum aestivum* and *Vicia faba*	Germination and elongation parameters	Ramadan et al. (2018)
Solanum muricatum and *Eichhornia crassipes*	sunflower (*Helianthus annuus* L.)	Seed germination and seedling growth	Sivaci et al. (2018)
Imperata cylindrical	*Aristida stricta Michx. var. beyrichiana* and *(Pinus elliottii)*	Specific root length, total root length, total mycorrhizal root length, percent mycorrhizal colonization and aboveround biomass	Hagan et al. (2013)
Artemesia monosperma and *Thymus vulgaris*	*Pisum sativum* L	Seedling length and proline/amino acid content	Al-Hawas and Azooz (2018)
Excoecaria agallocha L	*Eleusine coracana* (Finger Millet)	Germination and growth behavior	Desai et al. (2017)
Ageratum conyzoides, Cannabis sativa, Eclipta prostrata, and *Woodfordia fruticosa*	*Triticum aestivum* and *Pisum sativum*	Germination and percentage growth of root and hypocotyle	Devkota et al. (2013)
Silene villosa	*Triticum aestivum* L	Germination percentage, root shoot length and fresh and dry weight of root and shoot	Murad et al. (2016)
Azadirachta indica, Santalum album, and *Thespesia populnea*	*Oryza sativa*	Seed germination and seedling growth parameters	Neelamegam and Dhanusha (2013)

Table 1 (continued)

Plant	Test plants	Types of inhibition	References
Sorghum halepense	*Pisum sativum* subsp. *sativum, Pisum sativum* subsp. *Arvense*	Germ length, germ weight and seed germination	Georgieya and Nikolova (2016)
Erigeron canadensis L., *Solanum nigrum* L., *Amaranthus retroflexus* L.,*and Chenopodium album* L	*Pisum sativum* L., *Glycine max* L., *and Vicia sativa* L	Seed germination and initial development	Marinov-Serafimov (2015)
Euphorbia helioscopia L	*Cicer arietinum* L., *Triticum aestivum* L., and *Lens culinaris* Medic	Germination, seedling vigor index, and total dry weight	Tanveer et al. (2010)
Eucalyptus globules	*Ammi majus* and*Avena fatua*	Fresh and dry biomass	El-Rokiek and El-Din (2017)
Alternanthera tenella Colla., Croton bonplandianum Baill and *Xanthium indicum* Koen	*Vigna radiata* L	Germination, root length shoot length and vigour index	Patil et al. (2013)
Calotropis procera	*Cucumis sativus*, *Solanum lycopersicum, Triticum aestivum*	Root length, shoot length, fresh weight and dry weight	El-Khatib et al. (2016)
Trifolium alexandrium L	*Prosopis cineraria* L	Germination, morphological characteristics, photosynthetic pigments, and nutrients uptake	Ebrahimi et al. (2016)
Euphorbia guyoniana and *Retama retam*	*Bromus tectorum* and *Melilotus indica*	Germination efficiency, plumule and radicle length	Nasrine et al. (2011)
Colocynthis vulgaris (L.) Schrad, *Retama retam* L, *Traganum nudatum* Delile, *Pituranthos chloranthus* and *Artemisia herba-alba*	*Avena fatua* L. and *Polygonum convolvulus* L	Germination efficiency, germination index and radicle length	Nesrine et al. (2011)
Ocimum basilicum L., *Matricaria chamomilla* L., *Malva sylvestris* L., *Chelidonium majus* L., *Melissa officinalis* L. *and Levisticum officinale*	*Tripleurospermum inodorum* L	Germination and growth	Balicevic et al. (2015)
Euphorbia guyoniana	*Bromus tectorum* and *Melilotus indica*	Germination efficiency, plumule and radicle length	Nasrine et al. (2013)

Table 2 Major reports on the role of allelopathy in insect management

Plants	Insects controlled	References
Satureja montana L	Whitefly	Sucur et al. (2015a)
Salvia sclarea L	*Trialeurodes vaporariorum*	Sucur et al. (2015b)
Nepeta cataria, Thuja occidentalis, Salvia sclarea, Thymus mastichina, Origanum majorana, Pogostemon cablin, Mentha pulegium, Mentha citrate, O. vulgare, O. compactum, Melissa officinalis, and *Lavandula angustifolia*	*Spodoptera littoralis*	Pavela (2005)
Chenopodium ambrosioides L. and *Ocimum lamiifolium* Hochst	*Anopheles arabiensis* Patton and *Aedes aegypti* L	Massebo et al. (2009)
Salvia sclarea L	Several insect species including the common house flies (*Musa domestica*)	Fakoorziba et al. (2014)
Melia azdarach, Myrtus communis, Mentha longifolia, Pegnum harmala and *Cymbopogon citrates*	*Sitophilus oryzae* L	Saljoqi et al. (2006)
Olea europea, *Thea chinensis*, *Canabis sativa*, *Elephantia sp.*, *Allium sativum*, *Piper nigrum* and *Capsicum annum*	*Callosobruchus chinensis*	Zia et al. (2011)
Lycopersicon esculentum, Azadirachta indica and Capsicum annuum	*Taeniothrips sjostedti* and *Heliothis armigera*	Hongo and Karel (1986)

and become responsible for a great deal of damage and harvest loss. It is difficult to fulfil the feeding needs of the increasing global population because of persistent plant diseases. The main diligent agents for seed-borne and soil-borne diseases are bacteria, viruses, fungi, and nematodes. Chemical control mainly leads to ecological disturbances in food chains and food webs in natural and agricultural ecosystems. Allelochemicals encompass an affirmative job in controlling plant diseases in diverse ways like aqueous extorts, oil extracts, residues, etc. Allelochemicals extracted from *Decalepishamiltonii, Lawsoniainermis,* and *Mimosopselengi* were comparatively evaluated through the synthetic chemical fungicides viz., thiram, bavin, dithane, botox, captan, and M-45 at the suggested dosages and the impact was almost equivalent (Mohana et al. 2011). Thus, allelochemicals can be utilized for managing pathogenic seed-borne fungi and avoidance of degradation of crops in an environmentally friendly way. Table 3 highlights the allelopathic work done in plant disease management.

Table 3 Major reports on the role of allelopathy in management of the major plant diseases

Plant	Pathogen controlled	References
Ficus sycomorus	Bacteria	Salem et al. (2014)
Oryza sativa	Fungi and bacteria	Kong et al. (2004)
Ageratum conyzoides L	*Rhizoctonia solani* and *Pyricularia oryzae*	Nguyen et al. (2021)
Datura stramonium L., *Datura innoxia*, *Datura metal* L. and *Datura ferox* L	*Alternaria solani* and *Fusarium oxysporum*	Jalander and Gachande (2012)
Acacia nilotica, Caesalpinia coriaria, Decalepisha miltonii, Emblica officinalis, Lawsonia inermis and *Mimusops elengi*	*Alternaria alternata, Aspergillus flavus, Curvularia lunata, Drechslera oryzae, D. halodes, Fusarium moniliforme, Pyricularia oryzae* and *Trichoconis padwickii*	Mohana et al. (2011)
Solanum tomentosum	(Bacteria) *Bacillus cereus, Micrococcus kristinae, Streptococcus pyrogens, Escherichia coli, Salmonella pooni, Serratia marcescens, Pseudomonas aeruginosa*, and (Fungi) *Fusarium oxysporum, Aspergillus niger*	Aliero and Afolayan (2006)
Heracleum crenatifolium Boiss, *Heracleum platytaenium* Boiss, *Heracleum sphondylium* L	*Staphylococcus aureus, Staphylococcus epidermitis, Listeria monocytogenes, Pseudomonas aureginosa, Escherichia coli, Corinobacterium diphteria, Streptococcus pyogenes, Enterococcus feacalis, Candida albicans, Candida guilliermondi, Candida tropicalis, Candida crusei* and *Aspergillus niger*	Ergene et al. (2004)
Azadirachta indica, Emblica officinalis, Pongamia glabra and *Acacia nilotca*	*Magnaporthe oryzae* and *Bipolaris oryzae*	Pandey (2015)

Abiotic stress tolerance

Adverse environmental conditions (temperature, salinity, drought, humidity, UV radiations) lead to the development of stress in plants. Plant stress ultimately leads to the alteration in physiological and biochemical pathways and adversely influences plant growth and yield (Madani et al. 2019). Plants are braced with organized and systematized defence set-ups against abiotic stresses (Hasanuzzaman et al. 2012). Plant phenolic compounds act as promising phytoprotectants, which help plants to acquire forbearance against abiotic stresses. Phenolic compounds are amalgamated by the plants to adapt their defence contrivance against various stresses (Parvin et al. 2022). The propitious characteristic of these phenolic compounds (allelochemicals) for gaining plant tolerance against abiotic stresses is their antioxidant nature (Macias et al. 2007; Kaurinovic and Vastag 2019; Parvin et al. 2022). Under heavy metal stress, plant phenolics present themselves as chelators of metal ions, and conversely, they persistently forage molecular species of reactive oxygen. Phenolic compounds, mainly phenylpropanoids and flavenoids, perform H_2O_2 rummaging, and ascorbate/peroxidase coordination (Michalak 2006). Their chemical structure is primarily responsible for their antioxidant nature (Kaurinovic and Vastag 2019). Phenolic acids (subclass of plant phenolics) hold resonance stabilized structure and phenol moiety that contributes H-atom resulting in antioxidant property through radical scavenging. Radicle quenching through electron donation and quenching of active singlet oxygen adds to the antioxidant property of phenolic acids (Kumar and Goel 2019; Vuolo et al. 2019). Shreds of evidence are there, which highlight the production of plant phenolics as a response to abiotic stresses (Michalak 2006; Teklić et al. 2021). Some phenolic compounds protect plant tissues by acting as natural screening agents against harmful UV-B radiations. Hydroxycinnamic acids and flavonoids possess high UV absorbance and are almost present in all plants (Grace 2005; Agati et al. 2020). Evidence is in support of the fact that flavenoid synthesis is induced by UV-B radiation (Eichholz et al. 2012; Zhao et al. 2020). The presence of flavones and flavonols in higher quantities in the leaf epidermal surfaces depicts their role as UV protectants (Pfündel et al. 2008). Ultimately, there is an expectation to protect the stressed plants with these phytoprotectant constituents.

Conclusions and perspectives

Weeds and pests are reasons for yield loss more than any other abiotic stress. Because of enormous applications in weed and pest management, allelopathy can substitute harmful synthetic chemicals and expensive mechanical techniques being utilized in agricultural practices. Cost and environmental pollution are major issues in the use of synthetic pesticides. Allelopathic aqueous extracts provide improved substitutes for this purpose due to cost-effectiveness, environment-friendly nature, simple usage, efficiency, and safety. Future research must be on the selection of plants with more allelopathic potentials, exploration of flair cultivars fabricating extra allelochemicals and categorizing growth inhibitory and promoting allelochemicals in aqueous plant extracts. Other areas are the analysis of their (allelochemicals') mechanisms of action, the genetic and biochemical study of allelopathic plants, and the marketing of organic aqueous extracts as growth inhibitors (weedicides) and promoters (fertilizers). It could prove to be a radiant road, leading to achieving food security, agrarian maintainability, ecological security, resource preservation and management, and financial stability. Thus, allelopathy can be privileged as a natural substitute for mechanical and chemical methods for weed management, insect management, crop growth, and disease management.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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