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ABSTRACT

Plant allelopathy is a response to external stimuli by releasing secondary metabolites. It can be an effective sustainable strategy for weed control. Roots are the main point of release of allelochemicals. This phenomenon has the potential to facilitate environmentally cleaner weed control and avoid the concerns associated with the misuse of agro-chemicals for pest and weed management. The review comprehensively elaborates the mechanisms involving the release of allelochemicals by plants and the factors affecting its transport from a donor plant to a receiver. Although allelochemicals are produced by the entire plant, root exudation is the primary source of release of these chemicals into the soil environment. The study attempts to lucidly explain the physiology behind phytotoxic effects imparted by allelochemicals on target plants. We have discussed the various direct and indirect effect of allelochemicals on plant physiology and morphology. The review sheds light on the phytotoxic variation caused due to variable residue decomposition rates under changing climatic conditions. The various crop-weed, weed-crop and weed-weed allelopathic interactions and their possible response mechanisms have been briefly elaborated with reference to earlier works. We have shown the potential of integrating allelopathy and agronomic management practices for sustainable and environmentally safe weed management. The mechanistic insight of interferences caused by environmental factors on the bioavailability of allelochemicals is essential to develop an environmentally sound method of curbing the weed menace in agro-ecosystems. The studies on transport processes involving the release of allelochemicals from plants need more attention so as to exploit this knowledge in regulating the output of these compounds at a cellular level.

1. Introduction

Weeds are one of the most important constraints to crop productivity worldwide, causing yield losses in the range of 45–95 percent by competing for light, water, and nutrients with the main crop (Oerke, 2006; Das, 2008; Kumar et al., 2022). Hand weeding, mechanical weeding, and herbicide treatments have been the most common conventional weed management methods for reducing weed saturation (Abbas et al., 2021). Despite their substantial contribution, these methods are accompanied by several challenges, including the

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development of herbicide resistance in weeds (Harker, 2013) and exorbitantly high expenses incurred during weed control practices (McErlich and Boydston, 2014), thus necessitating the development of a more convenient, environmentally friendly, and low-input driven efficient strategy for weed management (Das et al., 2021). Allelopathy is gaining widespread popularity as a sustainable weed management strategy for combating the challenge of environmental pollution and herbicide resistance (Jabran et al., 2015). It is the phenomenon in which an organism secretes biochemicals (otherwise known as allelochemicals) that causes interference either positively or negatively, affecting the growth and development of other organisms. Allelopathy exploits the application of plant-derived secondary metabolites in disease and pest management, thus acting as a defense mechanism. The growing concerns over the excess use of herbicides and its ramifications on ecological sustainability have resulted in a shift toward other bio-rational alternatives. Allelopathy can offer a potent bio-rational option for weed management in cropping systems. Allelopathic plants transfer allelochemicals into the environment through root exudates, volatilization from above-ground plant parts, and leaching or decomposition of plant detritus when cultivated in intercropping systems (Scavo et al., 2018).

The historical developments of allelopathy, as per the records, started with the keen observations of Theophrastus (300 BC) and Pliny II (1 AD), relating to the marring of farmland by growing crops like chickpea, barley, fenugreek and bitter vetch (Weston, 2005). They were well aware of the sickening of fertile farmlands, which was accredited to the biochemicals released by the plants. However, proper scientific evidence of the allelopathic effect from root exudates was put forward by De Candolle (Singh et al., 2001). This concept was later extrapolated to address the weed menace by exploring the possible allelopathic effect of crops (cover crop, crop rotation, intercrop, crop residue incorporation or retention) to suppress weed growth in agricultural fields (Putnam and Duke, 1974; Behera and Das, 2019; Behera et al., 2019). The allelochemicals are mostly secondary metabolites with diverse chemical structures and properties, mostly belonging to the group of phenolics, flavonoids, terpenoids, alkaloids, momilactone, jasmonates, salicylates, hydroxamic acids, brassinosteroids, polysaccharides, glucosinolates, and amino acids that are released as byproducts during various physiological processes in plants (Faroog et al., 2011). The inhibitory or stimulatory effects of allelochemicals depend on their concentration and the recipient species. For instance, the aqueous leaf extract of Annona muricata inhibited the seedling growth of Vigna radiata and Eleusine coracana at high concentrations, whereas it stimulated the germination, seedling length, pigments, starch, protein, amino acid, carbohydrate, peroxidase, and catalase contents of the Vigna radiata seedlings at low concentration (1%) (Kannan and Palavian, 2022). The stimulatory effect of allelochemicals on plants can be exploited for producing biofertilizers (Hussain et al., 2017; Behera et al., 2021), while those with inhibitory effects may be used as weed suppressants and disease control agents (Farooq et al., 2011; Latif et al., 2017). The different types of allelopathic interactions are illustrated in Fig. 1. The sensitivity of the plants towards these biochemicals is selective, the knowledge of which is critical for targeted weed management with higher efficiency. Present-day researchers share their concerns regarding the ecological and physiological significance of weed-crop/crop-weed interferences and extend major emphasis on the mechanisms involved in allelopathy phenomena and the mode of action. Therefore, this review work has been lucidly synthesized with a broad objective of exploring the mechanism of action of allelochemicals, the factors affecting the efficacy of allelochemicals in managing the weed problem, and understanding the various types of plant-plant (crop-weed) interactions for extending its application at farm level for sustainable weed management.

2. Mechanism of release of allelochemicals

Allelopathy is a form of communication between plants, and they communicate by synthesizing various compounds through secondary metabolites (Yoneya and Takabayashi, 2014). The secondary metabolites are mostly released through the leaf, stem and roots of plants (Iqbal et al., 2020). The synthesis of these compounds is associated with the activation of some specialized genes and the presence of precursor molecules inside the plants. These activation processes often depend on environmental stimuli (Croteau et al., 2000). It is evident that not all bioactive metabolic compounds possess the allelopathic effect on surrounding organisms (Neori et al., 2000). Among all the pathways, root exudates are the most prominent source of release of allelochemicals



Fig. 1. A figurative illustration showing types of allelopathic interactions existing between donor and receiver plants. Allelopathic interactions have been classified on the basis of source (1 and 2), form (3 and 4) and action time of allelochemicals (5 and 6) (Das, 2008).

into the rhizosphere (Jilani et al., 2008). The mechanism of release of allelochemicals from the roots of the donor plant as exudate is described vividly in Fig. 2. However, other routes, such as washing out from the plant parts, volatilization from leaves, and residue decomposition, are also important alternative pathways for releasing these bioactive compounds (Singh et al., 2021). Apart from exudation, these may be released from roots by simple diffusion (low molecular weight metabolites) or by lysis of vesicles present at the surface of root caps (Latif et al., 2017). In the case of high molecular weight substances, membrane-bound proteins actively participate in inter- and intra-cellular transport by loading metabolites into vesicles and later removing the contents into the extracellular space (Weston et al., 2012). Some of the widely studied protein carriers include ATP binding cassette (ABC) family and the multidrug and toxic compound extrusion (MATE) family (Weston et al., 2012). The ABC protein family is one of the largest transporter families that are primary active transporters involving ATP hydrolysis to transport bioactive compounds (Dermauw and Van Leeuwen, 2014). Apart from nutrients, lipids, steroids, and xenobiotics, these transporters also transport a wide range of metabolites (Rees et al., 2009). They are localized in the plasma membrane, tonoplast, mitochondria, and chloroplasts, taking part in the plant defense mechanism and responding to abiotic stresses (Kang et al., 2011). For instance, a pleiotropic drug resistance (PDR)-type ABC protein (NpABC1) was involved in the defense response system in Nicotiana plumbaginifolia (Jasiński et al., 2001). In a study, a Arabidiopsis gene AtPDR12 (a member of the PDR subfamily) was found to be actively involved in the transfer of metabolites imparting resistance to the fungal pathogen, as shown by the pathogen signal metabolite treatment (Campbell et al., 2003). The MATE genes are also involved in transporting secondary metabolites along the electrochemical gradient of ions (Scavo et al., 2019). These were identified in the Arabidopsis family and carried DTX (from detoxification) initials, which are secondary active transporters (Li et al., 2002). An Arabidopsis gene named AtDTX1 encodes a protein that facilitates the export of alkaloids and other toxic compounds from roots (Li et al., 2002). The role of these genes in root exudation of secondary metabolites has been tested in various crops, viz., maize (ZmMATE2) (Kidd et al., 2001), rice (*OsPEZ1* and *OsPEZ2*) (Bashir et al., 2011), and sorghum (*SbMATE1*) (Zhang et al., 2019). A better understanding of biosynthetic pathways, enzymes, and genes responsible for the synthesis and release of allelochemicals could lead to selective weed management through allelopathy.

3. Factors affecting the release of allelochemicals

3.1. Environmental stress factors

Environmental factors may have a direct or indirect impact on a plant's ability to use allelopathy. The main environmental factors that regulate the net effect of allelopathy include temperature, radiation, availability of nutrients, and stressors (Meiners et al., 2012). For instance, stress imparted by UV radiation, nutritional deficiency, wounding, and plant pathogen invasion is known to cause an upswing in phenyl ammonia lyase (PAL) activity, which is the first step in the production of phenols (Dixon and Paiva, 1995; Croteau et al., 2000). Cinnamic acid, produced by cucumber, is ascertained to be the precursor of phenylpropanoids which is credited for peroxidation and decreased activity of H⁺-ATPase activity in the plasma membrane, ultimately reducing the root viability of target plants (Ding et al., 2007). Adverse environmental conditions also boost jasmonate synthesis and release. As a result, these hormones can up-regulate the expression of genes involved in secondary metabolism in plants (Wasternack and Parthier, 1997). The influence of environmental stressors on the generation of sorgoleone can be made worse by the presence of other plants around sorghum (Dayan, 2006). The generation of various allelochemicals is likewise influenced by environmental pressures brought on by plant interactions (Rivoal et al., 2011). The primary allelochemicals in rice have been identified as the diterpenes momilactone A and B, which were initially isolated from rice husks (Kato-Noguchi et al., 2010; Yazaki et al., 2017). Momilactone B concentration was approximately seven times higher in rice seedlings cultivated with barnyard grass (Echinochloa crusgalli L. Beauv.) than in rice seedlings raised alone (Kato-Noguchi, 2011). Low-land weed species such as Echinochloa crusgalli,



Fig. 2. A conceptual diagram depicting the possible mechanism of release of allelochemicals via root as exudates. The low molecular weight compounds are proposed to be transported by simple/facilitated diffusion, while those having high molecular weight mainly get released by protein transporters (ABC, MATE, etc.), or through vesicles. The aquaporins also take part in release of uncharged secondary metabolites.

Lactuca sativa, and others thrived more successfully next to rice plants lacking in momilactone production than they did next to wild-type rice plants (Toyomasu et al., 2014). At micromolar levels, momilactones also build up in the rice shoots, roots, and root exudates in addition to the husk (Hasegawa et al., 2010). Momilactone B is 17 times more effective than momilactone A at preventing growth in Arabidopsis thaliana (Kato-Noguchi et al., 2012). Momilactone B is therefore regarded as the rice allelochemical with highest potency (Murphy and Zerbe 2020). On the other hand, momilactone A has been primarily connected to rice resistance towards fungi pathogens (Hasegawa et al., 2010). Study shows that momilactone B is preferentially secreted from roots (Toyomasu et al., 2008). However, the increased production of momilactones by above-ground plant parts was also observed after the attack of pathogens like Magnaporthe oryzae, M. grisea, and Rhizoctonia solani (Lu et al., 2018). Allelochemical's effectiveness can be affected by environmental conditions that impact the ease of its degradation in the soil. In a study, 2, 4-dihydroxy-2H-1,4-benzoxazin-3(4H)-one (DIBOA) displayed a half-life of 43 h in non-sterilized soil. The final breakdown product of DIBOA and 2-aminophenoxazin-3-one (APO) had a low mineralization rate with more than 90 days half-life period (Macías et al., 2005). Additionally, soil bacteria accelerate the mineralization rate of flavonoid glycosides released by rice plants, resulting in aglycosylated compounds. The half-lives of flavonoid glycosides and aglycosides are 2 h and 30 h, respectively, suggesting that the second group has a stronger and sustained allelopathic activity (Kong et al., 2007). The synthesis of allelochemicals, their bioavailability and their impact on target species depend on the environmental conditions. Therefore, environmental variables and other processes that alter the fate of chemicals in the environment are crucial for the allelopathic relationship between plants in agroecosystems to aid weed management. Significant research findings support the hypothesis that environmental stress can boost the production of allelochemicals.

3.2. Plant factors

A plant root system serves various purposes, including anchoring the plant and absorbing nutrients and water. According to an estimate, higher plants create approximately 10,000 allelochemicals, with a wide variety of action mechanisms in the target plants (Weston et al., 2012). In response to biotic and abiotic stressors, the roots of several weed and crop species continuously secrete bioactive substances (low- and high-molecular-weight) into the rhizosphere (Bertin et al., 2003). The term "root exudate" refers to the substances that plant roots exude into the soil (Walker et al., 2003). Their amount and quality depend on the cultivar type, growth stage, plant and environmental stressors (Badri and Vivanco, 2009). For instance, it has been found that rice exudation rates were maximum during the flowering period while being very low in the seedling and maturity stage (Aulakh et al., 2001). Root exudations from sorghum and wheat were higher upon increasing soil compaction, drying and decrease in the available pool of nutrients, while it increased with the ageing of plants (Weil and Brady, 2017). Growing root systems typically exude more metabolites, which indicates its positive correlation with root growth (Lucas García et al., 2001). Additionally, the root system architecture and the type of root surface morphology are all factors that affect the determination of the qualitative and quantitative composition of exudates (Badri and Vivanco, 2009).

Higher plants with strong allelopathic properties are commonly incorporated into the soil for weed-control purposes. A study showed the phytotoxic variation with residue decomposition rate in the soil by using allelopathic plants, *viz*. alfalfa and kava as soil amendment (Xuan et al., 2005). Both alfalfa and kava strongly inhibited the growth of barnyard grass and *Monochoria* for up to 10 days (80–100% weed control). However, after 20–25 days, the magnitude of inhibition was drastically reduced, but it was still effective (50% weed control). Similarly, the allelopathic and decomposition patterns of *Jasminum officinale* L. f. var. *grandiflorum* were assessed by Teerarak et al. (2010). A decline in

allelopathic potency of the plant residues became apparent as the decomposition time lengthened. A crucial step in the ecosystem functioning, nutrient and carbon cycling, and ultimately climate change is the decomposition of plant litter. The effect of temperature on phytotoxic dynamics of Chrysanthemoides monilifera subsp. monilifera (boneseed) litter was studied by Al Harun et al. (2014). The results showed an increased concentration of water-soluble phenolics and dissolved organic carbon (DOC), with a decreased concentration of sulphate and nitrates in the soil under elevated temperatures. There was a considerable reduction in the germination rate, length and weight of hypocotyl and radicle of Lactuca sativa due to the higher release rate of allelochemicals from the litter at high temperatures. Therefore, identifying the suitable cultivar and growth stages of plant species with potential allelochemicals and evaluating them under the different plant and environmental stressors could open up new prospects for natural herbicides application.

3.3. Genetic factors

The proper genetic factors are required for plants to produce substances through secondary metabolism, including allelochemicals. For instance, understanding the enzymes and genes involved in momilactone B synthesis has aided the rice breeding program that sought to generate cultivars with a higher capacity to release allelochemical compounds (Toyomasu et al., 2008). Momilactone B, a diterpene molecule, is very effective against weeds. It is produced by the methylerythritol phosphate (MEP) pathway in the presence of the diterpene synthase enzyme (Dudareva et al., 2013). By employing reverse genetics, two genes were identified that were involved in the synthesis of diterpene synthase enzyme: 4-copalyl-diphosphate synthetase and kaurene synthase-like 4 (KSL4) (Xu et al., 2012). Momilactones are synthesized from the precursor geranylgeranyl diphosphate (GGPP) as diterpenes through a series of processes that occur in various cellular organelles and result in several intermediate products. On chromosome 4, a group of four genes have been identified that are involved in momilactone biosynthesis viz., Syncopalyl Diphosphate Synthase 4 (CPS4), Kaurene Synthase-Like 4 (KSL4), 9-β-Pimara 7, 15-Diene Oxidase (CYP99A3), and Momilactone A Synthase (MAS) (Shimura et al., 2007). Two more, CYP701A8 and CYP76M14, are located on chromosomes 6 and 1, respectively (De La Peña and Sattely, 2021). A single gene, CYP76M8, is located on chromosome 2, in another biosynthetic gene cluster required for oryzalexin production (Wu et al., 2013). Together, the products of these seven genes on chromosomes 1, 2, 4, and 6, synthesize momilactone B from GGPP. Thus, identifying and manipulating factors controlling gene expression involved in allelochemical synthesis could augment the allelopathic potential of plant species.

4. Interaction with soil environment

When an allelochemical is released into the environment, it undergoes a number of interacting processes (Fig. 3). These processes are broadly divided into three categories: transport, retention and transformation (Cheng, 1992; Weidenhamer, 1996; Cheng and Koskinen, 2002). Retention mechanisms impede the movement of chemicals from one point to another due to physical hindrances imparted by various soil constituents. The transformation processes will change the shape or structure of the allelochemicals, resulting in partial or complete molecular disintegration. The resulting transition product could be more potent, less potent or completely inactive than the parent compound. Transport processes control the movement of substances in the environment. The type of microorganisms present, the characteristics of the soil, and the soil environmental conditions are all important elements that can impact each step (Scavo et al., 2019). As a result, the fate of an allelochemical in the environment is determined by the kinetics and interaction of separate processes at a given site over time under a set of conditions. Although volatile allelochemical compounds play a



Fig. 3. An illustrative depiction of the various routes of release of phyto-allelochemical compounds and their interaction with various soil constituents. The bioavailability of these bioactive compounds is in direct correlation with the extent of retention and transformation it undergoes in soil before coming into the rhizospheric zone of the receiver plants for uptake.

significant role in plant-to-plant allelopathy interactions, allelochemicals released into the soil as root exudates or as secondary products of residue disintegration in soil remain the most important source of allelopathic interaction (Tharayil et al., 2008). Thus, the soil is the primary medium of transport of allelochemicals from the donor plant to the receiver. However, the current understanding of the mechanism of interactions between these chemical compounds and soil constituents is inadequate and remains ambiguous (Tharayil et al., 2008).

The quantity of allelochemical present in soil solution in a solubilized condition ultimately determines the degree of its bioavailability. Batch equilibration study is generally employed for studying the sorptiondesorption pathway of organic allelochemicals in soils which gives an idea of the extent of the effect the soil components (organic and inorganic) have on the release and bioavailability of these chemicals (Cheng and Koskinen, 2002). Studies show that the adsorption of phenolic acids is greatly influenced by soil properties, viz., oxides of Fe and Mn, organic matter content and pH (Inderjit and Bhowmik, 2004; Kobayashi, 2004). Upon comparing the retention behavior of phenolic acids released by poplar plantations in soil, Wang et al. (2011) inferred that p-HBA can exist in soil for a longer time compared to cinnamic acid and benzoic acid. The influence of pH on anion adsorption by soil components is particularly significant for organic biochemical, which particularly occurs by the electrostatic force of attraction with a positively charged surface of metal oxides (Gámiz et al., 2019). Salicylic acid, a phenolic compound type of allelochemical, is reported to show strong pH-dependent sorption in soils, particularly due to bidentate complex formation as attributed to its low pKa value (pKa = 2.9) (Calvet et al., 2007; Gámiz et al., 2019). Interestingly, the phytotoxicity of allelochemicals varies with pH and texture of the soil as evident from the study of Galán-Pérez et al. (2021). It was observed that scopoletin sorption in soil was strongly correlated with pH and fine texture of soils, thus expressing its phytotoxic effect in acid soil in contrast to alkaline soil. Gámiz et al. (2018) conducted a study to deduce the factor contributing most to the sorption and desorption of monoterpenes in agricultural soils. They found strong sorption by organic sorbents, viz., humic acid, as opposed to pH and mineral sorbents, viz. clay, silt, and carbonate content, as evident from the distribution coefficient values.

Numerous reports of the impact of soil pH on allelochemicals have been described in the literature (Batish et al., 2007; Norouzi et al., 2015). Norouzi et al. (2015) noted that decreased soil pH levels increased the allelopathic effects of powdered below- and aboveground parts of alfalfa (Medicago sativa), sorghum (Sorghum bicolor), and tobacco (Nicotiana tabacum L.) on several weeds. Leaching of allelochemicals and, consequently, their phytotoxic effects are strongly influenced by soil texture (Albuquerque et al., 2011). Additionally, because clay minerals vary widely from one another, clay typology affects the availability of allelochemicals. The highest specific surface area, ion exchange capacity, water retention capacity, and consequently, the strongest retention power towards allelochemicals are found in smectite-dominated soils like Vertisols, which are highly rich in montmorillonites (expanding 2:1 silicate clays). The preservation of allelochemicals, however, is relatively poor in soils predominately composed of non-expanding 1:1 silicate clays, such as kaolinites. In coarse substrate (sand), the allelochemicals released by roots of Hordeum vulgare L. ssp. vulgare showed higher toxicity (Bouhaouel et al., 2018). In another study by Shaukat et al. (2003), sandy soils showed higher levels of phytotoxic effects from aqueous shoot extracts of Conyza canadensis L., followed by loamy sand and sandy loam soils. This is likely because of the minimal adsorption of allelochemicals on coarse soil texture soils as well as the low levels of microbial and chemical degradation. In an early study by Ohno and First (1998), organic matter and manganese oxide content strongly affected the sorption of phenolic acids in soils, increasing their residual life in the soil. Arguably, the external addition of organic matter acts as a food source for microbes resulting in enhanced microbial activity, which may prevent the build-up of allelochemicals to below-toxic levels (Inderjit and Weiner, 2001). Numerous studies have shown that soil organic matter (SOM) affects the availability of allelochemicals in soil (Fageria, 2012). Allelochemicals adsorption is low in hot-semi arid soils, which typically have low SOM, facilitating the spread and dispersion of allelopathic plants like Rhaponticum repens (L.) Hidalgo and Centaurea maculosa Lam (Grossl, 2008). Redox condition of soil also has a significant role to play in determining the phytoavailability of allelochemicals in soil. Reduced conditions (<400 mV) present in the soils under Actinidia arguta plantation showed a 20-70% increase in

allelopathic phytotoxicity attributed to the slow pace of the humification process resulting in a more mobile form of organic allelochemical compounds in the soil matrix (Zaimenko et al., 2020). The ion exchange capacity of the soil also plays a crucial role in the retention and transport processes of allelochemicals (Scavo et al., 2019). Belz et al. (2009) revealed that clay soils with high cation exchange capacity favour parthenin breakdown, which is the allelochemical responsible for the invasive success of *Parthenium hysterophorus* L.

Soil microorganisms can have both positive and negative impacts on plants as pathogens, mutualists, and nutrient cycling drivers can alter the microbial ecology in the soil beneath the canopy and around the roots (Bever, 2003; Van der Putten et al., 2001). When allelochemicals reach the soil, the microorganisms are known to detoxify or increase the toxicity of allelochemicals, influencing the allelopathic effect (Inderjit, 2005). The low concentration of extremely phytotoxic compounds such as catechin and 8-hydroxyquinoline in soil has been related to soil microbial activity (Kaur et al., 2009). Microflora determines the microbial decomposition of allelochemicals. In a study, the chemical interaction between a grass, Agrostis capillaris and the monoterpene "carvacrol" produced by its thyme neighbour plant was investigated (Ehlers, 2011). The presence of carvacrol in the soil significantly reduced Agrostis plant survival, with mortality being higher when soil microorganisms were absent. Plants showed a minimal survival rate with monoterpene treatment when the soil was sterile, compared to higher survival rates ranging from 20% to 40% when the soil was not sterilized (Ehlers, 2011). The habitat type could also seriously impact the release of allelochemicals by plants. Plants cultivated in natural fields have substantially higher levels of cis-dehydromatricaria ester (DME), an allelochemical isolated from Solidago altissima, than those grown as hydroponic cultures (Nakamura and Nemoto, 1996). The interaction of allelochemicals with the soil environment affects the efficacy of allelochemicals released from the plants into the soil ecosystem. Knowledge of such interaction could be used in modulating the persistence of an allelochemical in such a way that allelopathic-based weed management could be availed for a longer time in crop fields.

5. Mechanism of phytotoxicity

Several researchers classified allelochemicals' mode of action as direct or indirect, which are referred to as true or functional allelopathy, respectively, by Aldrich (1984). Allelochemicals can either directly affect the target (direct allelopathy) or, when released into the soil, degrade to secondary degradation products, which can either harm plant development or modify the microenvironment, indirectly affecting the growth. Considering that there could be innumerable types of biotic and abiotic factors affecting the fate of allelochemicals released into the soil environment, it is impossible to secentate the dominance of direct allelopathy over indirect allelopathy is considered to be more important from an ecological point of view (Inderjit and Weiner, 2001). Different modes of action of allelochemicals (Fig. 4) are discussed hereunder, and some recent works are outlined in Table 1.

5.1. Cell morphology and multiplication

It is envisaged that the reduction in plant growth caused by the secretion of allelochemicals is the result of the suppression of mitosis and disorganization of the structure of cell organelles (Gniazdowska and Bogatek, 2005; Sánchez-Moreiras et al., 2008; Mushtaq et al., 2019). Several researchers have quantified this by estimating mitotic index (MI), which is an important prognostic factor for deciding a cell's ability to multiplicate at a particular time. Stem extracts of *Nicotiana plumba-ginifolia* at higher concentrations decreased MI in root tip cells of *Allium cepa*, which resulted in disruption of cell polarity, sticky metaphase, and telophase with abnormalities in chromosome arrangement (Mushtaq et al., 2019). Apart from cytological aberrations, they also found severe modifications in the ultrastructure of the leaf of *Cassia tora* leaves, as evident from the scanning electron microscopy (SEM) images of



Fig. 4. A schematic model illustrating the effect of allelochemicals on general metabolic function of cell. Allelochemicals affect the growth and development of the receiver plant by regulating the cellular processes and metabolism. Allelochemicals showed to have negative impact on the antioxidant system, photosynthetic systems and ATP synthesis in the mitochondria by inhibiting several rate limiting enzymes in these organelles. Moreover, allelochemical also regulate GS:GOGAT pathway which is a major rate limiting enzyme of nitrogen metabolism. These bioactive compounds also affect the cell wall loosening enzymes such as expansin which disturbs morphological traits and causes reduced growth. All these parameters result in lowering of cell energy status and ultimately deteriorating the growth and development of plant.

Table 1

Target crop	Allelochemical responsible	Physiological and biochemical process affected	References
Changes in the micro and Ultra-str	ucture of cells		
Cucumber	Cinnamic acid	Disrupted the ultrastructure of chloroplasts and mitochondria	Wu et al. (2004)
Mustard (<i>Brassica juncea</i> L.)	Benzoic acid	Disorganized cell arrangement and disrupted cell organelles in roots	Kaur et al. (2005)
Wheat and Arabidopsis thaliana L.	Citral	Disruption of microtubules	Chaimovitsh et al. (2012)
Arabidopsis thaliana L.	Citral	Disorganized cell ultra-structure, reduced intercellular communication and root hair formation	Graña et al. (2013)
Inhibition of cell growth and multip	plication		
Lettuce	BOA ^a	Inhibition of the mitosis (mainly at G2-M checkpoint)	Sánchez-Moreiras et al. (2008)
Cucumber	BOA and DIBOA ^b Slower regeneration of root cap cell		Burgos et al. (2004)
Soybean	Extracts of Datura stramonium L.	Inhibition root growth, reduced root hair length and density, increased	Cai and Mu (2012)
4.11.		chromosomal aberration and micronucleus indices	m 1 (1 (0010)
Allium cepa	Extracts of <i>Aglaia odorata</i> leaves (Ethyl acetate)	Disruption of chromatin organisation and the mitotic spindle along with hindered mitosis in roots.	Teerarak et al. (2012)
Imbalances in the antioxidant syste	em		
Mung bean (Phaseolus aureus)	Caffeic acid	Anomalies in the activities of proteases, peroxidases (PODs), and	Batish et al., (2008)
<u> </u>		polyphenol oxidases (PPOs) during root growth, and reduced concentration of total endogenous phenolics in hypocotyl cuttings	
Increases in cell membrane permea	bility		
Hordeum spontaneum, Avena ludoviciana, and wild mustard	Extracts of barley aerial parts	Increased lipid peroxidation	Farhoudi et al. (2012); Farhoudi and Lee (2013)
Potato (Solanum tuberosum L.)	Extract of combination of non-sterile	Accumulation of oxygen radical species (O ₂ ⁻ , H ₂ O ₂ and	Zuo et al. (2012)
	shoots of wheat and Alopecurusa	malondialdehyde) in leaves, increased membrane permeability and	
	equalis weed	altered superoxide dismutase (SOD) and ascorbate peroxidase (APX)	
Barnyard grass (Echinochloa	Lemongrass (Cymbopogon citratus) oil	activities Lipid peroxidation and electrolyte leakage	Poonpaiboonpipat et al.
crusgalli L.)			(2013)
Effect on the plant growth regulato	r system		
Wheat	Ferulic acid	Accumulation of indole-3-acetic acid (IAA), gibberellic acid (GA3), and cytokinin in seedlings, with a simultaneous increase of ABA concentration	Liu and Hu (2001)
Barnyard grass	Aqueous extract of rice	Stimulate IAA oxidase activity with reduced IAA levels, thereby damaging the plant growth regulation system	Lin et al. (2001)
Tomato Rice	Cyanamide (1.2 mM) DTD ^c from <i>Ageratina adenophora</i>	Hormone imbalance in plants (ethylene and auxin) roots' homeostasis The ABA content in rice seedling roots increased significantly, however	Soltys et al. (2012) Yang et al. (2008)
	HHO ^d from A. adenophora	this reduced dramatically after 96 h of treatment For 48 and 96 h, HHO ⁴ significantly increased ABA content	
Effect on enzymatic activity			
		No. 11. 1. 1. 1. J.	71 (0010)
Chrysanthemum (Chrysanthemum indicum L.)	Extract of above-ground parts and rhizospheric soil of Chrysanthemum	Root dehydrogenase and nitrate reductase activities were inhibited, the levels of soluble sugar and soluble protein were reduced, and root development of energy autience used incoded.	Zhou et al. (2010)
Greater duck weed (Spirodela	Diethyl phthalate (DEP)	development of stem cuttings was impeded DEP is toxic as it inhibits glutamine synthetase (GS) isoenzymes, which	Cheng (2012)
polyrhiza L.)		are involved in N assimilation and antioxidant enzymes	
Effect on respiration			
Corn and soybean Water melon	Juglone Ethanol extracts from corn pollen	Disruption of root oxygen uptake in seedlings Inhibits electron pathway and thereby reduced oxygen consumption	Hejl and Koster (2004b) Cruz Ortega et al. (1988)
Effect on plant photosynthesis		· · · · · · · · · · · · · · · · · · ·	
Galium spurium, Aeschynomene	Sorgoleone	Reduced efficiency of photosystem II (PS-II) of weeds (21 days old	Uddin et al. (2012)
indica and Rumex japonicus	-	seedlings) and growth inhibition	
Barnyard grass (Echinochloa crusgalli L.)	Lemongrass (Cymbopogon citratus) oil	Reduced chlorophyll a and b and carotenoid contents, affected seed alpha-amylase activity interfering with photosynthetic metabolism	Poonpaiboonpipat et al. (2013)
Effect on water and nutrient uptak	e		
Corn Wheat	Ferulic acid (250 mM) Ferulic acid, benzaldehyde and 4-tert-	Inhibition of NH_4^+ -N, NO_3^- -N and Cl^- uptake in seedlings Affects NH_4^+ -N absorption by seedlings	Bergmark et al. (1992) Yuan et al. (1998)
Cucumber	butyl benzoic acid Cinnamic acid and the root exudates of cucumber	Inhibits the uptake of $\mathrm{NO}_3^-, \mathrm{SO}_4^{2-}, \mathrm{K}^+, \mathrm{Ca}^{2+}, \mathrm{Mg}^{2+},$ and Fe $^{2+}$ by seedlings	Yu and Matsui (1997)
Peas (<i>Pisum sativum</i> L.), soybean and corn	Sorgoleone and juglone	Inhibited H^+ -ATPase activity and H^+ pumping in the root system which interferes with water uptake in plants	Hejli and Koster, 2004a; b
Maize	trans-Cinnamic, ferulic acid and p- coumaric acid	Inhibition of NO ₃ -N uptake and plasma membrane H + -ATPase activity in seedlings	Abenavoli et al. (2010)
		-	

(continued on next page)

Table 1 (continued)

Target crop	Allelochemical responsible	Physiological and biochemical process affected	References Geng et al. (2009)	
Tomato	Diphenylamine	Reduced root P uptake		
Effect on metabolism of proteir	and nucleic acid			
Eupatorium adenophorum	HHO ^d	Affected the expression of chalcone synthase (CHS) gene in roots (related to synthesis of amino acids)	Guo et al. (2011)	
Arabidopsis	Momilactone A and B (Rice allelochemicals)	Decreased seed germination by inhibition of degradation process of the storage proteins (cruciferin and cruciferina)	Kato-Noguchi et al. (2013)	
Tomato	Cyanamide	Altered expression of genes (LeEXPA9 and LeEXPA18) responsible for cell wall re-modelling thus inhibiting the tomato root formation	Soltys et al. (2012)	

^a 2(3H)-benzoxazolinone.

^b 2, 4-dihydroxy- 1,4(2H)-benzoxazin-3-one.

^c 4, 7-dimethyl-1-(propan-2-ylidene)1, 4, 4a, 8a-tetrahydronaphthalene-2, 6(1H, 7H)-dione.

^d 6-hydroxyl-5-isopropyl-3, 8-dimethyl-4a, 5, 6, 7, 8, 8a-hexahydronaphthalen-2(1H)-one.

15-day-old saplings. A similar effect was observed in the root cell ultrastructure of cucumber seedlings when exposed to allelochemicals like 2(3H)-benzoxazolinone (BOA) and 2,4-dihydroxy-1,4(2H)-benzoxazin-3-one (DIBOA) released from rye plant causing a decrease in root growth and suppression of cellular metabolisms (Burgos et al., 2004). These compounds exhibit such deleterious effects because of their ability to impede energy transduction and decrease ATPase activity in the cell membrane and chloroplasts (Burgos et al., 2004). Polyphenolic chemicals isolated from dodder plant inhibited mitotic activity in barley seedlings and onion root meristematic cells, with findings similar to treatments using 8-Hydroxyquinoline, a common cytotoxic drug (Ataei Azimi and Delnavaz Hashemloian, 2017). However, it should be noted that the concentration of the allelochemicals released into the soil environment is critical for staging such inhibitory effects in the growth of target plants. This was apparent when diallyl disulfide released from garlic at low concentrations showed growth promotion in tomatoes, while at higher levels inhibited root growth by affecting the activity of meristematic cells (Cheng et al., 2016).

5.2. Cell membrane integrity and its permeability

The cell membrane is an important component of the cell that serves as a barrier between the inside and outside environments. The integrity of the membrane is critical to protect the cell from external adverse environmental conditions (Xue et al., 2018). Allelopathy-induced alteration in membrane permeability and polarization triggers electrolyte leakage and lipid peroxidation, leading to decreased mineral nutrient uptake (Xue et al., 2018; Scavo et al., 2019; M'barek et al., 2019). Such changes in membrane permeability cause cell contents to spill and, as a result, plant tissues grow slowly or die (Li et al., 2010). The concentration of malonaldehyde (MDA) which is produced during lipid peroxidation, is often used as an indicator of cell membrane integrity. Early work on benzoic and cinnamic acids, commonly found allelochemicals in soil, showed increased electrolyte leakage and decreased catalase and peroxidase activity in soybean seedlings (Baziramakenga et al., 1995). They also cause a decrease in the electrochemical potential and depolarization of the plasma membrane resulting in the efflux of ions accompanying the increased membrane permeability (Blum, 1996; Ambika, 2013). In a study by Andriana et al. (2018), an increase in MDA activity was observed in radish seedlings in response to the oxidative stress caused by allelochemicals released from Tridax procumbens L. A similar effect was observed when leaf extracts of Tetraclinis articulata (Vahl) Mast. was treated with lettuce resulting in aberrations in the cell membrane, causing substantial electrolyte leakage as indicated by an increase in MDA activity (M'barek et al., 2019).

5.3. Interference with various enzymes activities and endogenous hormone synthesis

Allelopathic substances released from the weed and other plants

which is grown in the vicinity of main crops leads to the inhibition of various enzymatic system in the plant (Weston and Duke, 2003). The mechanism of allelopathy related to phenolic compounds has been extensively explored, and data show that phenolics interfere with a number of rate-limiting enzymes and physiological processes in plants. For instance, cinnamic and benzoic acids inhibit hormone function, membrane permeability, photosynthesis, respiration, and organic compound synthesis. The allelopathic molecules were reported to inhibit different enzymes which are present in the plant system, such as pectolytic enzymes, catalases, cellulases, phosphorylases, ATPases, peroxidases, phosphatases, proteinases, invertases, decarboxylases, and nitrates. According to Cheng (2012), diethyl phthalate inhibits glutamine synthetase isoenzymes in nitrogen for nitrogen absorption and antioxidant enzymes in larger duckweed (Spirodela polyrhiza L.). Moreover, the study by Mahdavikia and Saharkhiz (2016) suggested the beneficial effects of water extracts derived from peppermint leads to an improved morphological, physiological, and biochemical response of tomato. The extract concentration of about 10 percent (v/v) showed higher inhibitory action on proline, soluble sugar, and starch. Moreover, the phenolic compounds present in the extract also showed higher activities of antioxidant enzymes, including ascorbate peroxidase, catalase, peroxidase, and superoxide dismutase (SOD). Other reports suggest that the alkaloids might be considered to hinder the development of plants by various multiple mechanisms, which include interference with DNA, enzyme function, protein production, and membrane integrity in growing crops (Wink, 2004). Similarly, phytohormones like indole-3-acetic acid (IAA) and gibberellic acid (GA) are also affected by the allelopathic substances that regulate cell expansion. The earlier report also suggests that diverse allelochemicals inhibit the enzyme IAA-oxidase (Chou, 1980). Allelopathy stress enhanced ethylene and ABA (abscisic acid) synthesis (Bogatek et al., 2005). In their investigation of the influence of ferulic acid (FA) on the levels of endogenous hormones in wheat seedlings, FA caused a build-up of IAA, gibberellin, and cytokinin at doses of 2.50 mmol L⁻¹, but the accumulation of these four hormones created an accretion of abscisic acid. Brunn et al. (1992) revealed that the auxin transport is inhibited by some flavonoid aglycones that promote lateral root growth and inhibits negative geotropic growth.

5.4. Interference with plant respiration

Allelochemicals can either stimulate or inhibit respiration, thereby diminishing the vitality of the energy-producing mechanism (Batish et al., 2001). The allelochemical substances might inhibit the majority of the metabolic process, including O_2 uptake and the three phases of dark respiration, viz., glycolysis, the Krebs' cycle, and oxidative phosphorylation (Weir et al., 2004). Benzoxazolinone (BOA) is a benzoxazinone that is secreted by the roots of certain cultivated grasses and has a variety of physiological effects on plants. The generation of excessive reactive oxygen species (ROS) results in oxidative stress, which is a crucial event in the mode of action of BOA in the plant (Schulz et al., 2013). According to Burgos et al. (2004), the allelochemicals BOA and DIBOA from rye decreased the number of mitochondria, protein synthesis, and lipid catabolism in cucumber seedlings. However, photorespiration in chloroplasts obscures a number of allelochemical impacts on mitochondrial respiration (Weir et al., 2004). It is conceptualized that certain allelopathic substances interact directly with the mitochondrial membrane and impede mitochondrial respiration. The monoterpenes like camphor, pinene, and limonene significantly affected the respiratory activity of soybean radicular hypocotyl mitochondria, but their modes of action appeared distinct (Abrahim et al., 2003). Similarly, secondary metabolites such as flavonoid quercetin were reported to inhibit respiration in soybean hypocotyl mitochondria via three suggested hypothesized pathways. Quercitin appears to restrict substrate oxidation by directly interfering with electron transport, inhibiting phosphate intake and decoupling oxidative phosphorylation (Abrahim et al., 2000).

It has been demonstrated that allelochemicals have a deleterious effect on photosynthesis, while the underlying mechanisms are unknown. Allelochemicals can affect three primary photosynthetic processes (Zhou and Yu, 2006): (i) stomatal conductance and consequently gas exchanges between plant and atmosphere; (ii) "light reactions," which refer to electron transport; and (iii) "dark reactions" which refer to carbon reduction. Allelochemicals have a substantial effect on plant photosynthesis by accelerating the degradation of photosynthetic pigments, specifically chlorophyll (Pan et al., 2015). By decreasing chlorophyll content, benzoic and cinnamic acids inhibited soybean photosynthesis (Baziramakenga et al., 1994). The inhibition of photosynthesis and oxygen evolution via interactions with photosystem II (PSII) components is one of the best-studied phytotoxic effects of allelochemicals (Einhellig et al., 1993). Photosynthetic inhibitors consist of electron or uncouplers, energy-exchange inhibitors, electron acceptors, or a combination of these. Numerous PSII components are necessary for the formation of a flexible membrane-embedded scaffold. This scaffold organizes the ligands that bind an excitonically linked network of pigments and cofactors that capture, transmit, and utilize solar energy to drive water-splitting processes. Sorgoleone, a lipophilic benzoquinone found in the root exudates of S. bicolor, is a well-documented PSII inhibitor (Gonzalez et al., 1997; Nimbal et al., 1996). As a plastoquinone analogue, sorgoleone inhibits plastoquinone binding at the D1 protein of PSII (Czarnota et al., 2001) and also inhibits hydroxyphenylpyruvate dioxygenase (HPPD), which interrupts carotenoids biosynthesis and results in foliar bleaching (Meazza et al., 2002).

5.5. Inhibition of protein synthesis and nucleic acid metabolism

The phytotoxicity of certain allelochemicals is associated with their susceptibility to disturb normal metabolic processes in plants. This may also be a mode of action for other allelochemicals. For instance, L-canavanine, a L-arganine analogue identified in Canavalia ensiformis, inhibits plant growth because of its ability to disrupt L-arganine metabolism, resulting in a deficiency of L-arganine-derived compounds (Nakajima et al., 2001). In a study, radio-labeled C-14 sugars or amino acids were used to examine the effect of absorption of allelochemicals into protein, and the result showed an inhibition of protein synthesis (Bertin et al., 2007). Allelochemical reactions may generate ROS such as superoxide anions (O_2^{-}) , hydroxyl (OH^{-}) , or hydroperoxyl (HO_2) radicals, which can affect membrane permeability, nucleic acid structure, and protein synthesis, ultimately resulting in cell death (Weir et al., 2004). Allelochemicals can also interfere with gene expression (He et al., 2012; Fang et al., 2015; Ma et al., 2015), which is typically induced in recipient plants in response to an attack by the donor plants. Sarmentine and some other fatty acids, namely pelargonic acid, have the ability to improve the fluidity of leaf cuticle and the activity of peroxidase, which might be used as a potential desiccant (Huang et al., 2010).

5.6. Interference with plant-water relationship

There are many allelochemicals that might influence the water balance and target by clogging the xylem component, reduction of stomatal conductance, lowering of plant water potential, and thereby reducing the water uptake by the root system. Reports by Barkosky and Einhellig (2003) suggested that the concentration of 0.75 mM 4-hydroxybenzoic acid (p-HBA) significantly reduced water productivity and stomatal conductance in soybean seedlings. Sorgoleone and juglone affected cell permeability in crops like pea, maize and soybean by affecting the H⁺-ATPase activity and proton-pumping across the root cell plasma membrane (Hejli and Koster, 2004a; b). Bergmark et al. (1992) observed that ferulic acid (250 μ M) lowered NH_4⁺ and NO_3⁻ absorption in maize seedlings, with inhibition of NH_4⁺ absorption being less responsive than NO_3⁻ absorption.

5.7. Interference with soil microbial activity

The allelochemicals have a diversified effect on microorganisms dwelling in the rhizospheric soil. These plant-microbe interactions can be either stimulatory or affect the growth of microbes, influencing plant growth. The allelopathic effect of Alliaria petiolata (Alliaria) on mutualistic microbes has been widely studied. A study revealed that breakdown products generated during the decomposition of glucosinolate secreted by Alliaria might have harmful effects on mycorrhizal fungi (Vaughn and Berhow, 1999). Later on, various studies were conducted affirming the adverse role played by Alliaria on mycorrhizal species (Stinson et al., 2006; Wolfe et al., 2008; Barto et al., 2012a,b). However, the change in the community structure of soil microbes under the effect of allelopathic plant species varies with the age shift in plant population (Lankau, 2011). Evidences of the negative impact of allelopathic plant species on the beneficial soil bacteria are also replete. An early report by Mallik and Tesfai (1988) showed that shoot extracts of several weed species, including Chenopodium album, Cyperus esculentus, and Helianthus annuus inhibited nodulation by Bradyrhizobium japonicum. Similar works related to growth inhibition of various symbiotic (Rhizobium) and free-living (Azotobacter) bacteria in the presence of plant allelochemicals have been reported (Kloepper et al., 2004; Pollock et al., 2011). Such a relationship between allelopathic plant species and beneficial rhizospheric microbes will provide an added advantage to these plant species while competing with plants that are symbionts with such microbes (Cipollini et al., 2012). However, it must be noted that the adverse effect of allelopathy on soil microbes will also impact the growth of allelopathic plants, which also tend to benefit from the ecosystem services provided by these beneficial microbes (Devi et al., 2021). Allelopathy induces a series of physiological and biochemical changes in plants. Understanding the mode of action of different allelochemicals may aid in obtaining the basic information on the structure and biochemical forms of different allelochemicals for developing new bio-herbicides.

6. Application of allelopathy in weed management

Allelopathy plays an important role in overall weed suppression, and the residue of allelopathic plants enhances nutrient cycling processes in soil, thus having a significant effect on crop productivity. Application of water extract of sunflower curbed the problem of weeds like *Avena fatua* and *Phalaris minor*, thereby reducing the weed dry weight (10–62.0%) and increasing the yield (18.55–62.0%) of sunflower compared to control (Jamil et al., 2009). In a recent study by Sahoo et al. (2023) the positive effect of sunflower crop residue incorporation was observed on subsequent rice crop yield, which could be attributed to better weed suppression, nutrient availability and improved microbial activity. However, it must be noted that allelopathy of most of the crops is species-specific and discriminatory in their action, i.e., they inhibit the growth of some species but might not affect certain species and may have stimulatory effects (Cheema, 1988). Sorghum allelochemicals are specific in action and concentration-dependent in their effect (Cheema and Ahmad, 1992). Sturm et al. (2018) found that allelopathic effects were species-specific, with the weed *Stellaria media* showing greater sensitivity to allelopathy than *Alopecurus myosuroides* and volunteer wheat (*T. aestivum*). The release of allelochemicals and their activity depends on the environmental conditions, plant species, soil microbial properties etc. However, similar to synthetic herbicides, some allelochemicals also exhibit selectivity. Numerous woody and herbaceous plants, in addition to weeds, have allelopathic effects on both crops and weeds (Tesio and Ferrero, 2010). The most recent estimate showed 240 allelopathic weeds (Qasem and Foy, 2001), although many more plant species have been discovered to exhibit allelopathic qualities in the last two decades. Examples of allelopathic interactions between various plant species are given in Tables 2 and 3, including crops on weeds, crops on crops, weeds on weeds, and weeds on crops.

In general, manual removal of weeds or manual weed management operations is arduous, time-consuming, and expensive in this modern era. Developing several herbicide chemicals paved the way for more efficient and timely weed control. However, despite increased crop productivity due to herbicides, their uncontrolled usage has resulted in ecological threats such as the emergence of herbicide-resistant weeds and weed flora shifts in different ecologies. In order to overcome these issues, research should focus on alternative weed management strategies to reduce the use of synthetic chemicals for weed control. One of the strategies can be allelopathic weed management which is an effective plausible way toward sustainable weed management. These allelochemicals effectively inhibit weeds, leaving less to no phytotoxic residues and can substitute chemical formulations for weed control, thereby minimizing environmental pollution and ensuring better ecosystem functioning (Macias et al., 2003; Bhadoria, 2011). Allelochemicals can be used to develop novel eco-friendly bio-herbicides to inhibit weed germination and growth. However, some shortcomings that limit the use of natural herbicides are, (a) expensive due to structural complexity, (b) short environmental half-life, (c) non-target specific toxicity, and (d) potential mammalian toxicity (like AAL-toxin, fumonisin) and allergy (like sorgholeone) (Duke et al., 2000). The allelopathic weed management can be deployed at the field scale through a spatio-temporal arrangement of crops. However, heavy fieldwork and other interferences, such as competition for inputs, soil microbial impact, nutrient immobilization, etc., may make its execution difficult at the field scale (Cheng and Cheng, 2015). However, it must be noted that the selection of high-value crops with allelopathic properties (Sahoo et al., 2023) can provide better remuneration, which may pay off the laborious work incurred. Additionally, allelopathy could be a green alternative to hazardous chemical herbicides, thus maintaining and stimulating ecosystem functions and environmental health. The allelopathic weed management following different agronomic management methods is briefly discussed hereunder.

6.1. Crop rotation

Crop rotation gives the best results in reducing weed seed bank, i.e., maintaining weed communities at low densities, hindering weed establishment in early crop season and is most useful in avoiding invasive or noxious weed flora development (Buhler et al., 2000; Scavo and Mauromicale, 2020). Some crops commonly used in rotations with allelopathic potential are rice, wheat, sorghum, barley, rye, and sunflower (Abbas et al., 2021; Sahoo et al., 2023). Inclusion of these allelopathic crops in the cropping sequence controls weeds by releasing allelochemicals which will act against inhibition of weed seed germination and prevent the establishment of weeds (Scavo et al., 2019). Various studies report different crop rotations successfully suppressing the weed growth and establishment, for instance, sorghum-wheat (Shahzad et al., 2016); winter wheat–spring barley–peas (Scherner et al., 2016); and corn–soybean–oat/alfalfa–alfalfa (Hunt et al., 2017). All these studies agree upon the suppression of weeds through diversified crop rotations.

6.2. Cover crops

Allelopathic cover crops have several advantages in weed control, soil fertility improvement, soil erosion control and higher yield for subsequent crops (Tursun et al., 2018). Most noteworthy cover crops include canola, rapeseed, brown mustard, black mustard, oats, rye, crimson clover, red clover, cowpea, fodder radish, wheat, annual ryegrass, mustard, hairy vetch, and buckwheat, where all these crops may be employed in different cropping systems to inhibit the growth of weeds due to their vigorous initial growth, space capture ability and allelopathic effect (Mirsky et al., 2013). Some crops exude different allelochemicals, which may have serious implications on the seed germination and growth of weed seedlings (DeVore et al., 2012). For instance, taking up rye as a cover crop with cotton can control the establishment of the noxious weed Amaranthus by 67% over control (Tabaglio et al., 2013). This allelopathic weed management tactic of using cover crops can keep a check on the weed population below economic threshold levels but may not completely suppress the weed growth and reduces the use of existing herbicide formulations for weed management (Narwal and Haouala, 2013).

6.3. Green manuring

Green manuring includes the incorporation of crop biomass into the soil, mostly before taking the main crop. This practice of green manuring ushers diversification in crop rotational sequences. The aqueous extracts of some green manure crops show allelopathic weed control through their inhibitory action on weed growth (Adler and Chase, 2007; Purohit and Pandya, 2013; Anese et al., 2015; Rugare et al., 2021). Crop-specific allelochemicals are mostly responsible for weed suppression. For instance, black sunn hemp roots can have dehydropyrrolidizine alkaloids, while the leaves, stem, and seeds have isohemijunceines A, B, C, trichodesmine, junceine, and acetylisohemijunceines (Morris et al., 2015). The cruciferous plants contain ample quantities of glucosinolate chemicals which when hydrolyzed to isothiocyanates (Boydston and Hang, 1995) have potential to reduce weed growth and establishment. On the whole, green manuring helps in early-season weed control and thereby reduces the dependency on post-emergence herbicides.

6.4. Mulching

Allelopathic weed control using mulches has two main approaches, i. e., through the cultivation of live crops as mulch in the field, which covers the maximum ground space inhibiting the growth of weeds and the second approach being surface retention of crop residues to suppress the establishment of weeds (Scavo and Mauromicale, 2020). These cover crop residues used as mulch can hinder the growth of weeds by their physical presence on the surface of the soil or by releasing allelochemicals during microbial decomposition of residues (Weston, 1996). Mulches can be introduced into cropping systems in different ways, such as conservation agriculture, crop rotations, strip cropping, intercropping, and cover crops. Many research studies on different crop residue mulches, viz. rye (Schulz et al., 2013; Tabaglio et al., 2013), maize (Bajgai et al., 2015), sunflower (Rawat et al., 2017), have shown that they can be potentially used as a weed control strategy in field crops.

6.5. Intercropping

Allelopathic crops primarily aid in lowering weed intensity and therefore increase agricultural production when intercropped with other crop species. Because intercropping suppresses weeds more effectively than solo cropping, it provides the opportunity to employ crops as an efficient weed management strategy. By increasing the diversity of the soil microbial population and promoting the movement of

Table 2

Allelopathic effect of crops on other plants.

Allelopathic Crop (Donor)	Target plant (Receiver)	Response of weeds	Allelochemical	Type of experiment	References
Effect of cereal cro	ops on weed				
Rice	Echinochloa crusgalli, Cyprus difformis, Cyprus iria, Fimbristylis miliacea	Inhibition the seed germination and seedling shoot length and root length	Phenolic acid, indoles and terpenes	Pot experiment in glass house	Alam et al. (2018)
Rice	E. crusgalli	Inhibition of weed grass development by more than $\sim 41\%$	-	Laboratory	Rahaman et al. (2021)
Sorghum	Amaranthus hybridus	Reduce the emergence, plant height, leaf area and dry weight	Sorgoleone	Pot experiment in glass house	Tibugari et al. (2019)
Barley	Hordeum spontaneum	Reduced hypocotyl length, hypocotyl weight, radicle weight, seed germination and radicle length	Water soluble allelochemical	Green house and laboratory	Ashrafi et al. (2007)
Rye	Amaranthus retroflexus and Portulaca oleracea	Reduced germination and seedling growth	Benzoxazinones	Field experiment	Tabaglio et al. (2013)
Effect of legumes of	crops on weed				
Faba bean	E. crusgalli and A. retroflexus	Reduced the germination, root and shoot elongation and aerial biomass	-	Pot experiment	Álvarez-Iglesias et al. (2018)
Cow pea	Eleusine indica (L.) Gaertn.	Reduced germination, plant height and dry weight	-	Green house experiment	Adler and Chase (2007)
Common bean	Bidens pilosa, E. indica and Acanthospermum hispidum	Reduced germination percentage, radicle and plumule length	-	Laboratory and green house experiment	Runzika et al. (2013)
Effect of oil seed c	rops on weeds				
Black mustard	Phalaris paradoxa	Decreased plant biomass and leaf area by 94% and 92%, respectively	Ferulic acid, syringic acid and affeic acid	Laboratory and green house	Al-Sherif et al. (2013)
Groundnut	Lathyrus hirsutus L. and Anagallis arvensis L.	Reduced germination percentage	-	Petri dishes in controlled chamber	Abou El-Enin and Abdel-Ghffa (2017)
Sunflower	Parthenium hysterophorus L.	Reduced germination, root length, root and shoot biomass	-	Petri dishes in growth chamber and pot in green house	Javaid et al. (2006)
Effect of crop on c	rop				
Sunflower	Wheat and maize	Germination percentage germination index radicle and plumule length and seedling dry biomass	Alkaloids, phenolic compounds, flavonoids and terpenoids	Petri dishes in laboratory	Muhammad and Majeed (2014)
GM maize	Wheat	Decreased chlorophyll <i>a</i> , carotenoid, leaf soluble sugar, proline and activity of POD	-	Field experiment	Ibrahim et al. (2013)
Rice Straw	Rice	Reduction chlorophyll content	Phenolic acids	Field experiment	Asaduzzaman and Pramanik (2005)

allelochemicals into the soil, intercropping is said to improve the interactions between allelopathic weeds and cover crops and, as a result, the phytotoxic consequences (Brooker et al., 2015). Common mycorrhizal networks have been found to be operating as "superhighways" that directly connect plants underneath and transport allelochemicals to target plants (Barto et al., 2012a,b). Many researchers have witnessed reduced weed density and biomass production with intercropping in different cropping systems, viz. intercropping maize with fodder legumes (Khan et al., 2002); intercropping sesame, soybean, and sorghum with cotton (Iqbal et al., 2007); and pea intercropped with false flax (Saucke and Ackermann, 2006). Crops with allelopathic potential should be chosen for agronomic interventions like green manuring, crop rotation, cover crops, intercropping, mulches etc., in cropping systems. Research towards identifying and screening suitable or compatible allelopathic plant species in combination with other crop species in cropping systems can be a promising option for successful implementation of allelopathic weed control.

7. Conclusions and way forward

Dependency on synthetic herbicides in this modern era of agriculture severely affects the environment and the ecosystem. Alternate sustainable weed management strategies like allelopathy could be included in integrated weed management programs to reduce the usage of synthetic herbicides. The identification and augmentation of allelochemical synthesis and release pathways in donor plants could increase their concentration in the target environment. The allelochemicals interact differently with the soil environment based on their chemical nature, which could be used for inducing selectivity in weed management. Agronomic cultural practices like crop rotation, intercropping, and cover crops with crop species having allelopathic potential could be a part of conventional farming practices for economical and effective weed control. The extraction of allelochemicals from donor plants and their use as bioherbicide could be another approach to using allelopathy for weed management. Allelopathic weed management provides an opportunity to maintain ecological diversity while fulfilling the terms of sustainable agriculture. Promoting cross-disciplinary research on allelopathy and its application in agro-ecosystems will not only clarify the intricate role of allelochemicals in natural systems but also help us understand the communication channels between different organisms in soil environments that are prevalent at the micro level. Future research should address this and, in addition, should explore the application of biotechnological tools to enable plants to overcome biotic and abiotic stress in order to ensure a sustained defense mechanism system. Research must be done on introducing and regulating a multigene expression system to synthesize and localize the compatible allelochemicals in the appropriate plant tissue or organ. Using allelochemical consortia for weed management could be a more effective option for controlling weed growth for a sustainable agriculture.

Table 3

Allelopathic effect of weeds on other plants.

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Allelopathic weed (Donor)	Target plant (Receiver)	Response of weeds	Allelochemical	Type of experiment	References
Effect of weeds on we	eeds				
Persicaria lapathifolia	Echinochloa colona	Reduced germination, seedling root and shoot growth	n-Dodecanal, $\boldsymbol{\alpha}\text{-humulene}$ and limonene	Petri dishes in growth chamber	Abd-ElGawad et al. (2021)
Achyranthes aspera L.	Digera arvensis, Chenopodium album Trianthema portulacastrum, Parthenium hysterophorus, Convolvulus arvensis, Rhynchosia capitata	Reduced seedling establishment, emergence index and emergence energy	Gallic acid, caffeic acid, 4-hydroxy-3- methoxy benzoic acid, m-coumaric acid, chromatotropic acid and syringic acid	Laboratory condition	Safdar et al. (2021)
Ipomoea cairica	P. hysterophorus	Decrease chlorophyll content	3-3'-5-Trihidroxy-4'-7-dimethoxyflanove	Pot experiment	Srivastava and Shukla (2016)
Lantana camara	Rumex dentatus	Suppression of seed germination and decreased radicle and plumule length	Flavonoids, iridoid glycoside, furanonaphoquinones	Laboratory condition	Anwar et al. (2018)
Allelopathic effect of	weed on crop				
Tridax procumbens	Mung bean and cowpea	Inhibitory effect on germination, root and shoot elongation	Aqueous leaf extract	Petri plates in laboratory	Femina et al. (2012)
Eupatorium odoratum	Rice and groundnut	Reduced seed germination and seedling growth	Weed debris	Pot culture in Net house	Begum et al. (2021)
Lantana camara	Oat	Reduced germination		Petri plates in laboratory	Hayyat et al. (2020)
Polypogon hissaricus	Wheat	Reduced germination, growth and chlorophyll content	Aqueous leaf extract	Petri dish and pot culture	Siyar et al. (2019)
Phalaris minor L.	Wheat	Inhibition seed germination; reduced seedling dry weight	Alkaloids, quinines, phenolics	Petri dishes in laboratory condition	Ankita and Chabbi (2012)
Echinochloa colona L. and Cyperus iria L.	Rice and soybean	Reduced germination and suppressed early seedling growth		Petri dishes in laboratory condition	Chopra et al. (2017)

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

This review article has refered already published research work with due citations in the text.

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