BIOLOGICA NYSSANA
16 (2) December 2025:
DOI: 10.46793/BiolNyss.16.2.19V

Original Article

Exploring the applications of allelopathy in agriculture: A review

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Received: *August 16, 2025*
Revised: *November 26, 2025*
Accepted: *November 28, 2025*

Abstract:

This review delves deep into the world of allelopathy and its applications in agriculture, offering a detailed examination of its environmental, physiological, and ecological aspects. The review begins by dissecting the intricate factors that influence allelochemical production, including environmental and physiological determinants. It also explores the mechanisms underlying allelochemical activity, shedding light on how these compounds disrupt fundamental plant functions and signalling pathways. The review underscores the pivotal role of allelopathy in agriculture, emphasizing its dual impact on crop yields and weed management. Allelopathic interactions between crop plants and weeds are explored, revealing the intricate ways in which they influence each other. The review also highlights the effects of common plants on both crops and weeds, showcasing allelopathy's potential as a sustainable agricultural practice and an effective tool for weed control. The review provides valuable insights into the multifaceted applications of allelopathy in modern agriculture. Another crucial aspect discussed in the review is the persistence and degradation of allelochemicals in soil and their effects on soil nutrient dynamics. Understanding how these compounds interact with soil and impact nutrient availability is vital for optimizing their use in agriculture. This section emphasizes the need for a holistic approach to sustainable farming, taking into account the complex interplay between allelopathy and soil health.

Key words:
Allelochemical, agriculture, nutrients, weed control, soil health

Apstrakt:

Istraživanje primena alelopatije u poljoprivredi

Ovaj pregled dubinski ulazi u svet alelopatije i njenih primena u poljoprivredi, nudeći detaljnu analizu njenih ekoloških, fizioloških i ekoloških aspekata. Pregled započinje razlaganjem složenih faktora koji utiču na proizvodnju alelohemikalija, uključujući ekološke i fiziološke determinante. Takođe istražuje mehanizme koji stoje u osnovi aktivnosti alelohemikalija, osvetljavajući načine na koje ova jedinjenja narušavaju osnovne biljne funkcije i signalne puteve. Pregled naglašava ključnu ulogu alelopatije u poljoprivredi, posebno njen dvostruki uticaj na prinos useva i kontrolu korova. Istražene su alelopatske interakcije između useva i korova, otkrivajući složene načine njihovog međusobnog delovanja. Pregled takođe ističe efekte uobičajenih biljaka na useve i korove, ukazujući na potencijal alelopatije kao održive poljoprivredne prakse i efikasnog alata za suzbijanje korova. Na taj način, pregled pruža dragocene uvide u višestruke primene alelopatije u savremenoj poljoprivredi. Još jedan ključni aspekt obrađen u tekstu jeste postojanost i razgradnja alelohemikalija u zemljištu, kao i njihov uticaj na dinamiku hranljivih materija u tlu. Razumevanje načina na koji ova jedinjenja stupaju u interakciju sa zemljištem i utiču na dostupnost hranljivih materija od suštinske je važnosti za optimizaciju njihove primene u poljoprivredi. Ovaj deo naglašava potrebu za holističkim pristupom održivoj poljoprivredi, uzimajući u obzir složenu međuigru između alelopatije i zdravlja zemljišta.

Ključne reči:
alelohemikalija, poljoprivreda, hranljive materije, suzbijanje korova, zdravlje *zemljišta*

Introduction

For almost two thousand years, scientists have been studying plants and their relationship with other organisms. Many examples described by botanists, farmers, and horticulturalists provide strong evidence for allelopathic interactions among plants. Japanese literature also reports instances of plants harming other plants due to the formation of bane compounds in sediments, especially in *Pinus densiflora,* commonly known as Japanese red pine (Rice, 1985). In 1800, agronomists began to record repeated problems in a few perennial cropping systems (Weston, 2005).

The most fascinating fact was that most plant species with therapeutic value for humans are also reported to exhibit potential allelopathic effects later (Wink, 2018). The generation of allelochemicals from plant residues and the role of microbial interactions in their degradation are significant (Putnam & Weston, 1986). After the development of various techniques, such as extraction, bioassays, chemical isolation, and identification, in the 20th century, curiosity in the field of allelopathy developed (Willis, 1997).

First, Muller and his associates reported many compositions of volatile compounds induced by plants in the US, California, and Elroy Rice reported allelopathy in prairie-type ecosystems (USA, Oklahoma). He described the effects of allelochemicals on nitrogen-fixing and nitrifying microorganisms in soil (Rice, 1985). Research in this field can bring together various disciplines to build sustainable agriculture successfully.

In the 21st century, many weed scientists, physiologists, natural product chemists, and soil scientists began to take an interest in this challenging field of allelopathy (Macias, 2002). Studies have revealed crucial examples of allelochemicals in seed and growth suppression that alter vegetation patterns, order of plant succession, weed plethora, agricultural yield, and challenges in transplanting fruits and crops (El-Darier & Youssef, 2022; Hatata & El-Darier, 2009). These substances are produced by plants and microbes, referred to as “donor species,” while species whose growth and development are affected are referred to as “recipient plants.” Allelopathic interactions include those between plants, microorganisms, viruses, insects, soil, and plants, as well as interactions between plants and chemicals. The nature of the active chemicals and the targeted species defines whether allelopathic effects will be stimulatory or suppressive (Keating, 1999) (**Fig. 1**).

Secondary metabolites are substances emitted by plants, and some have allelopathic effects. The majority of allelochemicals are labelled as secondary metabolites from the shikimic acid or acetate pathways (Inderjit & Bhowmik, 2002). Allelopathic interference has been mainly linked to all kinds of secondary plant products (Weston & Duke, 2003). The plant kingdom contains hundreds of allelochemicals; many are phytotoxic, and several have been isolated from plant tissue and soil and are suspected of suppressing germination and growth. Biological and abiotic soil factors modulate the phytotoxic action of allelochemicals once they leave the plant. Some allelochemicals are water-soluble and can be washed away from leaves by rain, mist, dew, or fog drip (Kobayashi, 2004).

Plant parts that produce these chemicals are flowers, inflorescences, stems, leaves, fruits, roots, rhizomes, and seeds (Rice, 2012). Allelochemicals are synthesized in plant parts above, below, or both above and below the soil surface, and they cause allelopathic effects on many plant communities. Donor plant species that produce allelochemicals, such as lignins, salts, and tannins, often store them in an inactive form within plant cells. These hazardous compounds are produced by plant enzymes or by environmental stress (Weston, 1996). Allelochemicals are discharged through different mechanisms: (a) release of chemicals from the aerial parts (leaves and stems) by rainfall and dew, (b) release of chemicals from roots called root exudation through diffusion vesicle transport, and (c) disintegration by microorganisms (Keating, 1999).

Allelochemicals are the plant’s secondary compounds or breakdown products of degrading plant tissue. These compounds are frequently retained in vacuoles to protect the generating plant but are frequently extruded or filtered out of the tissues (Hall & Henderlong, 1989). Phytotoxic effects are shown to depend on the density of phytochemicals. Plant growth declines due to resource constraints, although phytotoxicity is highest at low plant densities (Weidenhamer et al., 1989). In most cases, early in the disintegration process, plant remains have the highest phytotoxic potential. Phytotoxicity lessens or is even eliminated as decomposition progresses. Activities in the soil, both biotic and abiotic, can influence the amount and activity of phytotoxins

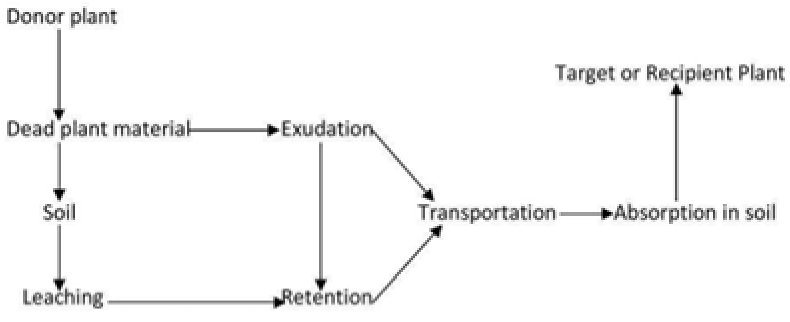

Fig. 1. Path of allelochemicals from a donor plant to recipient plant

(Sampietro et al., 2007). The concentration of allelochemicals in the plant tissue may fluctuate with time. For instance, bark leachates of a species of *Eucalyptus globulus* are more harmful to particular food crops than foliar leachates and leaf litter leachates (Rizvi et al., 1999).

Materials and Methods

Literature data

The data were collected from different types of secondary sources, including a systematic review of many web-based searches, and analysed published scientific articles and books on the allelopathic activity of several plants. The literature was searched by using Google Scholar, Research Gate, PubMed, Scopus, and Web of Science with particular search phrases like 'Allelopathy', 'Phytochemicals', 'Agriculture', 'Bioherbicides', 'Secondary Metabolites', 'Aromatic Plants', 'Weeds', and 'Abiotic factors'. The remaining literature was searched using the names of allelochemicals known to confer herbicidal activity to identify publications not found with these search terms. Additional searches were carried out for technical reports, student theses, government publications, agency reports, websites, and synthesis articles or book chapters. The collected material was published from 2000 to 2022. A total of 196 articles on allelopathy, allelochemical mechanisms, and allelopathy in agriculture were collected and included in this review (**Fig. 2**). Although it is difficult to compile all of the material from studies on allelopathy, we focused on the positive aspects of allelopathy that can be employed in weed management for sustainable agriculture. Finally, we examined the data to investigate the allelopathic activity of common aromatic plants in weed management.

Results and Discussion

Factors influencing the production of allelochemicals

Secondary metabolite deficiency, unlike primary metabolite deficiency, results in prolonged deterioration of the creature's survival, prolificacy, aesthetics, or possibly nothing noteworthy changed. They are also crucial in plant defence against herbivory and other interspecies protection. They have a relatively restricted range in the plant kingdom (Jain et al., 2019). They differ in quantity and quality for specific plant species that thrive in different locations. They are frequently produced in smaller quantities by specific cell types at various stages of development. Secondary metabolites are a diverse set of molecules found in plants, including alkaloids, flavonoids, phenolics, glycosides, terpenes, amines, and steroids, that have been widely exploited in the pharmaceutical industry (Sharanabasappa et al., 2007).

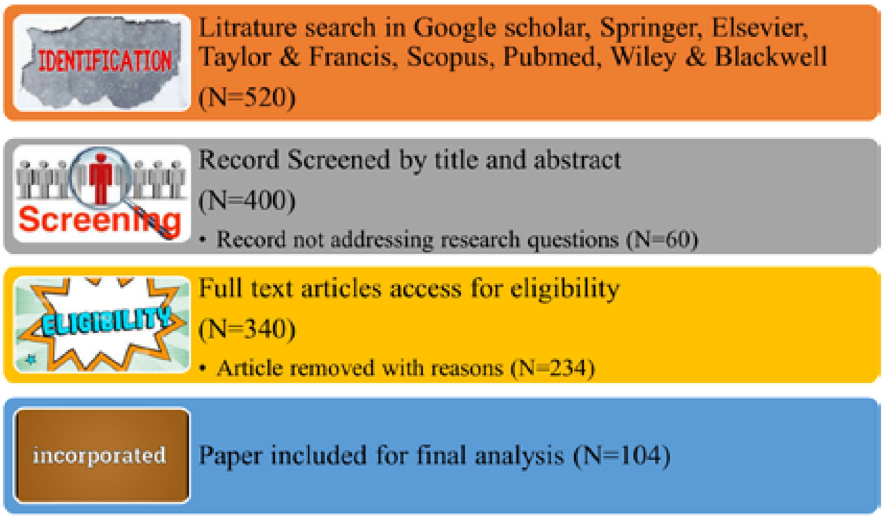

Fig. 2. Search strategy for the review

Climatic variables

Climatic variables have a significant impact on the generation of allelochemicals. Numerous allelochemicals are impacted by variations in light intensity, quantity, and duration. The majority are produced during protracted photoperiods and UV light exposure (Escobar-Bravo et al., 2019). Plants exposed to high ambient temperatures produced more allelochemicals. Water is essential to the phenomenon of allelopathy, as it serves as a solvent and a transporter of allelochemicals and leachate from plant aerial sections and the soil. Soil microorganism action is affected by soil moisture (Aliotta et al., 2006).

Allelochemicals are composed and concentrated differently, depending on the maturity, organ, and plant species (Qasem & Foy, 2001). Environmental factors can influence allelopathy expression. The plant's allelopathic capability in nature is likely to differ by location owing to edaphic and climatic conditions. Seasonal variables, such as soil temperature, air temperature, and soil moisture, significantly influence allelopathy. The separation and identification of molecules with biological activity from donor plants does not prove that these compounds interact in nature through allelopathic mechanisms. The retention and movement of allelochemicals in soil and the constituents of soil all affect the destiny of allelochemicals (Inderjit, 2001; Inderjit, 2005).

Physical, chemical, and biological variables

Physical and chemical parameters determine the quality, quantity, and number of allelopathic chemicals; soil texture, particularly, has a considerable impact on the manifestation of allelopathy in natural systems. Sandal loam soils absorb fewer phenolic chemicals than fine-textured soils. Allelopathic expression is influenced by soil chemical and biological factors, including nutrients, soil consistency, microbes, moisture, pH, and organic matter. They impact soil adsorption and transport, as well as allelochemical metabolism. The pH of the soil is vital for the absorption and immobilization of inorganic ions, as well as for the resulting nutrient buildup, and a high pH can enhance microbial activity (Kobayashi, 2004).

Similarly, soil chemical properties frequently change with the inclusion of plant waste, leaves, roots, or donor plant leachate, and these alterations have been shown to influence allelochemical activity. In soil settings, allelochemical interactions are heavily influenced by allelochemical turnover rates in the rhizosphere, and their interactions with organic matter, clay, and other soil variables further alter soil biological and physicochemical properties (Scavo et al., 2019). Blum reported that soil pH, texture, organic carbon, and nitrogen are all significant in regulating allelochemical absorption and persistence when soil microorganisms are present. As well as allelochemical phytotoxicity, it can also be influenced by the dynamics of soil moisture. According to data reported, increased evaporation-transpiration and reduced soil water content would result in the decline of allelochemical phytotoxicity of plants in the soil mixture (Blum, 2002)

Allelopathy is also influenced by soil microorganisms, which can alter outcomes by decomposing hazardous chemicals or producing toxic chemicals (Inderjit, 2001). They have the capacity to alter the availability of soil nutrients, as well as the release of chemical substances bound to soil particles. Allelopathic chemicals can exist in three states: irreversibly bound, reversibly bound, and free. In general, the last two types are relevant to allelopathy (Inderjit et al., 1999). Allelopathic plants enhance the synthesis of phytotoxic secondary metabolites when exposed to environmental challenges, such as excessive light levels, severe temperatures, mineral deficiencies, moisture stress, and exposure to fungicides, insecticides, herbicides, and plant growth regulators (PGRs) (Aliotta et al., 2006).

Determining the concentration at which each distinct reaction takes place is essential if allelopathic interactions are to be used in weed control programmes. Moreover, the allelopathic potential of different plant components may differ (Chon & Kim, 2002). The plants' leached metabolites contained various materials, including carbohydrates, amino acids, mineral nutrients, and more organic compounds. Depending on the season, leachability, concentration, and plant age, these substances can either promote or inhibit plant growth (Reganold, 2016). Biochemicals with complex structures are among the molecules plants use to interfere with each other, and inorganic elements may also be exploited in an allelopathic manner. In soil, elements like salts and heavy metals may build up due to hyperaccumulation, breakdown of litter, and changes in the chemistry of the rhizosphere (Morris, 2009).

In the ground, allelopathic plant residues can remain on the soil surface, and the subsequent crop can be planted into the remnants without tillage. Furthermore, entire leftovers may be incorporated into the planting region's soil via strip-till, allowing conventional equipment to be used. Biotic and abiotic variables, such as soil physical, chemical, and microbiological properties, may affect the phytotoxicity of chemicals released from integrated remnants (Popa et al., 2008). Thus, soil microorganisms can inactivate a phytotoxic chemical, make it more active, and transform it into new poisons (Kobayashi, 2004).

Mechanisms of action of allelochemicals

It can be classified as a direct or indirect mechanism. The direct action of allelochemicals involves biochemical and physiological effects on numerous critical plant developmental and metabolic processes. The indirect action is represented by changes in soil characteristics, nutritional status, and changes in the population or activity of microorganisms and nematodes. The allelochemicals should be soaked to have a direct effect on the target plant. Allelochemicals are absorbed mainly by recipient plants through their root network, either actively or passively, and the allelochemicals travel by way of the xylem by mass flow (Inderjit, 2005). When an allelochemical is absorbed, it alters the target plant's physiological activities. However, investigations have found that the allelochemical reaction might differ depending on concentration. Those allelochemicals that restrict the growth of one species at a particular concentration might promote the growth of a different species at other concentrations (Muzell et al., 2016).

Previously, allelopathy was known for its negative impacts on neighbouring plants, but in recent years, many researchers have adopted a more positive perspective, and the mechanisms underlying both perspectives are described in **Fig. 3**.

Allelochemicals can affect the growth and seed germination of nearby plants. When plants come into contact with soil-based allelochemicals, these effects primarily affect plant roots. Exposure to these compounds increases the physiological responsiveness of target plants, inducing oxidative stress and potentially leading to cell death. Lipid peroxidation, alterations in the cell membrane, protein abnormalities, and elevated protease activity are early indicators of cell damage. The plant's protoplast (the living component of the plant cell enclosed by the plasma membrane, excluding the cell wall) may degenerate through hydrolysis or necrosis if antioxidants are unable to eliminate these reactive oxidants, leading to the loss of cell organelle integrity and function. Moreover, variations in the structure and function of the apical meristem impact root development and water absorption. These allelopathic substances could provide a less harmful alternative to chemical pollution for controlling weeds and invasive plants (Šoln et al., 2022).

The mechanisms and modes of action of allelochemicals, which have since been studied, were identified by Rice (2012). Allelochemicals have several mechanisms of action to suppress and alter plant growth and development. Allelochemicals are known to target the following sites or processes: cell division, plant hormone balance and production, membrane permeability and stability, germination of pollens, uptake of minerals, movement of stomata, synthesis of pigments, respiration, photosynthesis, nitrogen fixation, amino acid synthesis, specific enzyme activities, nitrogen-fixing bacteria, and modification of nucleic acids. Allelochemicals may operate selectively, or plants may respond selectively. These problems are exacerbated by the presence of several active compounds in a single plant. For example, *Sorghum spp.* include flavonoids, cyanogenic glycosides, tannins, phenolic acids, and quinones; all of these have repressive activities, and most cause various biological effects (Weir et al., 2004).

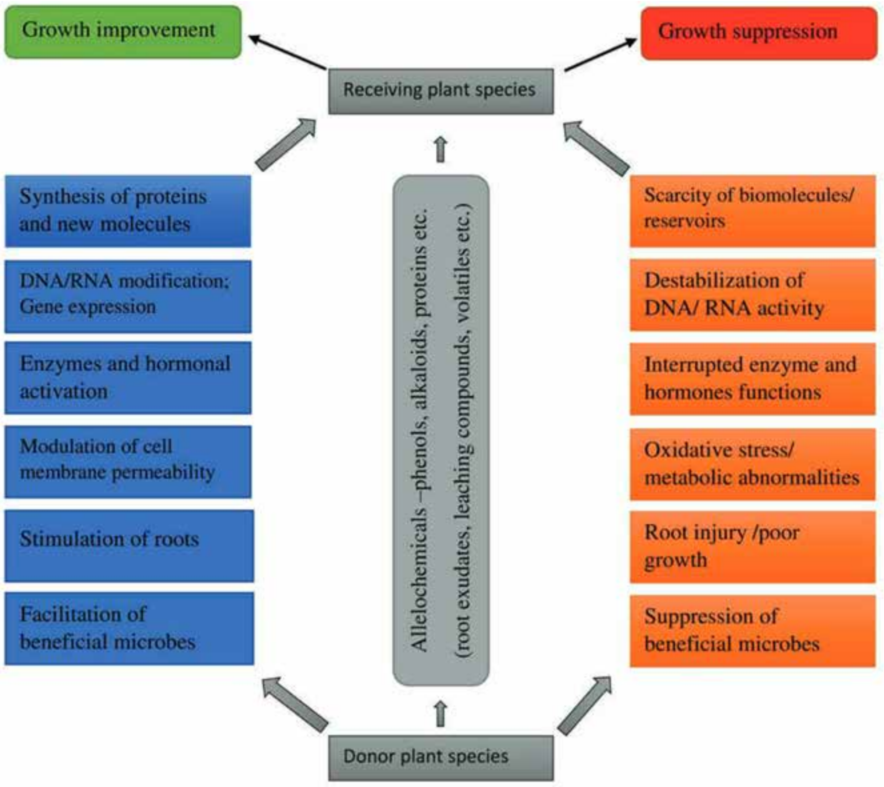

Fig. 3. Mechanism of action of allelochemicals that can influence receptor plants harmfully or beneficially

The suppressive actions of most of the *Artemisia* spp. foliar extracts appear to contain a variety of chemicals, including terpenoids, polyacetylenes, and coumarins (Weston & Duke, 2003). Sesquiterpenes are a broad family of naturally occurring chemical compounds that are represented by several physiologically active molecules, including those with intriguing herbicidal potential. Other studies have shown that trichomes on the leaf surface generate substantial amounts of camphene, cineole, and camphor, as well as considerable amounts of artemether and artemisinin, among other compounds, with camphor proving to be the most effective in seed suppression, i.e., inhibition of seed growth (Barney & Weston, 2002). A sesquiterpene endoperoxide lactone known as artemisinin, separated from *Artemisia* species, was originally found to have phytotoxic action. Artemisinin has the greatest impact on chlorophyll content and root network development (Duke et al., 2000). In the meristem of wheat root tips, Romagni discovered that monoterpenes such as 1,8-cineole impede the respiration of mitochondria and substantially inhibit all phases of mitosis. Camphor possesses mitotic and respiration effects comparable to those of 1,8-cineole (Romagni, 2000).

Amylase activity regulates the breakdown of starch and is necessary for providing substrates for respiratory metabolism, which in turn affects the germination of cereals. The leachates of *Eucalyptus globosus* leaf inhibited germination by decreasing amylase activity in finger millet (*Eleusine coracanta*) seeds (Padhy et al., 2000). Comparable results were achieved with *Lepidium sativum* seeds due to the presence of MBOA (6-methoxy-2-benzoxazolinone), which is widely found in cereals (Kato-Naguchi & Macias, 2004).

Mobilization of lipids was inhibited in the presence of *p*-coumaric and ferulic acids, while the seeds of *Brassica napus* and *Helianthus annus* were germinated in the presence of *Datura stramonium* (Baleroni et al., 2000). Allelopathic chemicals affected isocitrate lyase activity and the expression of the isocitrate lyase gene. Thus, isocitrate lyase seems to be a highly sensitive enzyme in response to allelopathic pressure, and its reduced performance may cause the retardation of seed germination or delay. Furthermore, it has been proposed that the observed reduction in enzyme activity is a side effect of allelochemicals, which damage proteins. As a result, allelochemicals' impacts on seed germination are mediated by disturbances in basic cellular metabolism rather than by organelle destruction. Reserve mobilization, which normally occurs rapidly during the early phases of seed germination, appears to be slowed or reduced under allelopathic stress (Weir et al., 2004).

Disruption of photosynthesis is among the most frequently documented physiological consequences of several allelochemicals. Allelopathic chemicals have the potential to be widely employed in organic agriculture, for example, as natural herbicides in sustainable weed control (Gniazdowska & Bogatek, 2005). In *Lactuca sativa* treated with artemisinin and its sesquiterpene, the amount of chlorophyll was reduced, and the quantity of carotenoid was also reduced (Dayan et al., 1999). When exposed to *Helianthus annuus* allelochemicals, leaves of *Sinapis alba* exhibited lower photosynthetic rate. However, it coincided with a decreased transpiration rate, suggesting restricted CO_2 absorption in the chloroplasts owing to stomatal closure (Bernat et al., 2004). The proposed reason for the interruption of bine growth under allelopathic stress is a change in mitochondrial respiration, leading to a lower ATP supply for all energy-dependent activities. Coumarin decreased the pace at which mitochondria in *Allium cepa* root cells respired; monoterpenes are the allelochemicals that reduce the respiration of mitochondria by enhancing the rate of electron transport via an alternate pathway. Cinnamic acid and pinene similarly reduced oxygen consumption in *Glycine max* cotyledons while increasing the relative splitting of electrons toward the alternate route (Cheng & Cheng, 2015).

The monoterpenes inhibited mitochondrial respiration in *Zea mays* main roots, resulting in complete inhibition of respiratory regulation. It was proposed that such chemicals may operate as oxidative phosphorylation uncouplers. The capacity of allelochemicals, such as monoterpenes, hydroxamic acids, and coumarins, to permeate plant tissue may be responsible for their inhibitory influence on O_2 uptake (Abrahim, 2000). The hydroxamic acid can also influence gene expression and chromatin modification in target plants by inhibiting histone deacetylases (Venturelli et al., 2015). The *Helianthus annuus* leaf extract impeded seed germination of *Sinapis alba* (Bogatek et al., 2006), thereby reducing the respiration rate of seeds during the initial three days of seedling development. This demonstrates a connection between dark respiration suppression and germination delay when allelopathic substances are present (Gniazdowska & Bogatek, 2005).

Seedling growth inhibition under allelopathy stress circumstances may therefore be due to reduced ion uptake. The impact of allelochemicals on onion uptake is crucial, as the root is the rhizosphere organ that initially comes into contact with them. *Cucumis sativus* root discharge reduced ion uptake by cucumber seedlings (NO_3^-, K^+, Ca^{2+}, Mg^{2+}, Fe^{2+}) (Mushtaq, 2020). Salicylic acid, a phenolic compound, has been shown to inhibit potassium absorption in plants. Both salicylic acid and ferulic acid inhibited K+ absorption by the roots of oats, especially when the pH is lower. Various additional investigations using entire plants and cell cultures have found that the absorption of macro- and micronutrients is decreased when phenolic acids are present (Sahu, 2013).

Phenolic acid inhibits the absorption of NO_3^-, K^+, PO_4^{3-}, and Mg^{+2} ions, and altered mineral ion uptake affects plant growth and development. (Einhellig et al. 2002). Vanillic and p-coumaric acids were more harmful when the seedlings of barley were low in phosphorus or nitrogen. They determined that the toxicity of phenolic compounds depends upon the nutritional quantities. As a result, the impact of allelochemicals on anion absorption may be due to a lowered respiration rate and an inadequate quantity of adenosine triphosphate generated in cells of roots (Gniazdowska & Bogatek, 2005). Terpenoids are known to be emitted from plants in drought-stricken areas. Volatile organic compounds have been found to have dual effects on germination and plant growth, both promoting and inhibiting. Volatile allelochemicals may impede the competitiveness of weed species and have piqued public interest (Xie et al., 2021).

Many secondary metabolites, such as terpenoids, flavonoids, phenolic compounds, and alkaloids, operate as plant allelochemicals. In natural and agroecosystems, these phenolic acids are recognized as allelopathic agents. They have been observed to affect seed germination, chlorophyll content, respiratory activity, seedling growth, enzyme activity, and cell division. However, there is little information on how phenols and other substances interact and alter seed germination and seedling growth; evidence suggests that combining phenols enhances their degrading activity. It is phytotoxic to various weedy plants and can be used as both a pre- and post-emergent herbicide (Bachheti et al., 2020). Allelopathy's most frequent phenolic chemicals include benzoic and cinnamic acid derivatives, coumarins, tannins, other polyphenolic complexes, and some flavonoids. The amount of these chemicals produced and released by plants varies greatly. The various coumarins, tannins, and phenolic acids appear to have identical modes of action, limiting plant development through a variety of physiological effects that impart broad cytotoxicity (Macias et al., 2004). The mechanisms of action of flavonoids are less understood than those of phenolic acid. Some flavonoids powerfully regulate energy metabolism and inhibit chloroplast and mitochondrial processes (Mierziak et al., 2014). Generally, the phenolic acid concentration necessary to impede seed germination is larger than that required to prevent growth in plant seedlings (Einhellig, 2002). A reduction in photosynthetic efficiency is a persistent side effect of phenolics. Sorgoleone, a p-benzoquinone, was found to block oxygen evolution in leaf discs and isolated chloroplasts, leading to decreased growth and photosystem II electron transport (Zhou & Yu, 2006).

Bioassays in allelopathy

The initial step for investigating probable allelopathic involvement is a laboratory bioassay. Bioassays are valuable tools for assessing the allelopathic potential of plant extracts and for monitoring their activity during the purification and identification of allelochemicals. Most allelopathic papers describe some form of bioassay procedure to demonstrate allelopathic activity (Macias et al., 2000). Bioassays for this type of study often involve tests of seed germination and growth, seedling, radicle, and coleoptile length, seedling fresh weight, and photosynthetic activity under controlled laboratory conditions. These tests can detect potential allelopathic effects (Gawronska et al., 2006). Although bioassays using plant aqueous extracts are valuable for demonstrating the presence of allelopathic chemicals in plants, these effects often disappear in the field due to adsorption onto soil particles, degradation, and leaching. Screening bioassays using entire plant seedlings have been developed in response to complaints about aqueous extract bioassays. Allelopathy research has employed plants at the seedling stage (Wu et al., 2000). The biosynthetic pathways of the major allelopathic substances are shown in **Fig. 4**.

Role of allelopathy in agriculture

In India's agroecosystems, weeds are predicted to cause a 13.2% loss in the eight most important cash crops worldwide. To manage weeds, hand weeding, like mechanical approaches, is used, which takes a lot of effort and time. At the same time, excessive herbicide use can lead to environmental contamination, hazardous agricultural products, and a risk to human health (Kordali et al., 2009).

Allelopathy is crucial in agriculture, resulting in diverse interactions among Crop–Weed, Crop–Crop, and Tree–Crop systems (Singh et al., 2001). Some plants hinder weed growth. They are an

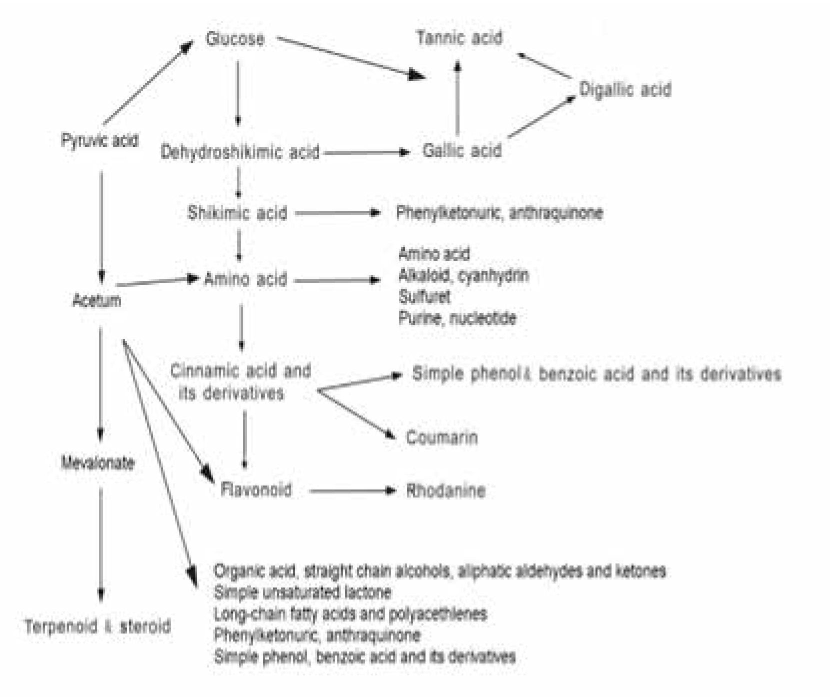

Fig. 4. Biosynthetic pathways of the major allelopathic substances (Seigler, 2006)

excellent, strategic source of natural compounds for developing natural herbicides. Plant allelopathic properties can be efficiently used for biological weed management in agricultural production (Vashishth et al., 2023). The allelochemicals in these plants can be the same or distinct, and when combined, they may have synergistic or additive effects. Allelopathic crops can be used to influence weeds in a variety of ways, including surface mulching (Cheema et al., 2000), spraying of aqueous extract (Cheema et al., 2002), blending with the soil (Sati et al., 2004), and intercropping and mixed cropping (Hatcher & Melander, 2003).

A number of papers have been published on screening plants for allelopathic potential in ecosystems. *Grewia optiva, Acacia* spp., *Eucalyptus* spp., *Albizzia lebbeck, Glircidia sepium, Moringa oleifera, Leucaena leucocephala*, and *Populus deltoides* are examples of tree species that affect crop production through allelopathy (Singh et al., 2001). The variety of weeds, particularly those in agroecosystems, is also known to exhibit allelopathic traits that increase their competitiveness and, consequently, negatively impact crops (Weston & Duke, 2003).

Allelopathic effect of crop plants on other crop plants and weeds

The majority of research has focused on the impact of cover crops on weed control, and crop growth research has focused on legumes or winter cereals (Dhima et al., 2006). The extract of the root, seed, seed coat, and aerial parts of *Arachis hypogaea* can hinder the development of rootlets and hypocotyls and the germination of seeds of *Lactuca sativa.* The separation of ethanol-based seed extract into dichloromethane, n-hexane, butanol, ethyl acetate, and aqueous residue also exhibits positive allelopathic potential. In some large-scale crops, the dichloromethane fraction of ethanolic seed extract can be used as an eco-friendly herbicide to control weeds (Casimiro et al., 2017). The effective field treatment of purple nutsedge using plant extracts from a variety of allelopathic crops (Sorghum, Brassica, and Sunflower) was reported by Iqbal and Cheema (2007). The *Brassica* spp. water-based extracts significantly inhibited *Physalis angulata,* a troublesome weed in Turkey's cotton, maize, and soybean fields (Uremis et al., 2005). Sorghum mulches dramatically decreased the dry biomass and density of *Cyperus rotundus*, one of the worst weeds in the world (Mahmood & Cheema, 2004), and an alfalfa aqueous extract inhibited the germination and seedling growth of *Lepidium sativum* (El-Darier & Youssef, 2000). The findings indicated that alfalfa pellets effectively prevented the development of rice weeds, suggesting that they could be used as a natural pesticide in rice fields (Xuan & Tsuzuki, 2001). The leaves, roots, and stems extract of *Coriandrum sativum* at the flowering and maturity stage was applied in Petri plates on seeds of *Triticum aestivum*, and some weeds (like *Lolium multiflorum*, *Sinapis alba*, and *Amaranthus retroflexus*), and the leaves extract showed more allelopathic activity, followed by stem and root extracts, but only on weeds seeds and not on *T. aestivum* seeds. Also, the extract of mature *C. sativum* was less allelopathic than the one obtained from the flowering stage (Pannacci et al., 2025)

Allelopathic effect of weeds on crop plants and other weeds

Seed germination and plant growth of *T. aestivum, Cucumis sativus,* and *Sinapis arvensis* were tested when treated with different concentrations (5%, 10%, 15%, and 20%) of the aqueous extract of *Euphorbia heterotophylla*. It was reported that the germination percentage of *Sinapis arvensis* and *T. aestivum* was reduced. At the 20% concentration, *Sinapis arvensis* showed the highest inhibition, i.e., approximately 44.44%, whereas at the 5% concentration, germination in *Cucumis sativus* seeds was stimulated and did not affect 10%, 15%, or 20%. In the case of growth, the peduncle length of *T. aestivum* was inhibited at all concentrations, the peduncle length of *Sinapis arvensis* was inhibited only at 15% and 20% and was stimulated at 5% and 10%, and the peduncle length of *Cucumis sativus* showed stimulation at all concentrations, with the highest stimulation noted at 10%, i.e., 66.90%. While the growth of rootlets at 5% concentration *of T. aestivum* and *Sinapis arvensis* showed stimulation, while inhibition at all other concentrations, and rootlets of *Cucumis sativus* showed inhibition at all concentrations, the highest inhibition was noted in *T. aestivum* at 20% concentration, i.e., 44.71% (Fandah et al., 2020). The allelopathic and antioxidant activities of *Euphorbia heterophylla* against the weed *Cenchrus echinatus* were investigated, and it was found that shoot growth was reduced by approximately 57.8%, root growth by 84.6%, and germination by 93.95% at a concentration of 100 µL/L of the essential oils. Hence, essential oils from *Euphorbia heterophylla* can be used as a biocontrol agent against the weed (Elshamy et al., 2019).

On the other hand*, Lactuca sativa* and *Sorghum bicolor* are indicator plants whose root and shoot growth at the early seedling stage are inhibited by 100% with the methanol extract of *Euphorbia heterophylla* at 2.0 mg mL/L. GC–MS analysis is performed using methanol-derivatized extraction, yielding the first study of the roots of *Euphorbia heterophylla* in a series of allelopathy interactions and the metabolic activity of their organic acids (da Silva et al., 2018). The allelopathic effect of *Euphorbia hirta* and *Parthenium hysterophorus* leaf extract on seed germination and seed elongation of *Capsicum annum*. They treated the seeds of *Capsicum annum* with different concentrations (25, 50, 75, and 100%) and found that an increase in the concentration of plant extract of *Euphorbia hirta* showed a stimulatory impact on germination of seed and seedling elongation of *Capsicum annum,* and a fresh and dry weight of seeds showed a positive allelopathic effect. Similarly, the plant extract of *Parthenium hysterophorus* also shows a stimulatory effect on the weight, both fresh and dried seeds of *Capsicum annum* (Pathare et al., 2014). The allelopathic effects of the parts of *Euphorbia thiamifolia* on seedling growth and pigeon pea germination were studied. The inflorescence, root, stem, and leaf parts of *Euphorbia thiamifolia* are extracted in water, and research is performed to comprehend the impact of this extract on the dry weight of the shoot and plant germination after 4 days, and the root length of *Cajanus cajan* over a range of different concentration levels. Seeding growth and pigeon pea seed germination are relatively l*ower* in all aqueous extractions compared with the standard distilled water control; also, these factors are significantly affected by extract concentration, as growth is lower at higher concentrations. During the study, it was also demonstrated that seedling length and weight, and pigeon pea germination, are more inhibited by Euphorbia thiamifolia aqueous extract from stems than from leaves. The root of *Euphorbia thiamifolia* on the 6th day has *a* relatively lower effect on growth than the leaf and inflorescence parts of the weeds (Kumbhar et al., 2011).

An enhanced concentration of leachate of *Euphorbia hierosolymitana* caused a substantial decrease in the length of the roots and shoots, the dry and fresh weight of wheat (*Triticum durum*) seedlings, and a decrease in total protein and chlorophyll content (Abu-Romman et al., 2010). Furthermore, the herbicidal activity of *Peganum harmala* residue on seedling growth of *Avena fatua* and *Convolvulus arvensis*, as well as the tendency of its phytotoxins to degrade in soil, was investigated. They also found that *C. arvensis* showed greater declines in plant growth metrics, and *that P. harmala* residue exhibited strong herbicidal activity and could be used as a natural pesticide for weed control (Sodaeizadeh et al., 2010).

The aqueous extract derived from *Lantana camara* was observed to promote the growth of *Cucumis sativus, Brassica juncea, Raphanus sativus, Phaseolus mungo, Cicer arietinum,* and *Vigna unguiculata*. The inhibitory effect on germination, root, and shoot length was reported because of aqueous leaf extracts of *L. camara*. This was proportional to the extract concentrations, with higher concentrations having stronger inhibitory effects and lower concentrations having a stimulatory effect in some circumstances. The inhibitory impact is significantly stronger on primary and lateral root growth than on shoot and germination development (Ahmed et al., 2007). Using a Lemna (*Lemna aequinoctialis*) bioassay, Allan and Adkins (2007) examined the ability of allelochemicals from medicinal herbs to inhibit plant growth. The aqueous extracts from plant components of *Acacia farnesiana, Acacia melanoxylon, Ageratum conyzoides, Castanospermum australe, Chamaesyce hyssopifolia, Alphitonia excelsa, Melaleuca quinquenervia*, and *Phyllanthus virgatus* hindered the growth of *L. aequinoctialis*, in which leaf, stem, and bark extracts inhibited the most growth. The water extract of *Cirsium arvense* and *Ageratum conyzoides* can decrease the germination and growth of seedlings of various weeds associated with wheat (Akhtar et al., 2001).

Allelopathic effect of common plants on crop plants and weeds

However, little is known about the allelopathic effects of therapeutic and aromatic herbs on weeds, crop germination, and seedling growth (Qasem, 2002). Allelopathic medicinal and aromatic plants have recently been proposed as feasible solutions for managing weeds in sustainable agriculture (Mekky, 2008). The compounds derived from medicinal or aromatic plant residue may aid in the reduction of the use of synthetic herbicides for the control of weeds, resulting in lesser pollution and better agricultural services (Khanh et al. 2007). The effects of aromatic plants on crops and weeds, whether employed as cover crops, absorbed into the soil as green manure, used in the soil as mulch, or used as an aqueous extract, are sparse in the literature.

The ethanolic extracts of *Tephrosia purpurea*, *Prosopis juliflora, Abutilon indicum*, and *Cassia occidentalis* were tested for their potential bioherbicidal activities on *Parthenium hysterophorus,* and it was reported that *Prosopis juliflora* and *Cassia occidentalis* had stronger phytotoxic activity than *Tephrosia purpurea* and *Abutilon indicum*. However, all four plants had phytotoxic properties and can act as natural biodegradable herbicides against weeds such as *Parthenium hysterophorus* (Andhare, 2019). The wheat yield is adversely affected by allelopathic interactions; hence, Shah et al. (2018) suggested that wheat should not be sown near *Quercus coccifera, Moringa oleifera, Prosopis juliflora, Eucalyptus camaldulensis, Acacia nilotica*, and *Acacia salinga* to prevent destructive effects on various developmental stages of the crop. The effect of six aromatic and therapeutic plants, basil (*Ocimum basilicum*), chamomile (*Matricaria chamomilla*), common mallow (*Malva sylvestris*), greater celandine (*Chelidonium majus*), lemon balm (*Melissa officinalis*), and lovage (*Levisticum officinale Koch*), on the germination and growth of the scentless mayweed (*Tripleurospermum inodorum Schultz*). Weed seed germination was reduced by 32.2% when lovage seeds were used in Petri dishes. Extracts from fresh plant biomass inhibited weed germination and development at 5% and 10% concentrations, with extracts from chamomile and common mallow having the greatest inhibitory effect. The inhibitory impact of extracts from dry plant biomass was greater. Weed seed emergence and growth were reduced when dried plant wastes were introduced into the soil at rates of 10 and 20 g/kg. The greatest allelopathic impact was observed with lovage and higher celandine residues (Baličević et al., 2015). The allelopathic effect of extracts of roots and leaves of donor species (*Lonicera maackii, Ranunculus ficaria,* and *Alliaria petiolata*) on recipient species (*Elymus hystrix, Anemone virginiana, and Blephilia hirsuta*) was studied, and it was found that leaf extracts had more germination inhibition than root extracts and that increasing the concentration of extract also increased the effects. The leaf extract of *Alliaria petiolata* had the highest inhibition of germination. *Lonicera maackii* and *Ranunculus ficaria* extracts reduced the germination of *Anemone virginiana* and *Blephilia hirsute,* while *Lonicera maackii* and *Ranunculus ficaria* leaf and root extracts had minimal impact on *Elymus hystrix* (Cipollini et al., 2013).

The seed germination and seedling growth of *Avena fatua, Phalaris minor, Rumex dentated, and Amaranthus retroflexu* is hindered by the allelopathic activity of methanolic extracts of *Ocimum basilicum, Artemisia annua, and Eucalyptus globulus* (Mekky et al., 2008). The essential oil isolated from sweet basil and oregano populations inhibited barnyard grass and common lamb's quarters' germination and root development (Vasilakoglou et al., 2007). These results implied that aromatic plants capable of producing phytotoxic essential oils may be important for controlling weeds in sustainable agricultural systems, whether applied as green manure or as mulch (Dhima et al., 2009). The acetone extracts (n-hexane soluble fraction, acetone soluble fraction, and water soluble fraction) of the shoot of *Azadirachta indica* prevented the germination and development of roots and shoots of *Digitaria sanguinalis, Cirsium arvense, Amaranthus rotundus, Lactuca sativa, Sinapis arvensis,* and *Lolium ultiforum*. The water-soluble fractions had the highest inhibitory activity in all bioassays. As the extract concentration increased, germination and root and hypocotyl growth were significantly reduced. Allelochemicals may be present in all three fractions, based on the test plants' concentration-dependent responses, with the water-soluble fraction showing the most promise. These findings suggested that *Azadirachta indica* residue or aqueous extract might effectively control weeds (Ashrafi et al., 2009).

The phenolic chemicals found in the fruits of *Artemisia herba-alba* have the capacity to hinder the seedling growth and germination of *Anabasis setifera* (Modallal & Al-Charchafchi, 2006). The *Azadirachta indica* (Neem) severely suppresses the development and germination of numerous crops, including bean (*Vigna angularis*), alfalfa (*Medicago sativa*), radish (*Raphanus sativus*), carrot (*Daucus carota*), sesame (*Sesamum indicum)*, and rice (*Oryza sativa*). The aqueous extract of *Eucalyptus camaldulensis* could inhibit the development of *Echinochloa crusgalli, Rumex acetosella,* and *Avena fatua* (Moradshahi et al., 2003). Similarly, in a bioassay experiment, Assaeed (2003) found that the water extract of *Artemisia monosperma* leaves and flowers reduced seed germination of some plant species from sandy areas, including *Pennisetum divisum, Lasiurus scindicus, Scrophularia hypericifolia,* and *Plantago boissieri*. The aqueous-acetone extract of *Melissa officinalis* decreased the germination and growth of seeds and seedlings in *Lepidium sativum, Amaranthus caudatus, Phleum pratense, Digitaria sanguinalis, Lolium multiflorum,* and *Lactuca sativa*. It was stated that the efficiency of the extract on the roots is larger than that on the shoots of the test plants and that the inhibitory effect is proportional to the extract concentration (Kato-Noguchi, 2001). An aqueous extract of *Artemisia herba-alba* had an inhibitory impact on the germination percentage of seeds of *Helianthemum squamatum* Escudero et al. (2000). Such inhibitors significantly slow or impair the development, production, and physiology of the agricultural plants linked with them (El-Darier & Youssef, 2007).

Interaction of allelochemicals in the ecosystem

Several aspects, such as the physicochemical and physiological transformations of volatile organic compounds and water-soluble phytochemicals into the soil matrix, necessitate more innovative experimental approaches. Reference models are also needed to understand how plants naturally interact with their biotic and abiotic surroundings across various ecosystems, including crop ecosystems. Conventionally, the hunt for novel herbicides with several modes of action and little risk of resistance development is part of the strategy to leverage these powerful synergies for comprehensive weed control (i.e., crop rotation, intercropping, green manuring, or using plant residue) (Serino et al., 2021).

The fate of allelochemicals in nature and the complexity of the multiple and multiscale interactions can be explained using the example of the study of Pardo-Muras (2022), in which the efficiency of *Cytisus scoparius* leaf in controlling weeds, and likely that of other allelopathic plants, depends on intricate, many synergistic interactions involving soil-preferred volatile and water-soluble allelochemicals. The allelopathic activity of *Artemisia* species varied with extract concentration. With an increase in extract concentration in the soils, both the chlorophyll content and biomass production rapidly decreased. Soil obtained beneath plants of various *Artemisia genera* or from contaminated areas (the area around the treated area) inhibited the growth and germination of a range of test species. The allelopathic activities of *Artemisia* spp. have been related to the phenolic compounds and a few flavonoids found in aqueous preparations (Kong et al., 1999).

Several published studies show varying levels of organic carbon, fertility, and nutrient content across vegetation diversity (Adiputra, 2022). Complex agroforests increase soil organic carbon (Saputra et al., 2020), while Matos et al. (2020) reported that litter quality supports soil restoration. According to the findings, soil fertility and organic carbon levels increase with plant population diversity. The interaction of allelochemicals and both inorganic and biological materials between plants and the soil environment is a complex process (**Fig. 5**).

Herbicides are harmful to plants and soil quality because of their direct action on the soil surface. Allelopathy in the sorghum crop significantly impacted weeds and improved soil quality. Ullah et al. (2022) observed that the water extract of sorghum residue can suppress weed growth. Implementing sorghum residue may improve weed control, soil health, and seed yield of spring-planted mung beans. Future research should concentrate on how micronutrients interact with one another in the soil environment when using various allelopathic weed control methods in the working environment. Furthermore, there are yet problems with managing weeds using different allelopathic techniques and with monitoring the allelopathic relationship between the treated crop and crop leftovers.

Conclusion and Future Aspects

In conclusion, this review sheds light on the complex world of allelopathy, in which plants communicate with their neighbours via allelochemicals to influence them. The complex interplay between allelopathy and crop plants and weeds underscores its promise as a natural tool for sustainable weed management and increased crop output. Furthermore, the destiny of allelochemicals in soil highlights the complexities of allelopathic interactions in ecosystems. This review gives an in-depth look into allelopathy's potential to influence future agricultural practices and ecosystem management. Further avenues of study emerge

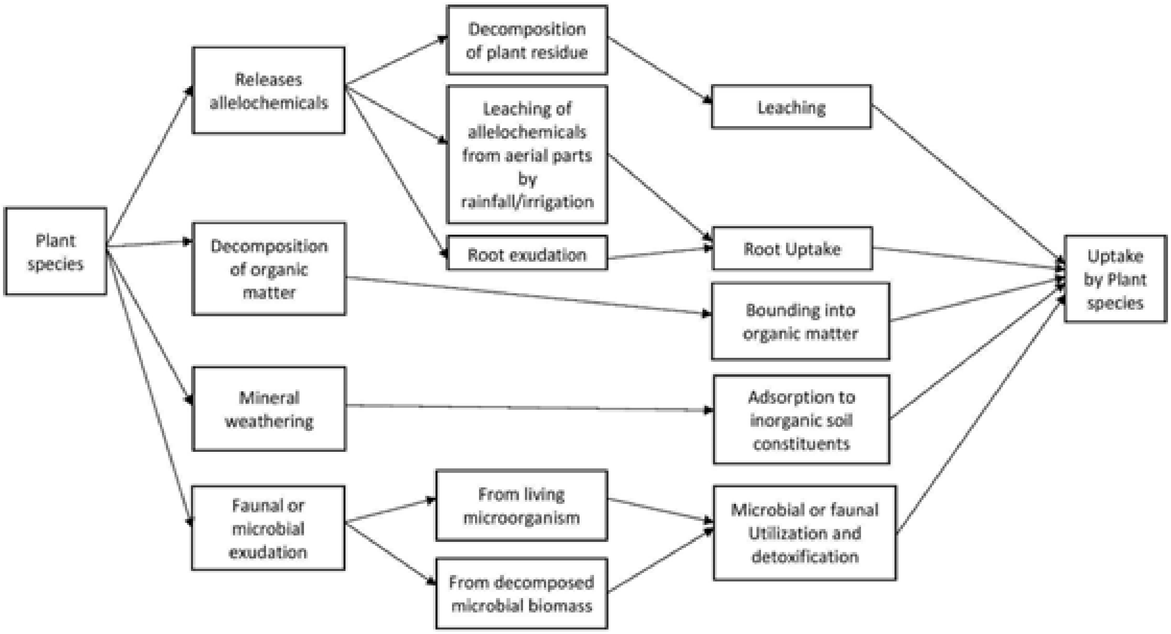

Fig. 5. Cycle of allelochemicals, organic and inorganic matter between soil and plant species (Scavo et al., 2022)

from this review. Mechanistic research could delve deeper into the specific molecular mechanisms by which allelochemicals affect plant physiology and signalling. Understanding the genetic basis of allelopathy, as well as the potential to develop crop varieties with improved allelopathic traits, could revolutionise weed management tactics. Exploring the ecological dynamics of allelopathy across various contexts, as well as its interactions with other factors such as climate change and soil health, offers significant potential. Using modern approaches such as metabolomics and molecular profiling could yield new insights into allelochemical diversity and relationships. Finally, as knowledge progresses, the potential for allelopathy to revolutionise agricultural practices, improve weed management, and contribute to ecological sustainability remains a viable route for future research and innovation.

Acknowledgments: The author wishes to thank Santosh Arya, Shiv Kishore, and Manoj Singh for their support.

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