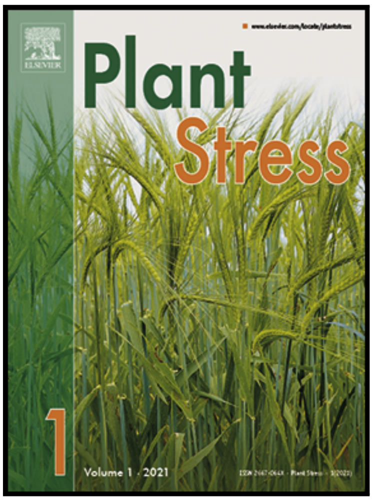

Phenolic profiling unravelling allelopathic encounters in agroecology

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Highlights

- Phenolic compound's structure impacts their availability and activity in the soil
- Phenolic allelochemicals interact with plant roots, hindering nutrient uptake by altering the plasma membrane gradient
- Phenolic allelochemicals influence plant succession by shaping plant communities
- Phenolic mixtures can show synergistic and additive effects of weed growth inhibition
- Phenolic allelochemicals enhance plant resilience to environmental stresses

Phenolic profiling unravelling allelopathic encounters in agroecology

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Abstract

Allelopathy, a biological phenomenon involving the production and release of secondary metabolites known as allelochemicals, plays a critical role in plant interactions and agroecosystem dynamics. Phenolic compounds are a significant class of allelochemicals that profoundly affect plant competition, soil health, and microbial communities. When released into the soil, their action depends on the soil's physico-chemical characteristics and microbial communities. This review comprehensively inspects phenolic allelochemicals' structure-function relationship, their direct combat with root cells in the rhizosphere, ecological functions, and their role in plant succession and stress tolerance. Phenolic allelochemicals, characterized by their diverse structures and ecological roles, offer a sustainable alternative to synthetic herbicides due to their minimal residual impact on the environment and rapid biodegradation. Additionally, the review addresses the challenges and future directions in applying phenolic allelochemicals, aiming to bridge the gap between ecological theory and practical agricultural applications for environmental protection and crop productivity enhancement.

Keywords: allelopathy; agroecosystem; bioherbicide; phenolic compounds; rhizosphere; stress

Abstract

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1. Introduction

Although the fundamental concepts of allelopathy were known to the ancient Greeks, Romans, Chinese, and Japanese, an Austrian botanist named Molisch first defined the term and identified its traits in 1937 (Mushtaq *et al.*, 2020a). Initially perceived as a process causing 'harmful' effects from one plant's (donor) chemical release on another plant (recipient), our understanding of allelopathy has evolved. It is now recognized as a complex mechanism triggering both beneficial (positive) and harmful (negative) interactions between plants and between plants and microorganisms or animals (Muhammad *et al.*, 2019; Mushtaq *et al.*, 2024). The allelopathic effects of one plant on another may come to the forefront either in succession or simultaneously alongside autotoxicity (Xie *et al.*, 2019). The mechanism behind allelopathy is multifaceted, with plants producing a wide array of organic compounds that play active roles in plant defences against diseases, pests, herbivores, and environmental stresses (Ain *et al.*, 2023). Among the myriads of compounds involved, phenolic allelochemicals stand out for their profound influence on the rhizosphere - the nexus of plant-soil-microbe interactions.

Phenolic compounds, including phenolic acids and flavonoids, are among the most studied groups of allelopathic activity (Hoang *et al*. 2021). These compounds are crucial in shaping plant community dynamics through their complex interactions with soil and microbial communities. Phenolic allelochemicals influence plant competition by inhibiting the growth of rival species, thereby affecting plant succession (Kumar *et al*., 2024). Recent studies have shown that phenolic compounds contribute more to the variation in understory plants than soil factors (Gavinet *et al*., 2019; Li *et al*., 2023). They play a vital role in soil health by impacting microbial communities and nutrient cycling (van der Heijden, 2015; Misra *et al*., 2023). Moreover, these compounds contribute significantly to plant stress tolerance, enabling plants to endure abiotic stresses such as drought and salinity (Tak and Kumar, 2020; Kiely *et al.*, 2023),

From a practical perspective, phenolic allelochemicals present promising alternatives to synthetic herbicides. Their natural origin, rapid biodegradation, and minimal residual impact on the environment make them ideal candidates for sustainable weed management. However, challenges such as variability in effectiveness and complex soil interactions must be addressed to optimize their application. While significant progress has been made in understanding the ecological implications of phenolic compounds, there remains a need for a comprehensive and up-to-date review that addresses their diversity and specific roles in rhizosphere interactions. Through this detailed review, we endeavour to bridge the gap in our understanding between the ecological importance and practical benefits of phenolic allelochemicals in agroecosystems. The ecological importance of phenolic allelochemicals is closely tied to their diversity and structure-function relationships, which will be discussed in the next section. Furthermore, we will explore the dynamic interactions of these compounds within the rhizosphere and understand the mechanisms involved, highlighting the complex interplay between plant roots, soil properties, and microbial communities. Finally, the review will discuss the inferences of phenolic allelochemicals in succession, their role in stress tolerance in plants and their potential for enhancing sustainable agricultural practices through allelopathy management.

2. Phenolic allelochemicals diversity in relation to structure-function relationship

Many classes of allelochemicals from a variety of plant species have already been studied and identified. These allelochemicals come in a wide variety of chemical forms, including alkaloids and nitrogen-containing chemicals (benzoxazinoids, cyanogenic glycosides), terpenoids (monoterpenes, sesquiterpenes, diterpenes, triterpenes, and steroids), phenolic compounds, and many other chemical families (Kostina-Bednarz *et al*., 2023). Phenolic compounds are characterized by a hydroxyl group (-OH) that bonds to an aromatic hydrocarbon group (Pompeu *et al*., 2018). More than 8,000 phenolic structures are currently known, ranging from simple molecules to highly polymerized substances (Dai and Russell Mumper, 2010). Phenolic profiling of agroecosystems involves both living and dead plants. Living allelopathic plants can produce and release a variety of phenolic allelochemicals including simple phenolics, flavonoids, coumarins, and quinones, however, phenolic allelochemicals from dead plants or crop cover mainly are lignin-related phenolic acids (Xu et al., 2023).

Phenolics are diverse compounds with varying structures within the same species. Different phenolic allelochemicals may have variations in the number and arrangement of phenol rings, as well as substitutions on the aromatic ring. This diversity results in a range of products, including simple aromatic phenols, hydroxy and substituted benzoic acids, aldehydes, hydroxy and substituted cinnamic acids, tannins, coumarins, and flavonoids (Roleira *et al.*, 2018). Phenolic allelochemicals like caffeic acid, vanillic acid, protocatechuic acid, *p*-hydroxybenzoic acid, syringic acid (benzoic acid derivatives), *p*-coumaric acid, ferulic acid (cinnamic acid derivatives) and sinapic acid have been largely determined in the rhizosphere soil (Hu *et al*., 2018. Kumar and Goel, 2019; Wilhelm *et al.,* 2021). The biological activity of phenolic compounds is closely related to their chemical structure, with different functional groups and substitutions affecting their allelopathic potential (Ladhari *et al*., 2020). For example, the presence and position of functional groups such as hydroxyl, methoxy, and carboxyl groups can significantly affect the compound's bioavailability and toxicity (Scavo and Mauromicale, 2021). The molecular weight, degree of polymerization, and aromaticity of phenolic compounds influence their interactions with target organisms and their mode of action (Mushtaq and Mehdizade, 2020; Avila-Roman *et al.*, 2021). For example, some phenolic compounds have been found to inhibit plant root elongation and cell division, while others can change cell ultrastructure and interfere with normal plant growth and development (Li *et al*., 2010).

Once in the soil, the phenolic compounds may exert their influence on the recipient plant either directly or the effect may be modified by biotic and abiotic factors (Scavo *et al*., 2019) as shown in **Fig. 1.** Hoang *et al*. (2021) have given a detailed classification of phenolic allelochemicals. **Table 1** presents a structured table that categorizes phenolic allelochemicals found in the soil rhizosphere according to their forms: free, reversibly bound, and bound. These first two forms are significant in the context of allelopathy, as they determine the availability and activity of phenolic allelochemicals in the soil rhizosphere. However, some phenolic acids like ferulic acid, can exist in more than one form. This is due to the presence and position of functional groups such as hydroxyl, methoxy, and carboxyl groups on their molecular structure. These groups can undergo hydrolysis under certain environmental conditions (such as changes in soil pH or microbial action), affecting the compound's bioavailability and reactivity. **Fig. 2** displays the typical structures of phenolic allelochemicals. To fully appreciate their ecological impact, it is crucial to understand the underlying mechanisms through which phenolic allelochemicals exert their effects.

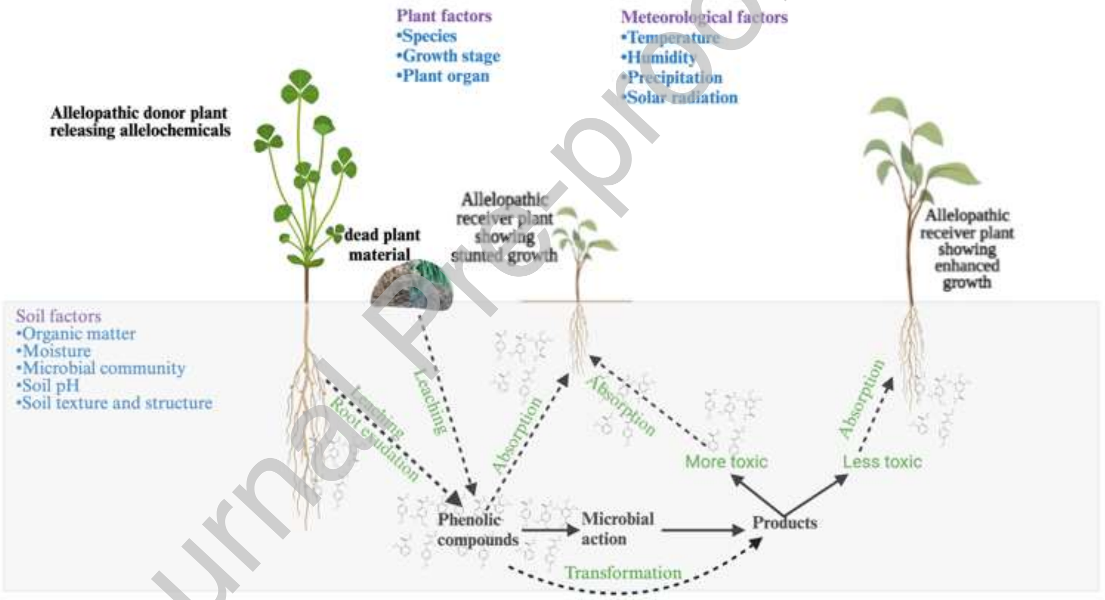

Figure 1. *Interactions of Phenolic Compounds in Soil*

The fate and effects of phenolic compounds in soil are influenced by a complex interplay of biotic and abiotic factors. They exhibit a multifaceted impact on recipient plants within the soil ecosystem.

Table 1: Comparative analysis of phenolic allelochemicals in soil

Form	**description**	**relevance to allelopathy**	**Phenolic class**	**Phenolic Compound(s)**	**Allelopathic Effect**	**References**
Free	Phenolic compounds that are dissolved in the soil solution and readily available for plant uptake or microbial degradation or be modified by biotic/abiotic factors.	Directly involved in allelopathic interactions, can influence plant growth and development.	Benzoic Acids and derivatives	*p*-coumaric acid	inhibit the growth of seedlings and change rhizosphere soil microbial communities	Zhou and Wu, 2012
				vanillic acid	Inhibits root and shoot growth and can alter the rhizosphere's total bacterial, *Pseudomonas*, and *Bacillus* spp. communities	Chotsaeng *et al*., 2017; Zhou and Wu, 2018
				caffeic acid	inhibits seed germination and plant height	Pan *et al*., 2023
				ferulic acid	inhibit plant root elongation and cell division, change cell ultrastructure, and interfere with normal plant growth and development	Hussain and Reigosa, 2021
				gallic acid	Inhibits plant growth and	Anwar *et al*., 2023

					biochemical pathways	
Reversibly Bound	Phenolic compounds that are adsorbed onto soil particles but can be released back into the soil solution under certain conditions, such as changes in soil pH or microbial activity. Like free phenolics, they can also influence the recipient plant directly or be modified by biotic and abiotic factors	Can become bioavailable and contribute to allelopathic effects when released into the soil solution.	Hydroxycinnamic acids	Ferulic acid	idem	
			Hydroxybenzoic Acids	vanillic acid	idem	
Bound	Phenolic compounds that are tightly bound to soil organic matter or	Less directly involved in allelopathic interactions due to lower bioavailability but may	ortho-Substituted phenolics	salicylic acid	inhibits radicle elongation	Li *et al.*, 2010 ; de Lima *et al.*, 2022
				o-coumaric acid	Inhibits root growth	Li et al., 2010 ; Xu et al., 2023

	minerals by forming chelate complexes with metals and are not readily available for uptake by plants or microbes.	still contribute to soil allelopathic potential over time.	dihydro-substituted phenolics	protocatechuic acid	could affect the phycosphere (the immediate environment surrounding algal cells), influencing algal growth, decay, and nutrient cycling	Li et al., 2010; Chen et al., 2020
				caffeic acid	idem	

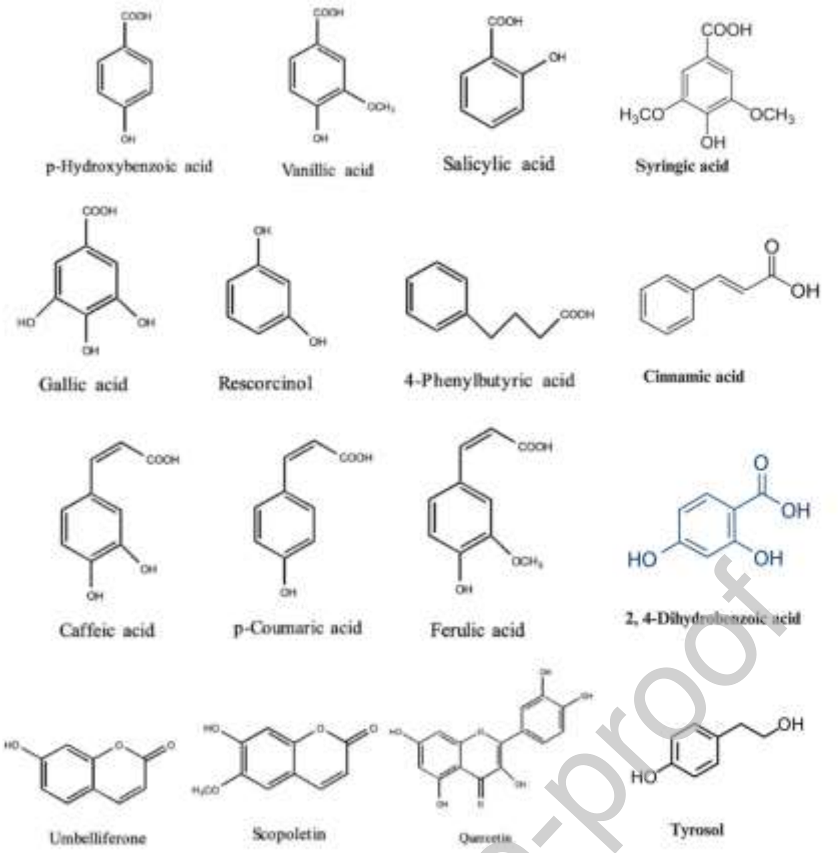

Figure 2. *Typical structures of phenolic allelochemicals*

3. Mechanisms of phenolic allelopathic interactions

3.1. Why study allelopathic mechanisms?

Phenolic compounds, prevalent in the soil at an average concentration of <1 mM, are crucial players in allelopathic encounters. These allelochemicals released during the putrefaction of crop residues act synergistically to adversely affect the germination and growth of succeeding crops (Pardo-Muras *et al.*, 2022). Similarly, weeds influencing crops have been reported for so long (Mushtaq e*t al.*, 2020b; Mushtaq *et al*., 2020c; Mushtaq *et al*., 2020d; Mushtaq *et al*., 2021). The inhibitory effect of diverse waste-land weeds on germination and seedling vigour index of sunflower, cotton, maize, and rice has been reported by Safdar *et al*. (2019).

Harvesting of crops leaves behind the roots of old plants that are buried deep in the soil, which is considered the principal cause of crop autotoxicity due to the release of phenolic allelochemicals (Jabran *et al*., 2015; Liu *et al*., 2018). These phytotoxins directly distress the succeeding crops, alter the organic matter content of the soil, cause microbial imbalance, alter nutrient uptake and lead to immobilization and an increase in ion leakage (Okumu *et al*., 2019). Rice (Hameed *et al*., 2019), maize (Guerrieri *et al*., 2019), alfalfa (Ghimire *et al*., 2019) and many other crops like cucumber, fennel, carrot, watermelon, tomato, eggplant, and pea (Yang *et al.*, 2019) are the most investigated crops showing autotoxicity.

3.2. Phenolic interactions in soil: root-soil-microbes face off

Synthesis, accumulation, and active secretion of secondary metabolites occur in the soil rhizosphere (Mushtaq *et al*., 2020c; Singh *et al*., 2023). It can be therefore considered the main site for allelopathic interactions. Phenolic allelochemicals released by plant roots can significantly modulate the composition of the soil microbiome, attract beneficial microbes, and affect the decomposition of plant litter (Cheynier *et al*., 2013; Clocchiatti *et al*., 2021; Oppenheimer-Shaanan *et al*., 2022).

Simple phenolic acids *viz*. caffeic acid, ferulic acid, hydrocinnamic acid, coumarin, *m*-coumaric acid, *p*-coumaric acid, *p*-hydroxybenzoic acid and salicylic acid are the most prevalent phenolic acids present in soils (Marchiosi *et al*., 2020). The action of phenolics in the soil is influenced by various elements such as soil organic matter, ion-exchange capacity, inorganic ions, reactive mineral surfaces, and biotic barriers (de Albuquerque *et al*., 2011; Scavo *et al*., 2019).

Phenolic acids react with soils abiotically by soil surface-catalyzed oxidation, ligand exchange reactions and/or integration into soil organic matter can get them blocked and thus become biologically unavailable (McGivern *et al*., 2021). Consecutive oxidization and chemical reactivity of several allelochemicals by soil have been stated (Kostina-Bednarz *et al*., 2023). One key abiotic factor that can alter the fate of allelochemicals in the soil is the influence of soil pH, ammonia loss, net nitrogen deposition/reduction, and changes in the chemical composition of rainfall reaching the soil. The pH of the soil also plays a key role in the uptake of allelochemicals by plant roots (Ding *et al*. 2022).

The physical characteristics of the soil, such as texture and structure, further influence the behaviour of phenolic allelochemicals. Soil texture, determined by particle size and distribution, significantly influences soil properties like water retention, aeration, and nutrient availability. This in turn affects the behaviour of plant allelochemicals in the soil, including their retention, transport, and transformation processes (Scavo *et al*., 2019). For instance, soil texture can influence the accumulation of phenolic allelochemicals, with sandy soil accumulating higher levels of phenolics than sandy loam soil (Kaur *et al*., 2014). Clay soils, with their fine texture and high cation exchange capacity, tend to retain allelochemicals more effectively than sandy soils, which can lead to their slower degradation rates and potentially greater phytotoxic effects. The presence of specific clay minerals, such as kaolinites and smectites, can further enhance the retention and availability of these compounds through surface chemical reactions (de Albuquerque *et al.*, 2011).

In addition to texture, soil structure, on the other hand, refers to the arrangement of soil particles into aggregates, which affects the porosity and the balance between the soil's solid, liquid, and gaseous phases. The formation of aggregates is influenced by rhizodeposition, both directly through the adsorption of root exudates with colloids and indirectly through microorganisms involved in aggregation. Soil structure also affects the availability of allelochemicals in the soil, primarily through the retention process (Scavo *et al*., 2019). The size and shape of soil pores, particularly micropores, are crucial in determining the adsorption and retention capacity for allelochemicals, which in turn influences their release and spatial distribution in the soil (Blum 2006).

The interaction between phenolic allelochemicals and soil microorganisms further complicates their ecological roles. Soil microorganisms can metabolize phenolic compounds, influencing their bioavailability, degradation, and transformation in the soil environment (Wang *et al*., 2021). Simple phenolic acids, such as ferulic and *p*-coumaric acid, can be utilized by microorganisms and transformed into other phenolic acids before the aromatic ring structure is broken (Ziolkowska *et al*., 2020). This microbial metabolism is a significant factor in determining the magnitude and duration of the allelochemicals' phytotoxic effects. In another study, specific strains of bacteria and fungi have been reported to degrade a wide range of phenolic allelochemicals (Chang *et al*., 2022). These microbial processes can mitigate the harmful effects of allelochemicals, such as in the case of tobacco bacterial wilt, by degrading the phenolic compounds that contribute to the disease (Chang *et al*., 2022). Etzerodt *et al.* (2006), Fomsgaard *et al.* (2006) and Chen *et al.* (2010) provide details of microbial transformation of allelochemicals into more biologically active compounds. Additionally, the presence of soil microorganisms can lead to higher concentrations of phenolic compounds in live soil compared to sterile soil, suggesting that microbes can influence the concentration and activity of allelochemicals (Xiao *et al*., 2020). This interaction can be complex, as microbes can sometimes reduce the allelopathic effect of these compounds and other times promote it (Xiao *et al*., 2020). Figure 1 illustrates how the combined actions of soil and microbes modify the allelopathic effect.

3.3. Phenolic allelochemicals' primary mode of action: root-phenolic interaction in soil affects nutrient dynamics.

The first organ to meet phenolic acids found in soil is the plant root. Given that root nutrient uptake is dependent on the proton gradient across the plasma membrane, there is evidence that phenolic acid absorption can hinder it by altering the gradient across the membrane. Politycka *et al*., (1997) confirmed this mechanism for benzoic acid and cinnamic acid. It is plausible to believe that phenolic acids act predominantly at the plasma membrane level, lowering electrical conductivity and absorbance of nutrients by the roots (Cheng and Cheng, 2015) as shown in **Fig. 3**.

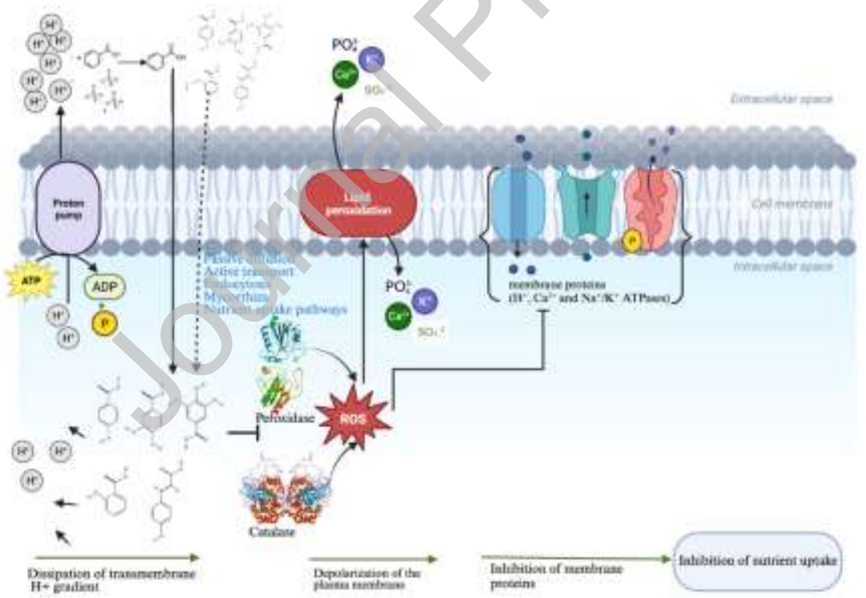

Figure 3. *Uptake and Transport of Phenolic Compounds in Plant Roots and their Effects on Plant Cell Membranes.*

The schematic representation illustrates the journey of phenolic compounds from the soil to the plant cells, emphasizing pH-dependent protonation, their passive/active transport across the cell membrane, the inhibition of antioxidant enzymes, ROS generation, lipid peroxidation, ion loss, membrane depolarization, and increased membrane permeability ultimately inhibiting nutrient uptake by plants.

The apoplast (cell exterior) is typically more acidic than the cytoplasm. At acidic pH levels, a portion of the phenolic acids are protonated. They are hydrophobic in this state and can easily flow through the membrane. When inside the cells, they encounter a higher pH and dissociate, thus reducing the H^+ gradient across the membrane (Lee 1977). The route by which phenolic compounds reach root cells varies depending on the phenolic compound, its size, polarity, and the plant species involved. Passive diffusion across the lipid bilayer (cell membrane) for small phenolics with low molecular weights, active transport of larger or polar phenolics by carrier proteins/transporters of the cell membrane, endocytosis of larger/complex phenolics, mycorrhizal fungi aided phenolics transport from soil to the root cells and nutrient uptake pathway by ion transporters of the cell membrane is possible.

Inside the cells, phenolic allelochemicals inhibit the enzyme activity of peroxidase and catalase (antioxidant enzymes), which increases reactive oxygen species (ROS) and causes lipid peroxidation. The breakdown of membrane lipids and proteins causes the loss of K^+, Ca^{2+}, PO_4^{2-}, and SO_4^{2-} ions, depolarizing the plasma membrane. Moreover, through the oxidative degradation of their sulfhydryl groups, simple phenolic acids also reduce the activity of carriers, pumps, ion channels and membrane proteins including H^+, Ca^{2+}, and Na^+/K^+ ATPases. The degradation of membrane lipids and proteins can also lead to an increase in membrane permeability due to which cell contents may spill and cause death or reduced growth of plant tissue.

3.4. Succession

Succession, or changes in species incidence and structure, happens over time in natural communities. Phenolic allelochemicals, through their allelopathic effects, play a significant role in shaping plant succession (Basaran, 2021). Studies have shown that certain phenolic compounds, such as juglone produced by black walnut trees (*Juglans nigra*), inhibit the germination and growth of nearby plants, influencing the composition of plant communities (Cipollini *et al*., 2012). Allelopathy succession occurs when plants produce and release phenolic allelochemicals over time in response to various factors, including plant development stage, environment, and interactions with other species (Basaran, 2021; Xu *et al*., 2023). Initially, the early stages of plant growth, when allelopathic effects are more noticeable, may see higher quantities of phenolic chemicals. Allelochemical production and release may decline or switch to various molecules as the plant ages. Through several methods, phenolic allelochemicals can affect succession. They can prevent nearby plants from absorbing nutrients, growing long roots, or germinating seeds. By interfering with different physiological and biochemical processes like photosynthesis, respiration, and hormone signalling pathways, phenolics can also have an impact on a plant's physiology and growth (Kumar *et al*., 2020). Additionally, phenolics can alter the soil's microbial population (Xia *et al.*, 2022), which can affect how quickly organic matter decomposes and how nutrients cycle through the soil.

The dynamics and composition of plant communities can vary over time because of the allelopathic impacts of phenolic allelochemicals (Xu *et al*., 2023). These substances may at first reduce the development of rival plants, providing the allelopathic species with a competitive edge. The allelochemicals may, however, become unavailable by binding to organic matter/soil particles or lose their inhibitory effects due to microbial action, allowing other plant species to establish and thrive (Wang *et al*., 2021).

The effects of phenolic allelochemicals on succession vary based on context, including plant species, habitats, and the timing and concentration of allelochemical release (Devi, 2017). Overall, phenolic allelochemicals influence plant growth, competition, and community dynamics, which are important factors in allelopathy succession as shown in **Fig. 4**. Understanding these ecological functions opens the door to practical applications in agriculture, where phenolic allelochemicals can be leveraged to enhance sustainability. Moreover, their role in mitigating abiotic stresses such as drought and salinity highlights their importance in plant resilience and adaptation.

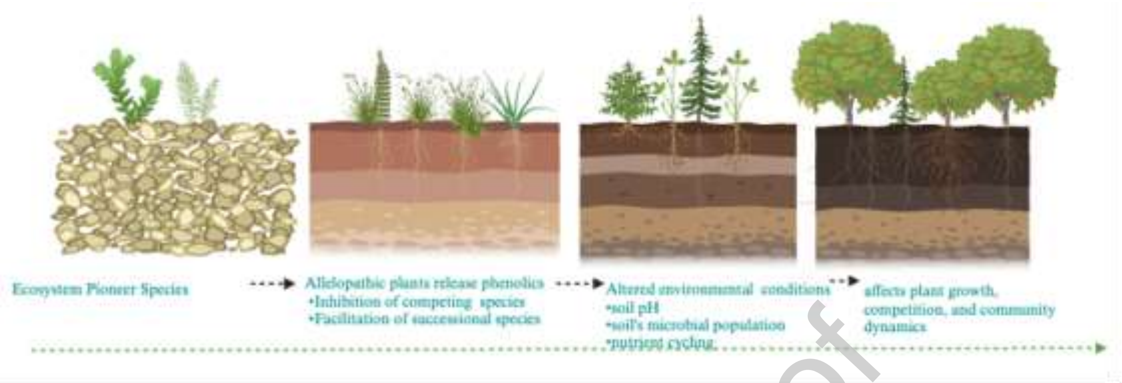

Figure 4: *Allelopathy Succession Mediated by Phenolic Allelochemicals*

Figure 4 depicts the dynamic process of allelopathy succession influenced by phenolic allelochemicals. It showcases how these compounds affect plant growth, competition, and the composition of plant communities over time. At the early stages of plant growth, higher quantities of phenolic chemicals are released, leading to noticeable allelopathic effects. Initially, rival plants may be suppressed, giving the allelopathic species a competitive advantage. However, the availability of allelochemicals may diminish as they bind to organic matter or soil particles or lose their inhibitory effects through microbial action, allowing other plant species to establish and thrive.

4. The Role of phenolic allelochemicals in biotic and abiotic stress tolerance

4.1. Biotic stress tolerance

How phenolic allelochemicals perform chemical warfare against plants has already been discussed in detail in the previous sections of this review. Phenolic allelochemicals do play a crucial role in plant defence against biotic stresses like herbivores and pathogens (Tak and Kumar, 2020; Chowdhary *et al*., 2021) and accumulate in plants under biotic stress conditions (Chowdhary *et al*., 2021).

During herbivore attacks, plants increase the production of phenolic allelochemicals like flavonoids, tannins, and lignins (Tak and Kumar, 2020; Chowdhary *et al*., 2021). These compounds act as toxins against insect pests, providing an induced defense mechanism (Chowdhary *et al*., 2021). The enhanced phenolic levels negatively correlate with larval growth, development, and survival of herbivores (Chowdhary *et al*., 2021). Moreover, plants accumulate phenolic allelochemicals at infection sites to slow the growth of microbial pathogens and restrict them (Chowdhary *et al*., 2021). Phenolics like salicylic acid induce systemic acquired resistance against pathogens. Specific phenolic compounds produced depend on the plant species and stress type.

4.1.1. Pathogen Defense

Plant pattern recognition receptors can detect conserved pathogen-associated molecular patterns (PAMPs), triggering an innate immune response known as PAMP-triggered immunity (Kumar *et al*., 2021). This recognition of PAMPs by plant receptors leads to the increased synthesis and accumulation of phenolic compounds which helps restrict the progress of the infection, preventing the pathogen from gaining complete control over the plant. This rapid induction of phenolics as part of the plant's defense mechanisms occurs before the pathogen can fully establish itself within the plant. Moreover, phenolic compounds act as antimicrobial agents, disrupting the structural integrity of pathogen cell membranes and interfering with their cellular processes (Lattanzio *et al*., 2006).

4.1.2. Herbivore deterrence

Phenolic compounds act as plant defences against herbivores by either directly harming them or making the plant less palatable, thus reducing herbivore feeding and survival rates (Lambers *et al.*, 2008). Herbivore-responsive phenolics are induced in plants like cotton upon insect attack (Dixit *et al*., 2017). These induced phenolics can impact insect performance and biochemistry, acting as toxins or deterrents. They can have anti-nutritive impacts on the growth and development of a variety of insects (Dixit *et al*., 2017). Toxic phenolic glycosides in the bark of Salix (willow) species serve as deterrents against herbivores (Lambers *et al.*, 2008). Condensed phenolics in Oak leaves are negatively correlated with the abundance and richness of leaf-chewing herbivores (Lambers *et al.*, 2008).

4.2. Abiotic stress tolerance

Regarding abiotic stress, phenolic allelochemicals can enhance plant resilience to environmental factors such as drought, salinity, and heavy metal contamination by helping maintain cellular homeostasis and protect plants against oxidative damage (Kiely *et al.*, 2023). Moreover, phenolic compounds have been shown to influence water and nutrient uptake by modifying root membrane permeability and activity of transport proteins, thus aiding in drought and nutrient stress tolerance (Kiely et al., 2023).

Integrating allelochemicals in crop management practices offers a sustainable approach to enhancing plant stress tolerance, reducing reliance on chemical pesticides, and improving overall crop productivity (Kiely et al., 2023).

4.2.1. Drought stress

The role of phenolic allelochemicals in mitigating drought stress involves various mechanisms such as modulation of stomatal closure and osmotic adjustment. Phenolic compounds, including allelochemicals, play a crucial role in plants under drought stress by controlling water ion flux, inhibiting water loss through stomatal closure, and aiding in osmotic adjustment to maintain cellular homeostasis (Pratyusha, 2022). These compounds act as antioxidants, helping plants cope with oxidative damage during drought conditions (Kiely *et al.*, 2023). Additionally, phenolic allelochemicals contribute to enhancing plant resilience by influencing water and nutrient uptake, modifying root membrane permeability, and chelating metal ions to reduce their availability to plants (Maqbool and Sadia, 2017; Kiely *et al*., 2023).

4.2.2. Temperature stress

Phenolic compounds like anthocyanins, flavonoids, and phenolic acids accumulate in plants under heat stress, protecting cells from oxidative damage (Commisso *et al*., 2017; Wang *et al*., 2019). For example, in carrots, phenolics such as coumaric acid, caffeic acid, and anthocyanins prevent heat-induced oxidative damage by enhancing their accumulation (Wang *et al*., 2019). Salicylic acid, a phenolic compound, acts as a stimulant for phenol biosynthesis in plants under high-temperature stress, leading to enhanced accumulation of protective phenolics (Sharma *et al*., 2019). In the grass species *Festuca trachyphylla*, heat stress induced the accumulation of phenolic compounds including 4-hydroxybenzoic acid, benzoic acid, caffeic acid, coumaric acid, cinnamic acid, gallic acid, ferulic acid, vanillic acid, which contributed to enhanced heat tolerance (Wang *et al*., 2019).

Under chilling stress, phenolic compounds like suberin or lignin accumulate in plant cell walls, enhancing resistance by increasing cell wall thickness and preventing chilling injury and cell collapse (Naikoo *et al*., 2019). The enhanced biosynthesis of phenolics under low-temperature stress is due to the increased expression of key enzymes like phenylalanine ammonia lyase, cinnamylalcohol dehydrogenase, and hydroxycinnamoyl transferase (Zhou *et al*., 2018). This is supported by research on *Prunus persica* Batsch under chilling stress, where phenolic accumulation plays a crucial role in protection (Gao *et al*., 2016). Flavonoids, a class of phenolic compounds, protect plants against UV radiation, which often accompanies cold stress (Commisso *et al*., 2016).

4.2.3. Nutrient deficiency

Phenolic allelochemicals can help plants cope with nutrient deficiencies by improving nutrient uptake efficiency through several mechanisms. Phenolic allelochemicals modify root membrane permeability and activity of transport proteins, enhancing the uptake of water and nutrients like nitrogen, phosphorus, and iron (Jabran *et al*., 2013; Jabran and Farooq, 2013). They inhibit biological nitrification by reducing the activity of enzymes involved in the nitrification process, leading to improved nitrogen use efficiency and reduced nitrogen losses (Jabran and Farooq, 2013). Phenolic compounds promote the uptake and release of phosphorus and iron, making these nutrients more available to plants (Jabran and Farooq, 2013). Phenolic compounds like coumaric acid, caffeic acid, and anthocyanins accumulate in plants like carrots under stress conditions, contributing to enhanced nutrient uptake and stress tolerance (Jabran and Farooq, 2013).

4.2.4. Salinity stress

Phenolic compounds act as antioxidants, helping plants cope with oxidative stress induced by salinity, thus improving salinity stress tolerance (Reetu et al., 2023). These compounds regulate ion transport, osmotic balance, and redox homeostasis in plant cells under salinity stress, contributing to overall stress tolerance (Reetu et al., 2023). Phenolic compounds like chlorogenic acid, caffeic acid, ellagic acid, ferulic acid, gallic acid, syringic acid, and vanillic acid have been shown to increase under salinity stress, aiding in maintaining redox homeostasis and enhancing plant health (Kiani *et al*., 2021). Flavonoids and phenolic acids such as anthocyanins, flavonols, and phenolic acids accumulate in plants under salinity stress, protecting plant cells and improving salinity tolerance (Sharma *et al*., 2019).

5. Management of allelopathy in agroecosystems

The main objective of allelopathy research is to leverage observed allelopathic effects for practical applications in agriculture. Allelopathic crops, including those rich in phenolics, are currently being used in agriculture, such as cover crops, intercropping crops, green manure, and crop rotation components (Cheema *et al*., 2013; Mahmood *et al.*, 2013). In recent years, Pakistan has seen success with the utilization of allelopathy in agricultural production (Cheema *et al*., 2013). *Rottboellia cochinchinensis* (itchgrass) is used as mulch by farmers in Lampang, (northern Thailand) to control weed growth (Meksawat and Pornprom, 2010). Similarly, according to several recent studies from different countries, as the weed was reduced by allelopathic therapy, crop production increased (Vashishth *et al*., 2023; Fadhel *et al*., 2023; Yan et al., 2023). Additionally, there is a growing interest in extracting novel agrochemicals based on allelochemicals, contributing to the development of sustainable and eco-friendly agricultural practices (Cheng and Cheng, 2015).

The variety of phenolic allelochemical structures may provide prospective lead compounds for the creation of biopesticides or bioherbicides. These are suitable substitutes for synthetic herbicides that may address shifting customer preferences, the demand for food grown organically and the need to overcome weed resistance phenomena (Scavo and Mauromicale, 2021). Since most phenolic substances are completely or partially soluble in water (due to the presence of hydroxyl group), applying them doesn't require the use of extra surfactants. Natural materials are comparatively safer than synthetic ones in the environment because they break down quickly (Lengai and Muthomi, 2018). In comparison to their synthetic counterparts, phenolic allelochemicals have a more environmentally benign chemical structure (Scavo and Mauromicale, 2021). They lack "unnatural" rings and contain greater nitrogen, oxygen, and sp^3 hybridized carbon molecules, along with only a few so-called "heavy atoms," a halogen replacement. These characteristics shorten a substance's environmental half-life, minimizing soil buildup and interference with non-target plants and species (Mushtaq and Mehdizade, 2020).

5.1. Phenolic compounds as naturally occurring weedicides.

Free phenolic compounds interfere with the availability and accumulation of soil nutrients and have a direct impact on plant growth. For example, Batish *et al*. (2009) reported the release of phytotoxins in the root exudates and residues of *Ageratum conyzoides* L. Some key phenolic allelochemicals found in its rhizosphere include *p*-coumaric acid, gallic acid, ferulic acid, *p*-hydroxybenzoic acid, and anisic acid. When intercropped with citrus orchards, *A. conyzoides* significantly suppress the growth of weeds (Kaur *et al*., 2023).

Similarly, distinct weed control patterns have been observed in hilly regions of Taiwan due to the presence of bamboo vegetation. Among the 14 bamboo species selected for their allelopathic properties, *Sinocalamus latijlorus* was the most toxic followed by *Bambusa pachinensis*, *B. oldhami*, *B. ventricosa* and *Phylostachys makinoi* (Chou and Yang, 1982). The allelochemicals identified in bamboo foliage and rhizosphere include various phenolics such as *o*-hydroxyphenylacetic, *p*-coumaric, *p*-hydroxybenzoic, ferulic, vanillic, and syringic acids.

In another study conducted in leguminous plantations, it was observed that *Leucaena leucocephala*, primarily due to its production of phenolic allelochemicals, prevented understored growth (Kato-Noguchi and Kurniadie, 2022). To target specific weed species, plants that produce phenolics can be intercropped with major crops, effectively suppressing weed growth. Additionally, allelopathic crops can be cultivated in agricultural fields to hinder the germination of specific weed species.

5.2. Allelopathic cultivars

The breeding of allelopathic cultivars can utilize traditional or transgenic technologies. Successful cultivars require traits like early maturity, high yield potential, disease resistance, and weed suppression (Gealy and Yan, 2012). For example, *Rondo*, a rice cultivar with a high yield potential and resistance to rice blast has been successfully cultivated in Texas. It has outperformed several commercial cultivars in weed control (Yan and McClung, 2010; Gealy and Yan, 2012). In China, the *Huagan 3* rice cultivar, derived from crosses between local varieties, exhibits strong allelopathic traits (Kong *et al*., 2011). Allelopathic rice cultivars play a vital role in integrated weed control by producing phenolic allelochemicals (Amb and Ahluwalia, 2016; Serra *et al*., 2021).

Genetic variation in phenolic acid content in wheat varieties suggests the feasibility of breeding for high phenolic content (Li *et al*., 2008). Bertholdsson (2010) bred high allelopathic wheat lines, which reduced weed biomass but showed a decrease in grain yield. This observation underscores the need for further research into optimizing early biomass production to potentially offset the impact on grain yield.

Breeding allelopathic cultivars requires addressing obstacles like continuous cropping and metabolic costs (Cheng and Cheng, 2015). Sequestration of phenolic allelochemicals in root vacuoles may prevent autotoxic interactions

(Potter et al., 1999), but their synthesis and sequestration incur fitness costs. However, research on the energy costs of allelochemicals beyond autotoxicity is limited.

5.3. Phenolic mixtures

The extensive study of phenolic compounds reveals their inhibitory effects on weed growth, yet their interactions remain underexplored. Phenolic allelochemicals naturally occur in mixtures, not in isolation, and these mixtures often exhibit greater allelopathic activity than individual compounds due to synergistic and additive effects (Pardo-Muras *et al.*, 2022; Khatun *et al*., 2023). It's possible that in an allelochemical mixture, the concentration of each chemical may be considerably lower than the concentration required when that chemical is present alone to exert a limiting impact on plant growth (Blum, 2006). Consequently, comprehending the potential for allelopathic effects necessitates considering both the overall and specific activities of allelochemicals within the soil (Manivel *et al*., 2023).

Studies have shown that combinations of compounds, such as momilactone E and 7-ketostigmasterol, can exert stronger growth inhibition through synergistic effects than they do individually (Quan *et al*., 2019).

Similarly, interactions between phenolics and mimosine can disrupt cellular functions in water hyacinth (Chai *et al*., 2013) and a mixture of phenolic acids released by *Delonix regia* affects the surrounding plant's growth in a concentration-dependent manner. Additive effects are also observed with coumarin and phenolic acids (Haig 2008), and with scopoletin and caffeic acid (Korableva *et al.* 1969) demonstrating enhanced allelopathic effects when combined. Einhellig (1996) assessed that a blend of umbelliferone (coumarin), salicylic acid (phenolic acid), and rutin (flavonol) has a phytotoxic effect.

The molecular-level synergistic interactions between allelochemicals in mixtures (de Albuquerque *et al*., 2011) are crucial for understanding natural allelopathy and developing effective natural herbicides.

5.4. Limitations to the development of phenolic allelochemicals-based herbicides

The isolation of bioactive substances from plant extracts presents a significant challenge in the development of bioherbicides, primarily due to the low yield of extracted compounds. This makes the discovery and production of bioherbicides more complex compared to their synthetic counterparts, which can be produced in large quantities through chemical synthesis.

Phenolic compounds, identified in various plant components such as tissues, leachates, exudates, and residues, exhibit diverse mechanisms of action in controlled environments. However, their interaction with environmental factors in natural ecosystems remains poorly understood. Phenolic allelochemicals often degrade, chelate, oxidize, or adsorb to soil particles, reducing their effectiveness in soil and limiting their potential as herbicidal agents (Hoang *et al*., 2021). Consequently, only a few phenolic allelochemicals have been successfully utilized in field applications.

Industries have found it appealing to produce herbicides using natural ingredients. In reality, just a few naturally occurring substances are employed to control weeds. However, these products require more frequent application and incur higher costs than conventional synthetic herbicides. Notably, several well-known synthetic herbicides, such as phosphinothricin, glyphosate, sulcotrione, mesotrione, and cinmethylin, are derived from natural lead compounds. However, none incorporate phenolic chemicals, primarily due to their low stability and high production costs (Kostina-Bednarz *et al*., 2023).

6. Perspectives in allelopathy research

Many biotic (competition, parasites, pathogens, life cycle) and abiotic (soil properties, temperature, rainfall, light) elements affect the production and fate of allelochemicals (Kostina-Bednarz *et al*., 2023, Mushtaq *et al*., 2024) in nature. A holistic approach is needed to understand these influences. The development of new technologies and omics-based methods has made it easier to identify the allelochemicals, their biosynthetic pathways, their diverse functions in the soil rhizosphere, and the many environmental stresses on their production (Aci *et al*. 2022). Omics-based methods, including metabolomics, proteomics, transcriptomics, and genomics, offer comprehensive insights into the allelopathic phenomenon, enabling the identification of active metabolites and their roles in plant interactions (Rinschen *et al*. 2019). Despite these methods, the role of allelopathy in plant protection and agriculture might be underestimated. Many questions remain to be answered, some of which have been neglected for years. This gap is particularly evident in the transition from controlled to field conditions, highlighting the need for real agronomical assays. A focus on the molecular mechanisms of allelopathic phenolic effects, through the study of gene expression, enzyme activity, and signaling pathways, could provide valuable insights. The integration of analytical chemistry, platform technology, mass spectrometry, and nuclear magnetic resonance, combined with advanced data analysis, positions this field as a truly interdisciplinary science (Gaudencio *et al*., 2023).

Furthermore, metabolomics has emerged as a powerful technique for uncovering the molecular targets and mechanisms behind the distribution, metabolization, and target site binding of allelochemicals (Rinschen *et al*., 2019). Genetic modification of crop plants to enhance the production of phenolics, such as those providing weed suppression or pest resistance, may become a viable strategy (in case GMOs are allowed to be commercially produced).

7. Conclusion

The incorporation of allelopathy and allelochemical compounds into modern agriculture is increasingly seen as a sustainable approach to mitigate environmental risks. This review has illuminated the multifaceted role of phenolic allelochemicals in shaping plant interactions, influencing ecosystem dynamics, and revolutionizing agricultural practices. The spotlight falls on phenolic compounds' potential as natural weedicides in recent years. Their unique ability to interfere with soil nutrient availability and accumulate within rhizosphere soils provides an eco-friendly alternative for weed suppression. Case studies demonstrate their effectiveness in curbing weed growth when thoughtfully integrated into agroecosystems.

The development of allelopathic cultivars holds great promise for the future of agriculture. These cultivars come with an array of benefits, including early maturity, high yield potential, disease resistance, and weed suppression. The success stories of Rondo rice and Huagan 3 wheat serve as beacons, illuminating the path toward improved weed management through strategic breeding efforts. The complexity of natural allelopathic interactions, especially the synergistic effects of phenolic mixtures, warrants further study to harness their herbicidal potential.

Integrating allelochemicals into crop management practices offers a sustainable approach to enhance plant stress tolerance, reduce reliance on chemical pesticides, and improve overall crop productivity.

Nonetheless, challenges persist in the adoption of phenolic allelochemicals, such as their large-scale isolation, production, and cost-effective application methods. Ongoing research is vital to optimize their use, improve production techniques, and confirm their effectiveness in agriculture.

As agriculture continues to evolve, allelopathy stands as a valuable, evolving tool in the pursuit of environmentally friendly weed management and crop production practices. With a firm foundation in both tradition and science, phenolic allelochemicals hold the potential to shape the future of sustainable agriculture positively, offering a greener path forward for the global farming community.

Authors' Contributions

Review idea development and conceptualization by WM and MLF. The main draft was prepared by WM, proofread and edited by MLF, and Figures were drawn by WM. All authors have revised and agreed to the final version of the manuscript.

Conflict of interest

The authors have no financial/non-financial competing interests.

Data availability

Not applicable

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Declaration of interests

☒ 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.