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HARMONIZING SOIL ATTRIBUTES AND PLANT ACTIVITIES IN ALLELOPATHY

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ABSTRACT. *Allelopathy plays several roles in plant-environment interactions, with implications for the composition and functioning of plant communities and for agricultural and horticultural practices. They can regulate plant communities, natural weed management, soil fertility and health, crop protection, facilitate the management of Invasive Species, influence succession, and influence crop production and diversity. The objective of this study was to provide a comprehensive overview of allelopathy, emphasizing the intricate interplay between soil properties and plant interactions. A strong association exists between soil properties and allelopathy. When these compounds enter the soil system, they may undergo chemical retention and release, microbial degradation, transport and distribution, and interactions with nutrients. Physically, soil also influences the movement of allelopathic substances through transport and distribution mechanisms. Soil texture and water content influence the movement of allelochemicals from the source plant to the target plants, affecting the range and intensity of allelopathic interactions. The transport and distribution of allelochemicals in soil are influenced by the soil's physical properties, water dynamics, and biotic interactions. Allelochemicals, such as secondary plant metabolites, can cause crop disorders and, in other cases, promote growth and development. Soil attributes such as pH, nutrient content, and microbial communities significantly affect the production, persistence, and activity of allelochemicals. In soil, allelochemical compounds undergo absorption and release by minerals and soil colloids. The chemical retention and release processes in soil mean it can adsorb and release allelochemicals, controlling their availability and concentration in the environment and thereby affecting their impact on other plants.*

KEYWORDS: *allelochemicals, plants, retention, release, soil.*

INTRODUCTION

As the primary producers in ecosystems, plants constantly engage in many interactions to thrive and survive in their dynamic environments. One such fascinating and multifaceted mode of plant interaction is allelopathy. Allelopathy is a biological phenomenon in which one plant releases allelochemicals into the environment that influence neighboring plants' growth, survival, and reproduction. These biochemicals can be beneficial or detrimental to other plants and affect various processes such as seed germination, root growth, and plant development. Allelopathy plays a significant role in regulating plant communities and dynamics. It can be an essential factor in agricultural systems for weed control, crop protection, and crop re-establishment while considering environmental, human, and animal health (Scavo et al. 2018, Olff et al. 2009). Allelopathy plays several roles in plant-environment interactions, with implications for the composition and functioning of plant communities and for agricultural and horticultural practices. They can regulate plant communities, natural weed management, soil fertility and health, crop protection, facilitate the management of Invasive Species, influence succession, crop production, and diversity (Power 2010, Chester & Inderjit 2001). Allelopathy involves complex interactions as ecological dynamics, including species interactions and coexistence, resource availability and utilization, successional stages, microbial interactions, trophic dynamics, invasion biology, and ecosystem feedback (Semenchenko et al. 2020, Einhellig 1996). The role of allelopathy in species interactions and coexistence function can alter competition dynamics, affecting which plant species can survive and coexist. It can serve as interference competition, with allelopathic plants producing chemicals that inhibit other species, impacting community structure and biodiversity (Uddin & Robinson 2017). Given the multifaceted and intricate roles of plant allelopathy in ecology, it is evident that this phenomenon cannot be disentangled from soil, the fundamental medium upon which plants thrive. Soil plays a pivotal role in mediating allelopathic interactions through various mechanisms, including retention and release of chemical compounds, microbial degradation, chemical transformation, and physical transport (Shayler et al. 2009, Nanzyo & Kanno 2018, Inderjit & Weiner 2001, Kong et al. 2019, Inderjit 2005). Soil serves as a medium that modulates the fate and action of allelochemicals within ecosystems. The complex interplay between soil characteristics and allelochemicals contributes to the diversity of allelopathic interactions observed in nature and agricultural settings, shaping the dynamics of ecosystems within a given landscape. It can influence species distribution, vegetation patterns, and successional processes in various habitats. Research into allelopathy is not a novel endeavor in academia. Over the past two decades, there has been a notable surge in publications in the Scopus database that use the keyword "allelopathy." However, few studies have critically examined how chemical interactions between plants, mediated by allelochemicals, can influence and be influenced by soil properties and landscape features where these interactions occur. This paper aimed to provide a comprehensive overview of allelopathy, emphasizing the intricate interplay between soil properties and plant interactions.

METHODOLOGY

To carry out this study, a comprehensive review of relevant literature was undertaken using the ScienceDirect database as the primary source. The search strategy used specific keywords and phrases closely related to the core themes of allelopathy, soil science, and plant interactions. Terms such as "allelochemical relationship," "soil characteristics," and "plant activities" were strategically employed to capture a wide range of scholarly articles and publications that discuss chemical interactions between plants and their surrounding environment, particularly through the release of allelochemicals. To ensure the accuracy, relevance, and scientific rigor of the information gathered, the review focused primarily on research articles and academic books published without a year specified. Only literature from peer-reviewed and indexed journals was considered to maintain a high standard of credibility and to incorporate the most up-to-date findings in the field. This approach allowed the study to build a strong theoretical foundation and contextual understanding of how allelopathic interactions influence soil properties and plant behavior across different ecosystems.

RESULTS AND DISCUSSION

Soil properties and allelopathy

Soil serves several vital roles as a medium for plant growth, including supporting plant structures and anchoring roots, providing a water supply, serving as a nutrient reservoir, facilitating gas exchange, and hosting microorganisms (Ahmad et al. 2020, Kannojia et al. 2019). A strong association exists between soil properties and allelopathy. When these compounds enter the soil system, they may undergo chemical retention and release, microbial degradation, transport and distribution, and interactions with nutrients. For example, phenolics, a group of allelochemical compounds, are plants' most abundant secondary metabolites. They are ubiquitous across the plant kingdom and are essential in various interactions between plants and soil (Dai & Mumper 2010). Results of investigations by Kanjana et al. (2024) also support the view that this group of phenolic compounds is the most abundant allelochemical in soil. Phenolics are among the most abundant components of soil (Gerhards et al. 2024) and play a vital role in the cycling of essential nutrients beneficial to plants and soil microbes (Min et al. 2015). To deepen understanding of this interaction, we illustrated the dynamics of allelochemical behavior in soil (Figure 1).

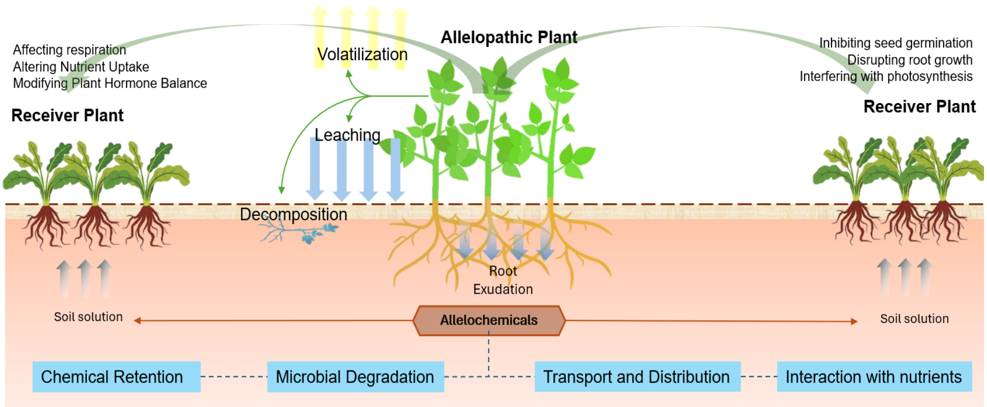

Figure 1. Soil properties influence allelochemical dynamics. (Figure created using www.biorender.com)

In soil, allelochemical compounds undergo absorption and release by minerals and soil colloids. Soil's chemical retention and release processes mean it can adsorb and release allelochemicals, controlling their availability and concentration in the environment and thereby affecting their impact on other plants. This can either decrease or delay allelopathic impact (Kanjana et al. 2024). Galán-Pérez et al. (2022) investigated the effects of the allelochemical scopoletin on sorption, degradation, and bioactivity in soil treated with organic and organo-clay amendments. Results revealed that amendments consistently increased scopoletin sorption, with greater affinity for allelochemicals. However, interactions between amendments and soil constituents altered the sorption behavior of two components of the mixture. Sorption and microbial activity changes both appear to contribute to increasing the persistence of allelochemicals in amended soil.

Not only do biotic particles in soil play an essential role in the process of Microbial Degradation, but living organisms in soil do as well. Soil microbes can break down allelochemicals, reducing their allelopathic effects or even transforming them into different compounds with different effects. Microbial degradation is crucial in the interaction between allelochemicals and soil microbes (Aamir et al. 2019). Microbial degradation in soil is a critical factor in allelopathy. Soil microorganisms, including bacteria and fungi, can break down allelochemicals released by plants into the environment. Numerous bacteria and fungi capable of degrading phenolic allelochemicals have been identified. Microorganisms such as *Aspergillus niger, Bacillus subtilis, Acinetobacter*, and *Klebsiella oxytoca* FZ-8 can degrade compounds such as caffeic acid, ferulic acid, p-coumaric acid, BA, and PHBA (Lubbers et al. 2021, He et al. 2017, Lu et al. 2021, Chang et al. 2022). This microbial degradation process affects allelochemicals by reducing their allelopathic effects, altering their transformation and biodegradation rates, detoxifying them, and altering the composition of soil microbes. As soil microbes degrade allelochemicals, their concentrations decrease, reducing their inhibitory effects on other plants. This process can alleviate potential negative impacts that allelochemicals may have on non-target species, including crops (Chen et al. 2003). Microorganisms transform allelochemicals into less harmful forms, detoxifying soil and making it healthier (Kannojia et al. 2019). Interestingly, soil toxic allelochemicals can also promote the growth of beneficial soil microbes (Lau et al. 2020). The dynamics of microbial-soil interactions and the rate of allelochemical biodegradation are influenced by factors such as soil type, temperature, humidity, and specific microbial communities (Selari et al. 2021, Yang et al. 2020).

Physically, soil also influences the movement of allelopathic substances through transport and distribution mechanisms. Soil texture and water content influence the movement of allelochemicals from the source plant to the target plants, affecting the range and intensity of allelopathic interactions. The transport and distribution of allelochemicals in soil are influenced by the soil's physical properties, water dynamics, and biotic interactions. For example, soil texture influences pore space and, thus, the movement of water and solutes. Coarse-textured soils like sand may permit rapid movement of chemicals, while fine-textured soils like clay can adsorb and retain them, limiting their movement. Water is the principal medium for soil transport. Where allelochemicals can be dissolved in soil water and move with water flow due to gravity, capillary action, or diffusion, the saturation level and direction of water flow within soil (upward, downward, or lateral) will influence distribution (Ismail & Ahmed 2022). The relative concentration of specific ions also influences the diffusion of allelochemicals, spreading them within the soil matrix. Some allelochemicals may evaporate and enter the atmosphere, where they can be transported by air currents and redeposited elsewhere by precipitation or settling.

Plant allelochemicals and their mechanism of release

Allelochemicals are present in all plants and tissues and can vary widely in their chemical structure and mode of action. Allelochemicals can be released into the environment through several mechanisms, such as decomposition of plant residues, volatilization, and root exudation. They can affect various physiological functions in target plants, impacting respiration, photosynthesis, ion uptake, seed germination, growth, and overall performance (Shu et al. 2020, Scavo & Mauromicale 2021). Plants produce a range of allelochemicals with different properties and functions (Macías et al. 2007). The table below shows allelochemical groups commonly found in nature and their functions in plants (Table 1).

The specific mix of allelochemicals a plant produces can depend on factors such as genetic makeup, plant age, environmental conditions, and interactions with other organisms (Belz 2006, Weston & Duke 2003, Chon & Nelson 2010). The environment can influence the production and efficacy of allelochemicals. Factors such as moisture stress, temperature fluctuations, and nutrient availability can enhance their production and potential for interference, sometimes in synergy with other stressors, such as herbicides (Einhellig 1996).

Allelochemicals affect target plants through several mechanisms, affecting various physiological processes. These chemicals can influence respiration, photosynthesis, and ion uptake within plant cells. Consequently, impacted plants may display reduced seed germination, hindered growth, and overall weaker performance.

Table 1. Main categories of allelochemical compound groups.

Groups of allelochemicals	Types	Function
Phenolic compounds	Catechins, tannins, flavonoids, quinones, coumarins, gallic acid, quercetin	Contribution to color, flavor, and defense mechanisms in plants (Huang et al. 2022, Zhang et al. 2023, Kiriyanthan et al. 2023).
Terpenoids	monoterpenes, diterpenes, sesquiterpenes, and triterpenes	Growth inhibitors or antimicrobials (Lokhande et al. 2023, Huang et al. 2022).
Alkaloids	Caffeine, Nicotine, Morphine, Piperine, Lupanine	Influence soil microbial communities, which, in turn, affect nutrient availability and soil health. They may inhibit harmful soil pathogens or disrupt beneficial symbiotic relationships between competing plants and soil microorganisms (Chou & Waller 1980, Yoneyama & Natsume 2010, De Alcântara et al. 2023).
Glucosinolates	cyanogenic glycosides, sinigrin, Glucobrassicin, Glucoerucin	Act as chemical defenses against herbivores, pathogens, and competing plants, influence the composition of microbial communities in soil and act as signaling molecules (Kato-Noguchi et al. 2024, Hoagland et al. 2008)
Hydroxamid Acid	DIMBOA, DIBOA	These are a type of secondary metabolite that can function as iron chelators and have roles in plant defense (Končić et al. 2011)
Organic Acids	acetic, butyric, and citric acid	Affect soil pH and metal availability, influencing plant growth (Zheng et al. 2022)

Specifically, allelochemicals can inhibit seed germination, preventing or delaying seed germination and affecting the early establishment of plants. A significant challenge in allelopathy research is elucidating specific mechanisms of action of allelochemicals, considering their varied chemical compositions and multiple target sites in higher plants. Researchers have designed various bioassays to investigate the direct effects of allelochemicals on plant growth rigorously and to evaluate their underlying mechanisms. This endeavour is particularly complex because bioassays targeting specific enzymes, which could be potential sites of allelochemical action, often necessitate detailed prior knowledge of the enzyme's catalytic or target site structure. In some instances, the precise target site of an allelochemical is not easily discernible from visual assessments of plant growth or morphology. Additionally, the validity of specific in vitro bioassays for providing definitive evidence of allelochemical mechanisms has been questioned, as has the relevance of these in vitro findings to natural settings (Inderjit & Weiner 2001).

It has been noted that the concentration of allelochemicals typically released into the environment is often low and transient, making it challenging to estimate or measure levels of individual allelochemicals or complex mixtures present in soil or the environment (Weir et al. 2004). Consequently, it is crucial to employ appropriate bioassays at relevant concentrations to evaluate potential inhibitory effects of allelochemicals on the growth of higher plants. In many cases, using multiple bioassays is necessary to assess these impacts accurately. For instance, assays that use local soils, plant species relevant to natural ecosystems, and that provide consistent, reproducible results are essential for generating useful datasets. Additionally, researchers in the agrochemical industry, who study the modes of action of synthetic and natural products such as allelochemicals, have developed robust models that utilize highly sensitive assays to evaluate plant growth.

Possible effects of allelochemicals on plants include altering cell permeability and membrane function, disrupting root growth, interfering with photosynthesis, affecting respiration, altering nutrient uptake, and modifying plant hormones. These effects are intricately linked to various biochemical and physiological processes in plants, making it difficult to isolate a single specific effect from the complex interactions within the plant system. Many secondary metabolites, including allelochemicals, can alter cell permeability and membrane function at sufficiently high concentrations. Such exposure can lead to leakage of cellular contents, resulting in cell death through apoptosis and necrosis (Li et al. 2010). This ultimately causes tissue death and loss of specific functions. For instance, several phenolic compounds are known to exhibit allelopathic effects by altering plasma membrane permeability. These compounds can readily cross cellular membranes via diffusion or assisted transport. Once membrane permeability is altered, potassium channels are affected, and chloride ion permeability often decreases. Monoterpenoids induced oxidative stress in the plasma membrane, disrupting its structural integrity and leading to cell death (Yoon et al. 2009, Singh et al. 2006). Chai et al. (2013) also discovered that phenolic compound concentrations exceeding 1 mM, as well as *mimosine* (a nonprotein amino acid) present in *Leucaena leucocephala* leachates, increased membrane permeability in leaf tissue of hyacinth (*Hyacinthus orientalis L.*). Membrane injury is typically assessed in vitro by measuring relative electrolyte leakage in treated plant culture bioassays compared to an untreated control.

Harnessing allelopathy for sustainable agriculture

Using allelopathy in agricultural production systems has the potential to revolutionize sustainable agricultural practices. In sustainable agriculture, allelopathy is harnessed to reduce reliance on chemical herbicides and pesticides, thereby minimizing environmental impact and enhancing the sustainability of agricultural practices. By integrating allelopathic plants into cropping systems, farmers can leverage their natural weed-suppressing properties, thereby improving crop yields and soil health (Bhadoria 2010). For example, allelochemicals from crops can be used to develop biological herbicides (Khanh et al. 2005), and the application of cover crops or mulches from allelopathic plants can benefit no-tillage farming systems (Trezzi et al. 2016). These strategies can help create more sustainable, environmentally friendly agricultural systems. approaches that can be taken primarily for practical weed management include intercropping, cover cropping, and residue incorporation. Certain crops possess allelochemicals that can selectively suppress weeds when rotated or intercropped with main crops. Intercropping allelopathic crops with other plants helps reduce weed density, thereby enhancing crop productivity. For example, several allelopathic crop species intercropped with maize have been shown to inhibit the growth of various narrow- and broad-leaved weed species (Rashid et al. 2020, Xuan et al. 2016). Similarly, intercropping white clover (*Trifolium repens L.*), black medic (*Medicago lupulina L.*), alfalfa, and red clover (*Trifolium pratense L.*) with wheat has proven effective for weed control and increased wheat yield (Miller et al. 2020). Fernández-Aparicio et al. (2010) also reported a reduction in the intensity of *Orobanche crenata Forssk* when berseem was intercropped with legumes such as broad beans and peas. Using cover crops. Apart from their numerous advantages, such as shielding plants from soil erosion, enhancing soil fertility and structure, and fixing nitrogen, allelopathic cover crops are also effectively applied in weed management (Restuccia et al. 2020). These crops reduce weed populations in agricultural fields through their allelopathic and competitive effects (Schappert et al. 2019). Canola, rapeseed, cereal rye, crimson clover, wheat, red clover, brown mustard, oats, cowpea, fodder radish, annual ryegrass, mustards, buckwheat, hairy vetch, and black mustard are a few of the significant cover crops. Cover crops are essential for controlling weeds in several cropping systems, including organic farming (Pittman et al. 2019). It was reported that cover crop mixtures of *Sinapis alba* L., (*Raphanus sativus var. niger J. Kern*), and *Vicia sativa* suppressed weeds. Cover crops smother weed growth by forming a physical barrier, reducing light and temperature intensity, or releasing allelochemicals from residues and microbes. Plants that produce allelochemicals can be used as cover crops or green manures (Kelton et al. 2012). When these are incorporated into soil or left as mulch, they release allelochemicals that can inhibit weed germination and growth. They outgrow weeds and outshade them. It has been noted that allelopathic crop plants substantially decrease weed crops. Cover crops' allelopathic potential and time in the field determine how effectively they control weeds; an allelopathic crop given enough time in the field can effectively control weeds (Bhowmik & Inderjit 2003).

Allelopathic plant residues, whether introduced accidentally or intentionally into the field, can reduce weed severity. Many allelochemicals, primarily phenolics, are released when plant waste decomposes and inhibit weed growth. For instance, it has been reported that crop residues from barley, rye, and triticale stored in a maize field in Greece exerted allelopathic effects on *E. crus-galli* and *Setaria verticillata (L.). P. Beauv*.; in this case, growth of *S. verticillata* and *E. crus-galli* was reduced compared to non-mulched treatment (Dhima et al. 2006). Moreover, applied mulches had no negative effect on maize. However, barley mulches applied to maize field increased grain yield by 45% in plots compared with non-treated control (Dhima et al. 2006). Remarkable reduction of weed infestation in broccoli (*Brassica oleracea* L.) crop when maize residues were added in the field after its harvest (Bajgai et al. 2013). Similarly, weed control potential in field crops has been reported with sunflower residues and surface mulches (Rawat et al. 2017).

The alternative application of allelopathy lies in its potential benefits as a biostimulant. Biostimulants, in contrast, are substances, including various compounds and microorganisms, that enhance a plant's growth, development, stress response, and overall health. They are employed to enhance yield, quality, and resilience to environmental stresses and comprise a diverse range of components, including humic and fulvic acids, seaweed extracts, amino acids, and microbial inoculants. Allelochemicals do not have a direct, standardized function as biostimulants. Nonetheless, the association between allelochemicals and biostimulation is considered indirect. When allelochemicals diminish weed competition, the target crop may experience reduced stress and better utilize available nutrients and water, potentially resulting in enhanced growth and yield. In this secondary context, it could be argued that suppression of competing plants by allelochemicals exerts a 'biostimulant effect' on the desired crop. However, it is important to note that stimulating plant growth is not the primary purpose of allelochemicals, nor are they directly applied or formulated for this purpose, as with conventional biostimulants. A comprehensive examination of allelochemicals in the context of biostimulants would require thorough research into their potential growth-promoting effects rather than focusing solely on their natural inhibitory roles.

Despite the numerous benefits of using allelopathy in agriculture, it faces obstacles and challenges in contemporary settings. Understanding intricate ecosystem interactions involving allelochemicals is complex and demands extensive research (Trezzi et al. 2016). Allelopathy's effectiveness can be influenced by diverse environmental factors, leading to inconsistent weed control and crop productivity outcomes. Furthermore, developing allelopathic plants through breeding is a time-consuming and challenging process that requires advanced expertise in plant genetics and breeding techniques (Khanh et al. 2005). Social factors also pose challenges, such as farmers adopting allelopathic crops. Farmers may exhibit reluctance to adopt new practices without clear evidence of long-term benefits and a comprehensive understanding of how to integrate allelopathy into their existing systems. Additionally, costs are a consideration, as initial expenses associated with developing allelopathic crops and persuading farmers to transition from traditional methods can pose financial barriers (Khanh et al. 2005). However, opportunities obtained will have many benefits in the agricultural sector, such as reducing pesticide use, providing economic and environmental benefits, providing healthier planting media, and supporting high soil biodiversity because they require less chemical input (Khanh et al. 2005). Research into allelochemicals may lead to the development of new, eco-friendly herbicides and pesticides, opening new markets and commercial opportunities (Khanh et al. 2005).

CONCLUSIONS AND FUTURE DIRECTIONS

Allelopathy is not simply a direct interaction between plants; the soil environment fundamentally mediates it. Their properties that can cause plant disorder or promote growth are closely related to soil attributes such as pH, nutrient content, and microbial communities. Soil acts as a dynamic buffer through chemical retention and release, in which minerals and colloids absorb compounds, controlling their availability, concentration, and persistence in the ecosystem. Over time, these retained chemicals are gradually released back into the soil solution, potentially moderating their impact on surrounding vegetation. Furthermore, soil microorganisms play a dual role: degrading these compounds to reduce toxicity and converting them into new bioactive forms. Harnessing allelopathy offers a transformative approach to modern agriculture, moving away from reliance on synthetic herbicides, fungicides, and insecticides toward environmentally friendly biological alternatives.

Compared with synthetic agricultural reagents, including herbicides, fungicides, and insecticides, allelochemicals offer an environmentally friendly alternative that reduces the need for chemical compounds. However, extracting allelochemicals from plants remains a time-consuming and labour-intensive process, and their degradation can pose technical challenges. Therefore, artificial synthesis of natural allelochemicals or their bioactive analogs will be essential to boost their industrialization. Additionally, a more forward-looking focus could be directed towards the development of allelopathic crop varieties, leveraging both conventional breeding techniques and advanced transgenic methods. These efforts aim to cultivate premium varieties that seamlessly integrate weed management capabilities, disease resistance, and breeding programs focused on incorporating strong allelopathic traits into high-yielding crops to reduce reliance on chemical herbicides and drought resilience, thereby advancing the sustainability and productivity of agricultural systems. Current research on allelochemicals' effects largely focuses on morphological and physiological aspects but lacks deep genetic and molecular insights into their mechanisms of action. To better harness the benefits of allelochemicals, an in-depth investigation into their mechanisms of action is required.

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