

Survival and Suppression: Black Walnut's Allelopathic Strategies

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Abstract From the perspective of chemosensory ecology, this study systematically explored the sources and types of chemosensory substances in black walnut trees, the mechanism of action of juglone and its target plant responses, and further analyzed its ecological functions in resource competition, community dynamics and symbiotic relationships. At the same time, the dual effects of the sensitization effect of black walnut in forestry and agricultural management were also discussed, as well as its adaptive significance in the context of global change. Research has found that by releasing sensitizing substances into the environment, especially the key compound Juglone, black walnuts can inhibit the germination and growth of surrounding plants, thus gaining an advantage in resource competition. This kind of "chemical war" not only affects the physiological metabolism and community structure of neighboring species, but also has a profound impact on community diversity and ecological balance. This study also proposed that in the future, efforts should be made to enhance the analysis of molecular target mechanisms, dynamic modeling of soil sensitizing substances, and the design of complex ecosystems. From the perspective of chemosensory ecology, exploring how black walnut achieves "survival and suppression" through chemosensory substances is of great significance for understanding the dynamics of forest communities and developing natural management methods in agriculture and forestry.

Keywords Black walnut; Chemosensory effect; Walnut ketone; Chemosensory substances; Ecological competition

1 Introduction

The black walnut (*Juglans nigra*) is native to North America and is a broad-leaved tree species with both economic and ecological value (Nicolescu et al., 2020). Its wood is hard and beautiful, and is widely used in the manufacturing of high-end furniture and flooring. Nuts are rich in oil and protein and are edible and used in the food processing industry. Meanwhile, the black walnut tree has a majestic posture and ornamental value. Its bark, leaves and green peels are used in traditional medicine to treat diseases (Nicolescu et al., 2020; Athaillah et al., 2024). For instance, the active substances contained in the green peel of black walnut are used in folk remedies such as antibacterial, deworming and pain relief (Jahanban-Esfahlan et al., 2019; Liu et al., 2022). In the ecosystem, the most prominent feature of black walnut is its strong inhibitory effect on adjacent plants: there are historical records as early as before the Common era that it is difficult for grass and trees to grow under walnut trees. This phenomenon was scientifically confirmed in the 19th century to be caused by the release of specific chemical substances from walnut trees (Liu et al., 2022).

Black walnut produces a typical chemosensitizing substance - juglone, which can inhibit the germination and growth of other plants in the soil (Nicolescu et al., 2020; Medic et al., 2021b). Allelopathic action, as one of the important strategies for competition and balance among plants, plays a crucial role in maintaining the competitive edge of black walnuts in the ecosystem. It not only won space and resources for black walnuts, but also to some extent changed the diversity and structure of the community, and might even affect the relationship between the animals and plants that coexist with them. The "black walnut effect" has become a classic example in the study of chemosensory effects. Studying the strategy of black walnut competing with surrounding plants through "chemical warfare" not only helps to reveal the interspecific relationships and species succession mechanisms of forest communities, but also contributes to the development of weed control measures based on plant natural products, serving ecological management in agriculture and forestry (Islam and Widhalm, 2020; Dolianitis et al., 2025).

Against the backdrop of increasingly intensified global environmental changes, the allelopathic effect of black walnut may demonstrate new ecological functions in resisting invasive plants and regulating community structure. This study aims to systematically sort out the sources and types of sensitivities in black walnut, the mechanism of action and ecological functions of juglanone, and further explore its adaptive significance in the application of forest farmers and in the context of global change, providing theoretical support for future research and management practices.

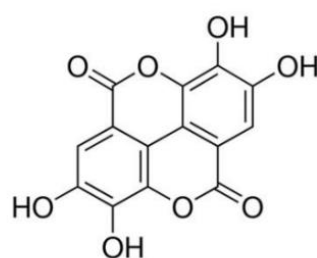
2 The Sources and Types of the Sensitizing Substances in Black Walnut

2.1 Chemosensory substances released from various parts of the tree

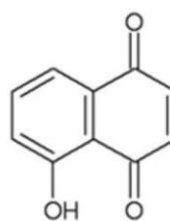
The sensitizing effect of black walnut stems from a series of secondary metabolites produced and released within its body. Studies have shown that various tissues of black walnut trees, such as root systems, bark, leaves, and fruit peels, all contain sensitizing active substances, which can be released into the environment through root secretion, leaching of leaf litter, and other pathways (Liu et al., 2022; Xu et al., 2023). Two representative secondary metabolites rich in walnut peels: Ellagic acid and Juglone (Figure 1). The green pericarp (unripe exocarp) of the walnut tree is regarded as the part with the highest walnut ketone content, with 20 to 40 milligrams of walnut ketone per 100 grams of green pericarp, while the content in leaves is approximately 5 to 23 milligrams per 100 grams. During the process of leaf fall and fruit peel decomposition in autumn, a large amount of substances such as juglanone and phenolic acids are released into the soil (Medic et al., 2021a; Liu et al., 2022).



Waluts husks



Ellagic acid



Juglone

Figure 1 Chemical composition of key secondary metabolites in the husk of black walnut (Adopted from Jahanban-Esfahlan et al., 2019)

Juglandone in black walnut trees is initially stored in living tissues in the form of non-toxic glycosides. Once it enters the soil, it will be hydrolyzed and oxidized to toxic free juglandone (Xu et al., 2023). In addition to juglanone, the leaves and green peels of black walnut are also rich in other phenolic compounds, such as tannins, caffeic acid, gallic acid, etc. They may jointly exert a complex chemosensory effect with juglanone (Zubay et al., 2021; Athaillah et al., 2024). Modern analysis has confirmed that the residues of black walnut harvesting (branches, leaves, shells, etc.) contain various phenolic substances, and these by-products can be used as raw materials for extracting natural products (Medic et al., 2021a).

2.2 Key sensitizing substances: Juglone

Juglandone (5-hydroxy-1,4-naphthoquinone) is the main allelopathic substance released by black walnut and other Juglandaceae plants, and it is also the earliest identified allelopathic component of walnut (Islam and Widhalm, 2020; Liu et al., 2022). Walnut ketone belongs to the naphthoquinone class of compounds. The pure product is yellow crystals and has high chemical stability in soil, which can exist for several months or even a year.

In walnut trees, juglanone exists in a non-toxic bound form. When plant tissues are damaged or metabolic products enter the soil, walnut ketone is transformed from a precursor (also known as hydrolyzed walnut ketone or walnut quinone glycoside) to a free state with strong inhibitory activity (Xu et al., 2023). Free juglandone is the main "weapon" of the chemical sensitivity of black walnut and has a significant inhibitory effect on seed germination and seedling growth of various plants (Nicolescu et al., 2020; Park et al., 2020).

However, recent studies have indicated that the inhibitory effect of walnut leaf extract on certain plants is stronger than that of pure walnut ketone solution of the same concentration, suggesting that in addition to walnut ketone, there may be other chemosensitic substances with synergistic effects in walnut tissue. For instance, polyphenols such as tannins contained in walnut leaves and peels may exert effects different from those of juglanone on certain receptor plants, thereby jointly constituting the chemosensory "chemical pool" of walnut trees (Medic et al., 2021b; Zubay et al., 2021). Despite this, juglanone is undoubtedly the core component in the chemosensory strategy of black walnut, and its mechanism of action and environmental behavior have also become the focus of chemosensory ecology research.

3 The Mechanism of Action of 3-Juglanone and the Response of Target Plants

3.1 Effects on the physiology of adjacent plants

Juglandone has significant inhibitory effects on seed germination, seedling growth and physiological functions of various plants (Ochekwu and Uzoma, 2020; Park et al., 2020). Plants affected by juglanone often show symptoms such as decreased germination rate, hindered root growth, and wilting and yellowing leaves. This is because when walnut ketone enters sensitive plants, it interferes with their basic physiological processes. For instance, sensitive crops (such as tomatoes and potatoes) grown under walnut trees often show slow growth, wilting and even death, which is attributed to the inhibition of the respiration and water and nutrient absorption functions of these crops by juglandone (Nicolescu et al., 2020). Greenhouse experiments have shown that the addition of juglanone significantly reduces the plant height, biomass and yield of sensitive plants (such as cucumbers and tomatoes) (Ochekwu and Uzoma, 2020; Medic et al., 2023).

Research has found that when the concentration of juglanone in the soil reaches 1 mM, the yield of cucumber seedlings drops significantly. Moreover, juglanone can also inhibit secondary metabolism in cucumbers, reducing the plants' resistance to diseases and adverse conditions. Similarly, it was observed in the field that there were few herbaceous plants and a single dominant species under the black walnut grove, and the population vitality was significantly limited (Nicolescu et al., 2020). This indicates that the effects of walnut ketone on adjacent plants are multifaceted: including direct toxic effects that inhibit seed germination and seedling growth, as well as disrupting the metabolic balance within the recipient plants, thereby weakening their competitiveness and viability (Ochekwu and Uzoma, 2020; Medic et al., 2023).

3.2 Research progress on cellular and molecular mechanisms

The chemosensory inhibitory effect of walnut ketone involves a series of disorder mechanisms at the receptor plant cell and molecular levels. Firstly, walnut ketone is an oxidized naphthoquinone that can generate excessive reactive oxygen species (ROS) in recipient plant cells, leading to lipid peroxidation and cell membrane damage. Walnut ketone has alkylation activity and can covalently bind to thiol groups on the cell membranes and enzyme proteins of receptor plants, interfering with the function of key enzymes (Han et al., 2021). In addition, juglanone can also interfere with the hormone balance and gene expression within plants. Research has found that the application of exogenous plant hormones (such as gibberellin and agonist) can partially alleviate the inhibition of juglandone on the germination and growth of water celery seedlings, suggesting that juglandone may inhibit growth by influencing the levels of endogenous hormones.

From the perspective of gene expression, some studies conducted transcriptome analysis using the model plant rice and identified a series of genes induced or inhibited by walnut ketone, including antioxidant, defense-related genes and signal transduction components (Medic et al., 2021b). This indicates that the recipient plants will initiate defense responses under juglanone stress, but it is often difficult to counteract its toxic effects.

3.3 Sensitivity differences of receptor plants

The sensitivity of different plants to walnut ketone varies significantly. Some species are highly susceptible, while others show certain tolerance (Nicolescu et al., 2020; Park et al., 2020). Generally speaking, dicotyledonous herbs and certain horticultural crops (such as tomatoes, potatoes, leguminous vegetables) are particularly sensitive to juglandone and often grow poorly or even fail to survive under black walnut trees, which has been widely reported in horticultural practice (Nicolescu et al., 2020). In contrast, some gramineous crops and shade-tolerant plants have a relatively mild response to juglanone. For instance, research has found that juglanone only slightly inhibits the sprout growth of cereal crops such as corn and wheat. In the intercropping system of black walnut and crops, crops such as wheat, corn, and oats only showed slight growth reduction and could coexist with walnut trees through reasonable planting density and management (Davies et al., 2011; Bishop et al., 2024).

Bishop et al. (2024) of the walnut alley cropping (intercropping of forest farmers) study indicated that wheat and barley showed only slight growth retardation under walnut ketone stress, while the germination of many dicotyledonous weeds was significantly inhibited. This selectivity may stem from physiological and biochemical differences among species: tolerant species may have higher detoxification enzyme activity or thicker rhizosphere microbial membranes, which can degrade juglanone more quickly. However, the cell membrane permeability and antioxidant defense of sensitive species are relatively weak, and they are more vulnerable to damage by walnut ketone (Kanatas, 2020; Park et al., 2020). Even in lower plants such as algae, similar phenomena have been observed: walnut ketone has a strong inhibitory effect on the growth of harmful cyanobacteria, but has a relatively small effect on some diatoms (Park et al., 2020). It can be seen that the chemosensory effect of walnut ketone varies depending on the type of recipient plant.

4 The Ecological Function of the Black Walnut Transformation Strategy

4.1 The sensory advantage in resource competition

Black walnut has gained a unique advantage in forest succession and resource competition through allelopathic effects. Substances such as walnut ketone released by its root system and fallen leaves can inhibit the growth of neighboring plants, thereby freeing up space for itself and obtaining more resources (Kanatas, 2020; Nicolescu et al., 2020). Research indicates that tree species with strong chemical sensitivity often reduce the plant coverage under the forest, weaken potential competitors, and thus consolidate their dominant position. This chemosensory competitive advantage compensates to some extent for the weakness of black walnut's intolerance to light and nutrients (Bertin et al., 2003). In fact, black walnut is a light-loving tree species with relatively weak competitiveness at the young tree stage. However, with chemosensory substances, it can "chemically clear the field", reduce the interference of shrubs and grass under the forest, and create favorable conditions for the growth of itself and its offspring (Nicolescu et al., 2020). Meanwhile, the sensigenic substances of black walnut can also have an impact on the soil microenvironment. For example, they can inhibit the activity of certain microorganisms that antagonize walnut, indirectly enhancing their own utilization efficiency of soil resources (Kanatas, 2020; Islam and Widhalm, 2020). Underground interactions and their effects on soil microbial communities, nutrient cycling, root growth patterns, etc. can also be achieved through Allelochemicals (Figure 2) (Xu et al., 2023).

4.2 Impact on species diversity and community structure

The allelopathic inhibitory effect of black walnut has a profound impact on the species diversity and structure of the community. Because walnut ketone can selectively inhibit the renewal of sensitive species, the composition of undergrowth plants often changes in the distribution area of black walnut, manifested as dominance of tolerant species and lack of sensitive species (Nicolescu et al., 2020; Zubay et al., 2021). In the long term, this selective pressure may reduce the species diversity of the community. On the other hand, from the perspective of community competition, the sensitization effect of black walnut may prevent certain highly competitive but sensitive species from invading, thereby maintaining its dominant position in the community. For instance, the survival rate of *Ailanthus altissima* seedlings, which are highly invasive, was significantly reduced in soil where walnut ketone was present (Ferus et al., 2020), which to some extent curbed the encroachment of *ailanthus altissima* on local vegetation. Therefore, the allelopathic effect of black walnut may both reduce local species diversity and protect the composition of the original community by inhibiting invasive species (Sujeeun et al., 2023).

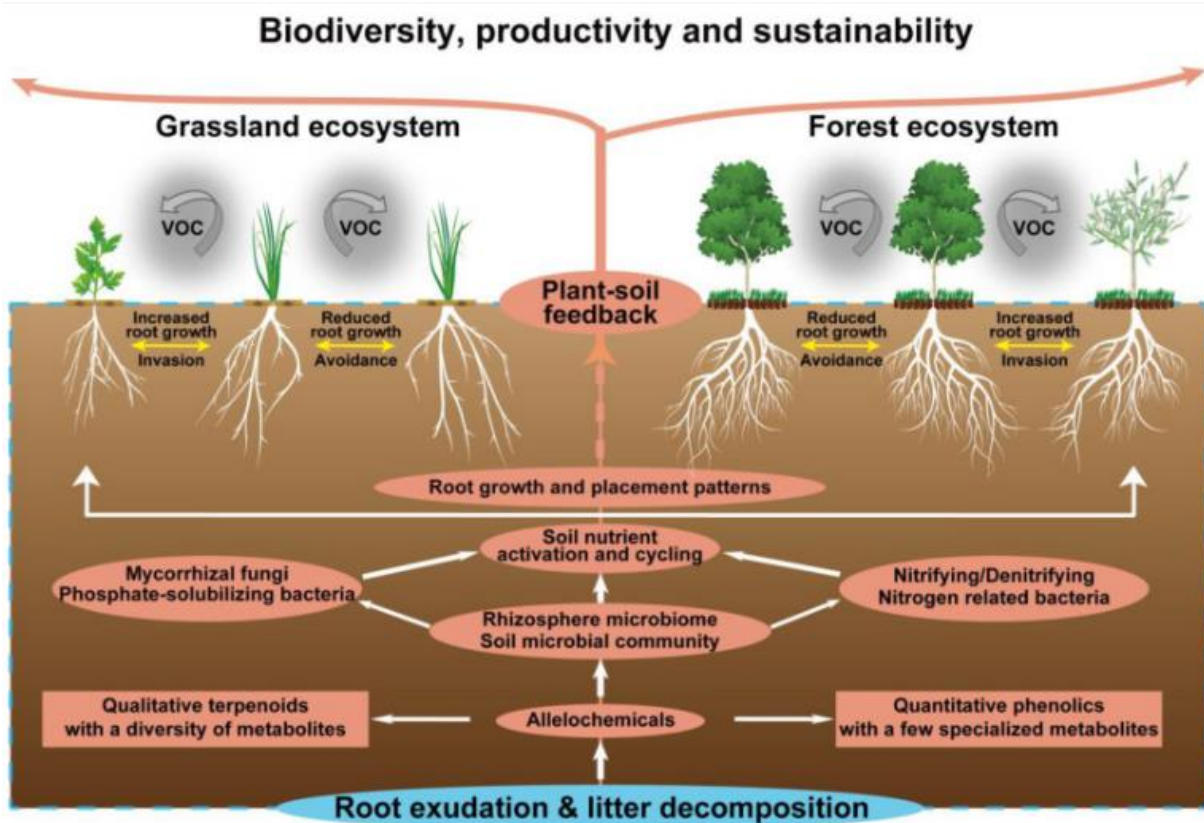


Figure 2 Allelochemical-mediated below-ground interactions and plant–soil feedback (Adopted from Xu et al., 2023)

4.3 Potential conflicts and coordination with symbiotic relationships

Chemicals released by black walnuts can suppress the growth of nearby plants, yet at the same time may interfere with their own symbiotic partners. This tension often results in conflict or requires delicate balance. Compounds such as juglanone not only hinder competitors but also influence beneficial soil microbes, including mycorrhizal fungi and nitrogen-fixing bacteria. As a result, the close associations between walnut roots and these organisms can be weakened. In walnut stands, shifts in AM fungal communities are common: sensitive groups decline, while tolerant ones gradually dominate, reflecting microbial adaptation under juglanone stress (Jose, 2002).

Intercropping experiments, however, indicate that carefully chosen plant combinations can mitigate or even offset these allelopathic effects, thereby fostering more stable symbioses. In southwest China, for instance, tea trees have been cultivated alongside walnuts. The results showed improved soil nutrient status, greater microbial diversity, and tea yields that were only minimally affected (Bai et al., 2022). Additional studies suggest that the roots of certain companion plants can secrete compounds accelerating juglanone degradation, reducing its accumulation and easing its harmful influence on the broader system.

5 Application Perspective: The Double-Edged Sword Role of Black Walnut in Forestry and Agriculture

5.1 Weed control potential and natural weeding strategies

The strong chemical sensation effect of black walnut provides a new idea for the development of natural herbicides. Research has found that juglanone, as a natural substance derived from plants, has a significant inhibitory effect on algicolor in various weeds, and thus is regarded as a potential candidate for bioherbicides (Ferus et al., 2020; Islam and Widhalm, 2020). The experimental results show that juglanone can not only significantly prevent the seed germination and seedling growth of common weeds in the field, but also has relatively low toxicity to certain crops (Bishop et al., 2024).

In forestry applications, black walnut reduces undergrowth weeds and competing trees by virtue of its own allelopathic effect, thereby lowering the management and tending costs of young forests (Ferus et al., 2020). In

agricultural production, the use of juglanone to replace some chemical herbicides can reduce the risk of environmental pollution and simultaneously delay or inhibit the spread of drug-resistant weeds (Lu et al., 2015). However, its field effect is often restricted by environmental factors such as the rate of soil adsorption and degradation. The grass suppression efficiency of juglanone still needs more field verification (Islam and Widhalm, 2020).

5.2 Adverse effects and planting management risks

The sensitization effect of black walnut may also have adverse effects on mixed crops and the environment, and requires careful management. The toxicity of walnut ketone to sensitive crops means that highly sensitive species must be avoided when choosing crop types in agroforestry systems. If susceptible crops such as vegetables and tobacco are planted under black walnut groves, it may lead to a sharp reduction in yield or even total crop failure, which is a major risk of black walnut intercropping (Nicolescu et al., 2020; Ochekwu and Uzoma, 2020). The accumulation of juglanone in the soil may have a continuous impact on subsequent crops. After the removal of walnut trees, walnut ketone in their soil can remain for several months (Xu et al., 2023). Therefore, when converting black walnut forest land into farmland, it is necessary to allow a certain amount of soil fallow or plant plants with strong detoxification ability to promote the degradation of juglanone and avoid residual chemical hazards to subsequent planting (Islam and Widhalm, 2020).

The allergenic substances in black walnut may also affect soil ecology: although juglanone can inhibit weeds, excessive amounts may also suppress the activities of beneficial organisms in the soil (such as earthworms and nitrogen-fixing bacteria), which is not conducive to soil health in the long run. Management measures can be taken to reduce this risk, such as enhancing soil aeration and organic matter input to promote microbial degradation of juglanone (Islam and Widhalm, 2020). It is notable that studies have found that the content of juglanone in some by-products of black walnut (such as nut shells and wood shavings) is very low, and it is usually safe to use it as mulch or substrate (Athallah et al., 2024).

5.3 Potential utilization prospects of chemosensitive substances in agriculture

The sensitization strategy of black walnut is a "double-edged sword" in agriculture and forestry. Future research and practice can be dedicated to making full use of the favorable aspects of this "double-edged sword". Walnut ketone, as a natural product, is expected to be developed into an environmentally friendly biopesticide or plant-based herbicide (Islam and Widhalm, 2020). Compared with synthetic herbicides, walnut ketone is derived from renewable resources and can be degraded by microorganisms in the environment, thus being more environmentally friendly (Liu et al., 2022). Juglandone has an inductive resistance effect on certain crops at low doses, which is known as the "hormone-like" or "positive stimulation" effect. Studies have shown that low concentrations of juglanone can induce the expression of antioxidant enzymes and detoxification enzymes in plants, enhancing their resistance to pests and diseases.

With the development of nanotechnology, loading walnut ketone onto nanocellators can significantly improve its water solubility and stability, and enhance its efficacy against target organisms (Ahmad and Suzuki, 2019; Gumus et al., 2020). Gumus et al. (2020) have demonstrated that walnut ketone encapsulated in PLGA nanoparticles has stronger and more persistent antifungal activity than free walnut ketone. The black walnut sensory transformation strategy also provides ideas in the design of ecological agricultural systems. For example, the natural weeding characteristics of walnut trees can be utilized to plant tolerant forage or medicinal plants under their forests, achieving a win-win situation of weed suppression and yield (Bishop et al., 2024); Or intercrop black walnut with certain species that can promote the degradation of its chemical substances to achieve a dynamic balance of "trees suppressing grass and grass protecting trees" (Bai et al., 2022).

6 The Adaptive Significance of Sensitization Strategies in the Context of Global Change

6.1 Interaction between walnut ketone release and environmental factors

Global climate and environmental changes may affect the effectiveness of the black walnut sensation strategy. Environmental factors such as precipitation, temperature, soil properties, etc. significantly regulate the release, migration and degradation of juglandone in the ecosystem (Nicolescu et al., 2020). For instance, in a humid and

rainy climate, juglanone in the soil is more prone to leaching and dilution, and its continuous inhibitory effect on vegetation may be weakened. In dry seasons or poorly drained soil, walnut ketone is more likely to accumulate, thereby enhancing the sensory effect (Choudhary et al., 2023). Similarly, it can be speculated that under drought stress, black walnuts may secrete more juglanone to reduce competition, or due to water shortage, juglanone may act more intensively on local soil areas, thus exerting more obvious suppression on adjacent plants. On the contrary, under conditions of high precipitation and irrigation, the concentration of juglanone is diluted and degraded more quickly, and its "medicinal power" will be weakened (Islam and Widhalm, 2020).

Temperature is an important factor in the sensory effects of black walnut. When it gets warmer, trees often produce more secondary metabolites such as walnutone. But higher heat can also make these compounds break down faster in the soil (Liu et al., 2022). This means climate warming has two sides. It can boost the release of sensitive substances inside the tree, but it can also shorten how long they stay in the soil because soil microbes become more active.

The rise of CO₂ in the air also matters. Extra CO₂ usually speeds up carbon use in plants and pushes secondary metabolism. Studies show that under high CO₂, the level of some sensitizing substances goes up, which may increase their inhibitory effect. Even though there is no full study yet on how walnut ketone acts under different climate conditions, current evidence suggests that global change will shape the adaptability of black walnut's chemical strategy. In dry areas, it may gain more strength because of its higher advantage. In wetter regions, or where soil microbes are active, its effect may become weaker (Islam and Widhalm, 2020; Kaur et al., 2024).

6.2 The Potential and Limitations of chemosensory strategies in combating Invasive plants

Whether the sensitizing effect of black walnut can play a "biological control" role in the global plant invasion problem is an aspect worthy of attention. Theoretically, broad-spectrum and long-lasting chemogenic substances like walnut ketone can inhibit many invasive alien plants and provide a certain protective barrier for native species (Ferus et al., 2020). For example, when introducing black walnut in some parts of Europe, studies have observed that the numbers of several invasive weeds under its forest (such as *Solidago canadensis*, *Delphinium*, etc.) are relatively small, which is speculated to be related to the inhibitory effect of juglandone (Nicolescu et al., 2020). In particular, the strong inhibitory effect of black walnut on the seedlings of *Ailanthus altissima* (a globally notorious invasive tree species) has aroused people's interest in using walnut trees to inhibit the spread of *Ailanthus altissima* (Ferus et al., 2020).

However, the transformation-based strategy also has clear limits in resisting invasive plants. Some species are not sensitive to juglanone, and some even show strong tolerance. Garlic grass is a typical case. This invasive crucifer can still thrive under black walnut forests and shows high resistance to juglanone. It may avoid its toxicity through its own metabolic system or by relying on symbiotic microbes. Invasive plants also spread fast and reproduce well. Even if many seedlings are suppressed, enough may survive and expand into the community edge. In addition, global changes may give some invasive plants stronger adaptability, further reducing the effect of the black walnut chemical barrier (Scavo and Mauromicale, 2021; Khamare et al., 2022; Murthy et al., 2025).

7 Concluding Remarks

Black walnuts rely on juglanone and related compounds to build a survival strategy of "inhibition and persistence." On one hand, they suppress surrounding plants and secure an advantage in resource competition. On the other, the strength of this effect shifts with environmental context, producing both gains and potential risks. Thoughtful management is therefore required. In natural ecosystems, allelopathy is seen as a driver of black walnut dominance during community succession. In agriculture and forestry, it provides insights for weed control and ecological planting. Plant-derived herbicides based on juglanone, or intercropping systems that reduce pesticide use, may also support sustainable production.

Several obstacles remain before broader and safer application can be achieved. Juglanone-based products require greater stability, and their impacts on non-target species must be clarified. The adaptive strategies of invasive plants present further complications. Future research directions are clear. First, molecular targets of juglanone and

the responses of affected plants should be explored. Genomic and transcriptomic tools can highlight key genes and pathways, revealing mechanisms of resistance and informing the breeding of tolerant varieties. Second, predictive models that integrate environmental variables and soil microbial activity are needed to simulate juglanone accumulation and breakdown under varying practices. Third, chemical regulation concepts should inform ecosystem design, with companion plants selected not only for tolerance but also for their ability to degrade juglanone or deliver indirect benefits to walnut growth.

By planning mixed systems such as “black walnut + tolerant forage + degrading microbes,” it may be possible to balance advantages, enhance positive effects, and reduce harm. Under climate change, attention should also be given to how weather affects chemical sensitivity. Research on the release and impact of juglanone in different scenarios will help guide its future use. The “winning by transformation” strategy of black walnut highlights the ecological secrets and practical potential of allelopathy. With deeper study, this “green tool” is likely to support ecological farming and sustainable forestry, and promote coexistence between people and nature.

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Conflict of Interest Disclosure

The authors affirm that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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