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Review

Allelopathy and Allelochemicals in Grasslands and Forests

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Abstract: Plants can produce and release allelochemicals to interfere with the establishment and growth of conspecific and interspecific plants. Such allelopathy is an important mediator among plant species in natural and managed ecosystems. This review focuses on allelopathy and allelochemicals in grasslands and forests. Allelopathy drives plant invasion, exacerbates grassland degradation and contributes to natural forest regeneration. Furthermore, autotoxicity (intraspecific allelopathy) frequently occurs in pastures and tree plantations. Various specialized metabolites, including phenolics, terpenoids and nitrogen-containing compounds from herbaceous and woody species are responsible for allelopathy in grasslands and forests. Terpenoids with a diversity of metabolites are qualitative allelochemicals occurring in annual grasslands, while phenolics with a few specialized metabolites are quantitative allelochemicals occurring in perennial forests. Importantly, allelochemicals mediate below-ground ecological interactions and plant–soil feedback, subsequently affecting the biodiversity, productivity and sustainability of grasslands and forests. Interestingly, allelopathic plants can discriminate the identity of neighbors via signaling chemicals, adjusting the production of allelochemicals. Therefore, allelochemicals and signaling chemicals synergistically interact to regulate interspecific and intraspecific interactions in grasslands and forests. Allelopathy and allelochemicals in grasslands and forests have provided fascinating insights into plant–plant interactions and their consequences for biodiversity, productivity and sustainability, contributing to our understanding of terrestrial ecosystems and global changes.

Keywords: allelopathic interference; autotoxicity; below-ground chemical interactions; plant neighbor detection; plant–soil feedback; qualitative and quantitative allelochemicals

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Citation: Xu, Y.; Chen, X.; Ding, L.; Kong, C.-H. Allelopathy and Allelochemicals in Grasslands and Forests. *Forests* **2023**, *14*, 562. https://doi.org/10.3390/f14030562

Academic Editor: Mark D. Coleman

Received: 30 December 2022
Revised: 5 March 2023
Accepted: 10 March 2023
Published: 13 March 2023

1. Introduction

Grasslands and forests are integral components of the global ecosystem, totally covering about 70% of the earth's terrestrial area. Both function as the crucial global pool of biodiversity to supply a wide range of species, and their productivity and sustainability modulate global changes [1–3]. Importantly, grasslands and forests play substantial roles in diverse ecological services to generate tremendous benefits for humans, such as water conservation, sand fixation, carbon sequestration, oxygen release and global biogeochemical cycles [4,5]. Understanding the biodiversity, productivity and sustainability of grasslands and forests and their underlying mechanisms has been of great interest to ecologists for decades.

The biodiversity, productivity and sustainability of grasslands and forests are the net outcomes of various biotic versus abiotic feedbacks between plants and their environment. These can arise through a variety of mechanisms such as resource partitioning, niche divergence, plant–soil and other species-specific interactions [6–8], but the central driver must be interspecific and intraspecific plant–plant interactions that can be neutral (consummation and recognition), positive (facilitation and kin selection) and negative (competition and allelopathy) to allow local coexistence. The interactions, either beneficial, harmful or commensal, eventually contribute to the biodiversity, productivity and sustainability of grasslands and forests. While most studies have focused on resource competition, environmental factors and global changes, relatively little is known about the importance of allelopathy in grassland and forest ecological processes [9].

A plant may interfere with the growth and establishment of neighboring plants through competition, allelopathy or both. Differing from competition for resources, allelopathy is an interference mechanism in which living or dead plants release allelochemicals exerting an effect (mostly negative) on co-occurring plants [10,11], even within a species (i.e., autotoxicity or intraspecific allelopathy). Four ecological processes, volatilization, leaching, litter decomposition and root exudation, can bring allelochemicals into air or soil. When allelochemicals contact or approach the associated plants, they directly demonstrate allelopathic action by disturbing the systems of photosynthesis, respiration, and metabolism, or indirectly affect target species by altering environmental conditions, particularly for soil physicochemical properties and microbial communities [12–14]. In fact, allelopathy originates from interspecific and intraspecific plant–plant interactions in grasslands and forests. The first classical case is black walnut (*Juglans nigra*), which produced and released a 1,4-naphthoquinone (juglone) to interfere with the growth of understory plants thousands of years ago [15]. The allelopathic interference of shrubs in grass through the release of volatile terpenes into southern California coastal grassland was reported in the 1960s [16]. Subsequently, an increasing number of studies have shown that many ecological events occurring in grasslands and forests are associated with allelopathy and certain allelochemicals [9–11,17,18].

Allelopathy in grasslands and forests is key for understanding terrestrial ecosystems and global changes. In recent decades, numerous control experiments and field investigations have been conducted to estimate the functional consequences of allelopathy for plant communities in natural and managed grasslands and forests. However, a comprehensive allelopathy, particularly for allelochemical-mediated below-ground and above-ground interactions in grasslands and forests, is rare. Understanding allelopathy with allelochemicals and their consequences for biodiversity, productivity and sustainability in grasslands and forests can provide new insight into terrestrial ecosystems and global changes. Hence, capturing recent advances and applications in allelopathy and allelochemicals is becoming valuable in advancing interdisciplinary research in grasslands and forests.

2. Allelopathy in Grasslands

2.1. Allelopathy Drives Plant Invasion in Grasslands

The occurrence of invasive plants threatens the structure and function of grassland ecosystems, especially in biodiversity and stability [17]. Several plant species have been confirmed to invade grasslands with an allelopathic mechanism. Spotted knapweed (*Centaurea stoebe*), native to Europe and introduced into North America, is an example of an invasive plant in western American grasslands. Spotted knapweed can take advantage of root-secreted allelochemicals against local grassland species and alter nutrition availability and underground microbial community composition [18,19]. However, the allelopathy of spotted knapweed is conditional, and there is discrepancy between geographical sites. Spotted knapweed does not exhibit allelopathic invasion in eastern American grasslands [20]. Additionally, sufficient light or infection with fungal endophytes can enhance the allelopathic invasion of spotted knapweed in American grasslands [20,21].

Allelopathic invasion of spotted knapweed in American grasslands results in the novel weapons hypothesis (NWH) that the success of plant invasion can be attributed to the allelochemicals of invaders [22]. Generally, allelochemicals of invasive species have little effect on their original neighbors due to long-term mutual adaptation, but as they are novel to the species of the invaded habitat, they exert a strongly allelopathic interference on the native species [22]. Much evidence has demonstrated that allelochemicals appear to confer a competitive advantage to the invasive plants [23–26]. However, some studies did not fully support the NWH, and questioned the necessity of secondary metabolites for nonnative species to ensure invasive success [27–29]. Another hypothesis, the biochemical recognition hypothesis (BRH), postulates that plant seeds can adaptively detect phytochemicals released from potential competitors and respond by extending their period of dormancy until better establishment conditions occur [30]. Leachates from spotted knapweed reduced the germination rate of grassland species. Importantly, they had no effect on seeding biomass, implying that the allelochemicals in the leachates are non-phytotoxic and do not impede plant growth [30].

Although both the NWH and BRH focus on plant-derived chemicals and predict similar results that phytochemicals released from invasive plants inhibit the emergence of native plants, their fundamental mechanisms are distinct. This can be explained either a negative exposure to toxic chemicals by NWH or a positive recognition of facilitative chemicals by BRH [22,30]. Nevertheless, whether the success of invasive plants is attributed to allelochemicals has been debated. Actually, allelopathy is pervasive in invasive plants [31]. Interestingly, allelopathy of native grassland communities seems to increase their resistance to invasion by introduced plants [32], but there was no evidence that native plant communities' tolerance to allelopathy contributes to the degree of invasiveness of introduced plants. A more vital linkage between allelopathic traits and invasive performance needs to be explored in further studies.

2.2. Allelopathy Exacerbates Grassland Degradation

Grassland degradation is a phenomenon in which grass struggles to grow or hardly survives, which usually leads to an irreversible reduction in grassland productivity and biodiversity [33]. Many factors have been regarded as the drivers of grassland degradation, of which the main factors are natural climate change and human disturbance [34,35]. One early sign of degraded grassland is that the originally dominant species are gradually replaced by other adaptable plants, such as toxic weeds with allelopathic traits [36–38]. Toxic weeds in degraded grassland are adapted to extremely harsh environmental conditions and exhibit high aggression toward surrounding plants, even poisoning livestock or humans [39,40].

In the process of grassland degradation, toxic weeds not only vigorously compete with forage plants for water and nutrition resources, but also produce a wide range of secondary metabolites to exert allelopathic effects on the establishment of the co-occurring plants, subsequently reducing species richness and exacerbating grassland degradation [41–43]. Several studies have shown that extracts of toxic weeds, regardless of plant tissues or growing soil, can reduce the seed germination rate and seedling biomass of the receiving plants [38,44,45]. However, the allelopathic effects have distinct differences among the extract concentration, extract source and tested species [44]. Many phytotoxic compounds, such as coumarins, flavonoids and terpenoids, have been isolated and identified from toxic weeds. These potential allelochemicals could jeopardize the photosynthesis, respiration, and metabolic system of plants [46–48].

Stellera chamaejasme and *Artemisia frigida* are representatives of toxic weeds and generally serve as bioindicators to characterize the degree of grassland degradation. *S. chamaejasme* is a common toxic weed in the degraded grasslands of northern China, which can restrict the growth of co-occurring plants via root exudates [38,49]. *A. frigida*, a perennial dicotyledonous semi-shrub species, has a wide distribution range in the global temperate grasslands, covering Eurasian steppes and northern mixed-grass prairies. Differing from the mainly allelopathic pathway of *S. chamaejasme*, *A. frigida* can significantly decrease seed germination and seedling growth by emitting volatile organic compounds (VOCs) as allelochemicals [50,51]. This environmental disturbance may severely influence the composition and abundance of VOCs emitted from *A. frigida*. Artificial damage can induce *A. frigida* to release more categories and greater concentrations of VOCs [51]. In particular, grazing activity can enhance the allelopathic effect on the growth of other grassland species, suggesting that allelopathy may interact with over-grazing grassland to accelerate the grassland deterioration by frequently simulating *A. frigida* [52].

Overall, allelopathy is one of the critical factors driving grassland degradation. Comprehensively understanding of how allelochemicals from toxic weeds mediate intraspecific and interspecific plant–plant interactions would be useful for rehabilitating degraded grassland.

2.3. Allelopathy in Pasture Management

A pasture is a piece of grassland that mainly grows forage grass for livestock. Its quantity and quality are closely related to grassland ecosystem health and animal husbandry development. Hence, the management of pasture, whether natural or managed, is essential to ensure adequate forage grass and to support livestock production.

Allelopathy-based interspecific and intraspecific interactions have ecological consequences for the productivity and biodiversity of a pasture. Particularly in a managed pasture, pasture weeds can immensely decrease forage yield and quality, negatively affecting livestock production. Fortunately, some forage species can take full advantage of allelopathy and allelochemicals to retard the emergence and growth of co-occurring weeds, from which they will obtain growing benefits [53,54]. For example, rye (*Secale cereale*) is a cool-season forage species with high frost and drought resistance; it is generally planted in infertile or acid soils due to its strong adaptability. Rye can produce and release benzoxazinoids to selectively inhibit broadleaf weeds, modifying the spectrum of weed species in the pasture [55,56]. Therefore, some fine forage cultivars with allelopathic traits can be used for weed control. In particular, natural allelochemicals released from allelopathic forage cultivars may act as biological herbicides to a large extent, lowering the consumption of chemical herbicides and the cost of pasture management [57,58]. Many studies have shown that the application of allelopathic forage cultivars can effectively control pasture weeds and increase pasture productivity [55,57,59]. Notably, allelopathic forage species such as rye not only suppressed the pasture weeds but also succeeding forage species. To avoid failure in rotation systems, it is warranted to select resistant succeeding forage species [60].

Autotoxicity (intraspecific allelopathy) is ubiquitous in pastures. Autotoxicity in pasture has been well verified in alfalfa (*Medicago sativa*) [61–63]. Alfalfa is a major forage legume used as a high-quality livestock feed and cultivated in pastures throughout the world. Several phytotoxic phenolics, saponins and medicarpin in alfalfa can remarkably suppress their own seed germination. To attenuate the autotoxicity, the most obvious solution is to develop a new autotoxicity-tolerant alfalfa cultivar. A recent study has picked out the most autotoxicity-tolerant alfalfa from 22 cultivars based on a technique for order of preference by similarity to ideal solution analysis [64], which provides a theoretical basis for the breeding of autotoxicity-tolerant alfalfa cultivars. However, a long-term and large-scale field verification is needed to assess the tolerance of different alfalfa cultivars to autotoxicity.

A mixture of diverse forage species is considered as another option to experimentally prove effectiveness in improving forage productivity [65,66]. Directly, some highly allelopathy-tolerant forage seeds can be used as a subsequent alternative for restoring sparse natural grassland caused by allelopathy [67]. Additionally, the pattern of mixing species also has another benefit for pastures. The mixture of rye with berseem clover (*Trifolium alexandrinum*) may promote rye pathogen-resistant capabilities [68]. In the coexistence system of *Artemisia adamsii* with *Stipa krylovii*, volatiles emitted by *A. adamsii* can strengthen photosynthesis of *S. krylovii* by enhancing stomatal conductance even with water deficiency [69]. When grown with the P-mobilizing species *Filifolium sibiricum*, *Leymus chinensis* exhibited greater shoot and root P content [70]. These positive interactions are prevalent in pastures and mostly attributed to plant–plant chemical communication.

3. Allelopathy in Forests

3.1. Allelopathy in Natural Forests

Natural forests usually possess plant diversity and stable productivity. The role of allelopathy and the mechanisms underpinning it remain poorly resolved in species-rich forests, but allelopathy does contribute to natural forest regeneration. Forest regeneration is commonly considered as a critical ecological process that sustains resource reproduction through the establishment of saplings and the replacement of dead trees; it has profound implications for the perpetuation of tree species in the temporal and spatial dimensions. However, long-term exposure to allelochemicals from woody species may create a barrier effect on the understory-regenerated saplings, resulting in forest regeneration failure. In particular, endangered and rare plant species are inherently difficult to generate due to their scarce propagules and low adaptability. Allelopathy additively reduces the likelihood of the sapling establishment and probably leads to locally rare species' extinction. *Cinnamomum migao* and *Metasequoia glyptostroboides* are two endangered woody species. Their regeneration is extremely restrained, and the natural population would be gradually diminished over time without active management. Generally, most natural populations only occasionally have 1~2 saplings in their understories [71,72]. Recent studies found that leaf extracts or litters of *C. migao* and *M. glyptostroboides* dramatically impeded their seedling growth by impairing the lipid structure of the cell membrane, suggesting that autotoxicity might aggravate the obstruction of the natural forest regeneration among some endangered tree species [72,73].

Apart from autotoxicity or self-inhibition, allelochemical-mediated interspecific interactions also hinder natural forest regeneration and impact the plant community's composition. In the context of forests dominated by two tree species, dominant tree species may chemically inhibit the sapling regeneration of the others. For example, *Kandelia obovate* and *Aegiceras corniculatum* are two dominant species in mangrove forests. Leaf litter leachates of *K. obovate* are detrimental to the propagule germination and sapling growth of *A. corniculatum*, ultimately modulating the natural regeneration of the whole mangrove forest [74]. In the later successional forests of maple-beech codominance (*Acer saccharum* and *Fagus grandifolia*), the abundance of beech progressively increases as maple decreases with the years. This result, in part, can be explained by the allelopathic advantage of beech leading to the regeneration failure of maple [75,76].

Monopolistic herbaceous plants grown in the floor layer may inhibit natural forest regeneration. For example, the natural regeneration of sessile oak (*Quercus petraea*) is often hampered by the dense moor grass (*Molinia caerulea*) understory [77]. When watered with root exudates of moor grass, a significant decrease in oak biomass occurred, suggesting the allelopathic interference of moor grass in oak growth. Even though this negative impact was lower than that of resource depletion, it demonstrated the crucial contribution of herbaceous allelopathy to natural forest regeneration [78].

Based on the understanding of the allelopathic mechanisms underlying natural forest regeneration, some appropriate methods of forest management are proposed to alleviate the adverse effects of allelopathy and promote long-term natural regeneration. One of the most direct and efficient ways is to reduce the frequency of allelopathic interactions by removing litter, or eradicating the allelopathic species. Prevention of saplings from potential allelochemicals facilitates the sustainability of forest health [78,79]. In addition, attempts to enhance the diversity of the shrub layer and floor layer may be an alternative way to promote natural forest regeneration [80].

3.2. Allelopathy in Tree Plantations

A tree plantation is an artificial forest for the large-scale production of wood; usually, easily established and fast-growing tree species are selected as a monoculture forest. The productivity and sustainability of tree plantations intimately links the economic and ecological benefits of forestry. However, successive rotations of some forestry species may cause a replanting problem or soil disease, resulting in a decline in productivity and the loss of biodiversity in plantations [81,82]. Although the underlying mechanism for this issue is still being disentangled, a growing amount of evidence has shown that allelochemicals enriched in soil are mainly responsible for this problem [83,84].

Eucalyptus is one of the most widely planted forestry genera on the planet, but it has suffered from autotoxicity for a long time. Most studies have demonstrated that allelochemicals of *Eucalyptus* penetrate into the soil through the decomposition of litter and leachates, exerting an allelopathic effect on understory plants, thus limiting the regeneration of native vegetation [85,86]. However, Zhang et al. (2016) argued that the poor establishment of indigenous vegetation on plantations mainly arose from *Eucalyptus* roots rather than *Eucalyptus* litter. Retention of understory litter is more likely to facilitate the performance of native species [87]. Whatever the case is, a consensus is that allelopathy is more crucial than resource competition in the replanting problem of *Eucalyptus* plantations [88]. Chinese fir (*Cunninghamia lanceolata*) is another tree plantation severely disrupted by autotoxicity. Regeneration failure and poor establishment have remained critical problems in monocultural plantations of this species [89]. However, root exudates contribute more to soil allelochemicals than the litter in Chinese fir plantations. Root-secreted allelochemicals, therefore, are considered a primary source leading to the decline in the plantation of Chinese fir [90].

The mixture of multiple tree species is an effective way to improve the self-inhibition and soil deterioration caused by allelopathy and allelochemicals in plantations [91–93]. In *Eucalyptus* plantations, *Albizia lebbeck*, an introduced N-fixing species, has been regarded as a 'good partner' to *Eucalyptus*. Mixed-species plantations of *Eucalyptus* with *A. lebbeck* increase productivity and maintain soil fertility compared with pure *Eucalyptus* stands [91]. Similarly, the establishment and productivity of autotoxic Manchurian walnut (*Juglans mandshurica*) can be improved in the presence of larch (*Larix gmelini*). Larch root exudates and soil in mixed-species plantations greatly stimulated the growth of Manchurian walnut seedlings and rapidly degraded the allelochemical juglone [92]. The growth and regeneration of Chinese fir is improved in *Michelia macclurei* and Chinese fir mixed-species plantations. One of the explanations for this beneficial promotion is that there may be interspecific facilitation mediated by the root exudates from *M. macclurei*, which not only attenuate the release of allelochemicals from Chinese fir roots but also induce a microbial shift to accelerate the decomposition rates of allelochemicals [93]. These studies illustrate the importance of mixed-species stands in plantations. However, most successful mixtures were empirically established from traditional practices, or were assessed from haphazard experimental combinations. We lack effective strategies for a priori selection of mixtures to achieve relevant benefits. Therefore, understanding intraspecific or interspecific allelopathy will be a key step in screening appropriate combinations of tree species to design plantations.

3.3. Tree-Understory Vegetation Allelopathic Interactions

The canopy position and soil occupancy of dominant forest trees remarkably reduce light and soil nutrient availability for understory vegetation. Even so, some shrub and herbaceous species in understory vegetation can adapt to these diverse conditions and coexist with trees. Apart from competition for resources, the allelopathy of the trees is an interference mechanism for the growth of understory vegetation [94,95]. The allelopathic trait of some trees is highly associated with forest abundance and biodiversity, particularly for woody invasive species. The presence of allelopathic tree species in forests can reduce the abundance of understory vegetation, ultimately becoming dense monospecific stands and extending to the whole forests [96–98]. In this process, allelochemicals may act as a meditator [99].

For the allelopathic effect of trees on understory plants, leaf litter and leachates have long been considered the main source [100,101]. Leaf litter and leachates from trees falling into the ground may prevent the colonization and development of understory vegetation [102,103]. This suppression is mainly attributed to their physical and chemical effects [104,105]. However, allelochemicals from leaf litter and leachates also have a measurable effect on understory vegetation [106–108]. Through the decomposition of leaf litter, allelochemicals can be gradually liberated into the soil and come into effect by altering soil pH, nutrient availability, the nitrogen cycle and microbial community structures [109,110]. Especially intriguing is leaf litter and leachates that may modify plant coexistence in the grass layer. For example, spotted knapweed and *Bromus tectorum* exhibit strong competition with each other, while leaf litter and leachates of *Pinus ponderosa* can mitigate the competitive effect of spotted knapweed on *B. tectorum*. In other words, the presence of

P. ponderosa shifted competitive outcomes through physical and allelopathic effects, thereby indirectly facilitating *B. tectorum* by more strongly inhibiting spotted knapweed [111].

In some cases, leaf litter and leachates cannot solely show allelopathic potential. It must unite other biotic or abiotic factors to jointly impact the ecological process [102,112]. *Prosopis juliflora* is one of the world's most aggressive invasive species, the leaf litter of which causes the increase of total phenolics in soil and toxifies understory vegetation [113]. When incubated with similar levels of leaf leachate from *P. juliflora*, the content of allelochemicals varies in different soil textures. Sandy soil accumulates higher levels of phenolics than sandy loam soil due to the greater absorption of inactive phenolics fettered in sandy loam soil [112]. In addition, the allelopathic effect of *P. juliflora* is also limited by soil moisture because their water-soluble allelochemicals in the soil are more likely to be washed away by rain. Therefore, *P. juliflora* could not manifest their allelopathic potential in humid soil. Only in dry environments, *P. juliflora* can create a depressive impact on understory plants [114].

Dense understory species with highly allelopathic potential, in turn, may directly slow the growth of trees and indirectly cause trouble by dissolving the fungal hyphae of trees. Garlic mustard (*Alliaria petiolata*) is a typical understory invasive species that may suppress fungal mutualists via allelochemicals, leading to significant declines in a series of physiological and metabolic functions [115–117]. Nevertheless, arbuscular mycorrhizal fungi (AMF) strains can be quickly selected by the allelopathic stress from garlic mustard. After the initial decline in AMF abundance, resistant AMF strains gradually displace sensitive AMF strains and the abundance rises again after the long-term invasion of garlic mustard [118,119]. Moreover, as an invader, the novelty of allelochemicals to resident species, regardless of the plant or microorganism, diminishes over time. Ultimately, garlic mustard may enter a new coevolutionary relationship with native competitors and slowly be integrated into the native community [120,121].

4. Allelochemicals in Grasslands and Forests

4.1. Category of Allelochemicals

All the occurrences of allelopathic phenomena can be attributed to a certain or a set of allelochemicals. Allelochemicals and their properties largely determine the allelopathic effectiveness. In the past decades, numerous old and new allelochemicals have been detected and identified from herbaceous and woody species in grasslands and forests. These allelochemicals involve a diversity of plant secondary metabolites, but are mainly divided into three categories of phenolics, terpenoids and nitrogen-containing compounds.

Phenolics have a wide distribution in plants and represent a diverse group of compounds with an aromatic ring possessing at least one hydroxyl group and possibly other substituents, including simple phenolic acids, coumarins, flavonoids and quinones. In forests, a tremendous amount of lignin from litter is decomposed into a variety of phenolic acids. These lignin-derived phenolic acids are main allelochemicals in forest soil, leading to a decline in forest species' abundance and biodiversity. For example, the soil of the *Eucalyptus urograndis* plantation contains high levels of hydroxybenzoic, vanillic, coumaric and ferulic acids (Figure 1), resulting in autotoxicity of *E. urograndis* [85]. However, the allelopathic effect of phenolic acids is concentration-dependent. In particular, individual phenolic acids are insufficient to effectively suppress the growth of co-occurring plants, but their mixtures exhibit phytotoxic effects [122].

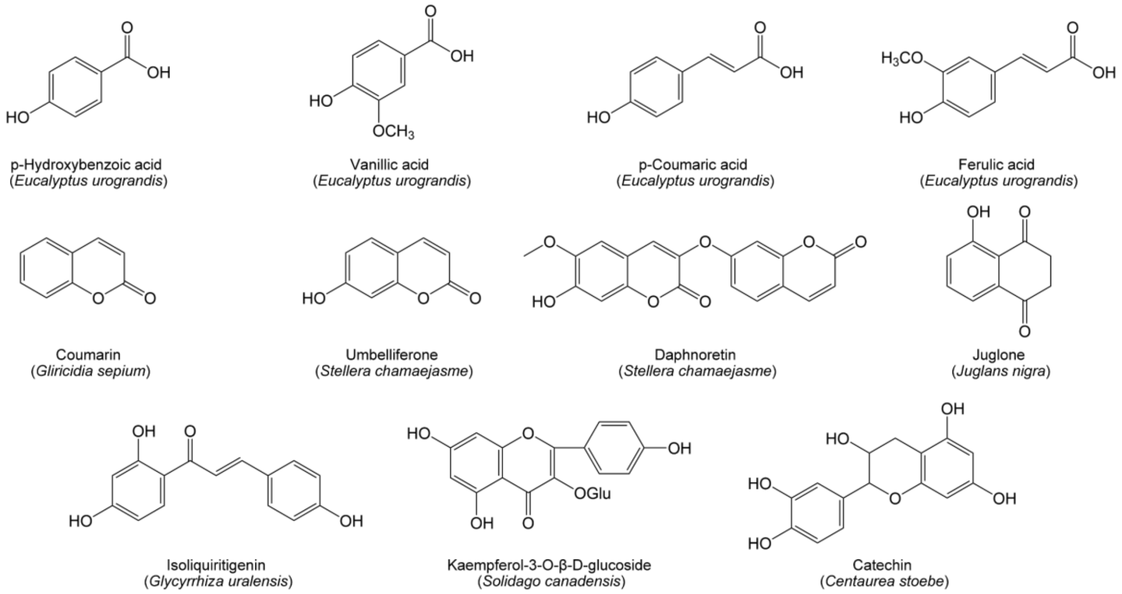

Figure 1. Phenolic allelochemicals from herbaceous and woody species in grasslands and forests.

Many coumarins possess phytotoxicity and act as potential allelochemicals in grasslands and forests. Coumarin exacted from the leaf of *Gliricidia sepium* was identified as an allelochemical to inhibit the growth of plants [123]. Umbelliferone and daphnoretin (Figure 1) are two coumarin allelochemicals in *Stellera chamaejasme* [38]. Umbelliferone can inhibit plant growth by inducing membrane lipid peroxidation and retarding cell division, while daphnoretin inhibits plant growth by arresting the mitosis process [124].

Flavonoids generally perform a broad range of ecological functions. Several flavonoids have proved to be allelochemicals in grasslands and forests. Isoliquiritigenin (Figure 1) is a flavonoid allelochemical in *Glycyrrhiza uralensis*. It is able to trigger a chain of reactions in plant cells, including the overproduction of reactive oxygen species, lipid peroxidation, and a decline in cell vitality and chlorophyll content, ultimately resulting in seedling growth inhibition [125]. Another flavonoid, kaempferol-3-O-β-D-glucoside (Figure 1), is an allelochemical of *Solidago canadensis* [126]. Catechin (Figure 1) is a controversial flavonoid allelochemical secreted by spotted knapweed. Many studies have found high catechin concentrations in spotted knapweed soils [127,128] and proposed that catechin acts as a novel allelochemical of spotted knapweed, which contributes to growth limitation of the native plants [18]. However, several studies pointed out that catechin was hardly present in the bulk soils of spotted knapweed, and possessed low phytotoxicity to a variety of plant species [27,28].

Quinones are the classical allelochemicals in forests. Juglone (Figure 1) is an exclusive allelochemical of *Juglandaceae* family and represents one of the best-known members of quinones [129]. Initially, juglone is stored in leaves, barks and roots in the form of non-toxic naphthol O-glycoside. When released from plant living tissues to the environment, it is hydrolyzed into a less phytotoxic naphthol, and subsequently oxidized into phytotoxic juglone. The allelopathic mechanisms of juglone are associate with the disruption of leaf photosynthesis, transpiration, respiration and stomatal conductance. Additionally, juglone has high stability in soil. The toxicity of juglone can maintain for up to a year in spite of the removal of the walnut trees [130].

Terpenoids, including monoterpenes, sesquiterpenes, diterpenes, triterpenes and steroids, are a class of compounds derived from the 5-carbon isoprene. Monoterpenes and their derivatives possess strong volatility and may interact with neighboring plants in their gaseous phase. Volatile allelochemicals emitted by donor plants generally impact surrounding plants through two main pathways, either forming 'terpene clouds' of directly impacted target plants [16], or leaching into the soil of indirectly affected target plants. The volatiles of *A. frigida* contain a copious quantity of terpenoids, among which monoterpene camphor is a key allelochemical affecting the neighboring species [36]. Another monoterpene, (−)-α-thujone, emitted from *Thuja occidentalis* (Figure 2), can display phytotoxic activities against seed germination and seedling growth of *Taraxacum mongolicum* and *Arabidopsis thaliana* [131]. β-Caryophyllene (Figure 2), a sesquiterpene within the needle litter of *Pinus halepensis*, exerts a deleterious effect on the germination and growth of herbaceous target species [132]. Dihydromikanolide (Figure 2) is another sesquiterpene allelochemical from *Mikania micrantha*, which contributes to promoting soil bacterial diversity but reduces fungal diversity [133]. Two diterpenes, ent-kaurene and phyllocladane (Figure 2), isolated from senescent needles of *Araucaria angustifolia* can act as allelochemicals to inhibit the germination and seedling growth of neighboring plants [134]. Similarly, diterpene allelochemicals, 7-oxodehydroabietic acid and 15-hydroxy-7-oxodehydroabietate (Figure 2), were found in the understory soil of *Pinus densiflora*. Both allelochemicals may be the underlying cause of sparse understory vegetation within the *P. densiflora* canopy [135]. Besides, some pentacyclic triterpenoids may function as allelochemicals, such as betulinic, oleanolic and ursolic acids (Figure 2) within the litter of *Alstonia scholaris*, limiting the growth of co-occurring species by inhibiting seed germination, radicle growth and the functioning of photosystem II [136].

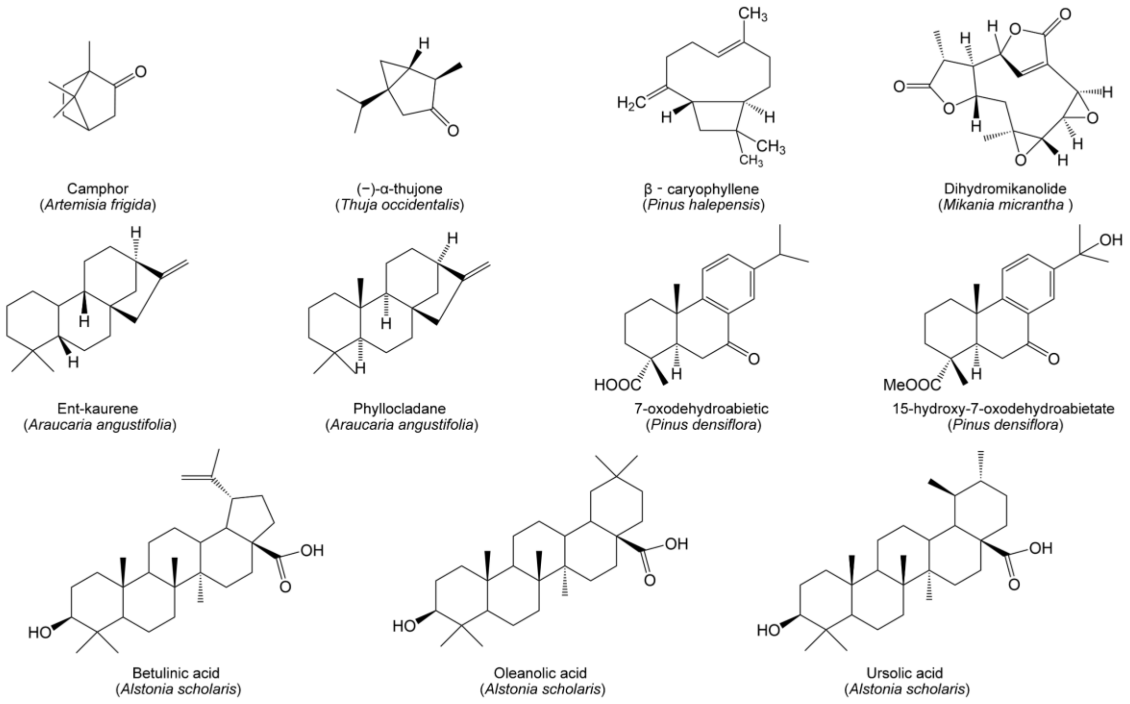

Figure 2. Allelopathic terpenoids from herbaceous and woody species in grasslands and forests.

Nitrogen-containing compounds mainly include alkaloids, non-protein amino acids, benzoxazinoids and cyanogenic glycosides. Compared with phenolics and terpenoids, nitrogen-containing allelochemicals are relatively unknown. However, several specialized nitrogen-containing metabolites have been identified as allelochemicals that have significant ecological implications for grasslands and forests. Hexadecahydro-1-azachrysen-8-yl ester (Figure 3), identified as a potential alkaloid allelochemical in *Imperata cylindrica,* can reduce root growth and mycorrhizal colonization [137]. There are many non-protein amino acids involving allelopathic interferences with co-occurring species in grasslands (Figure 3). *meta*-Tyrosine of fine fescue grasses (*Festuca rubra*) can interfere with the root development of competing plants [138]. Mimosine of *Leucaena leucocephala* can retard plant growth by blocking the cell division of protoplasts and disturbing the associated enzyme activity [139]. L-Canavanine of *Vicia villosa* not only exerts the phytotoxic effect by disrupting the arginine metabolism in the plants but also significantly alters the microbial community composition and diversity in soil [140,141]. A novel cyclic dipeptide (6-Hydroxy-1,3-dimethyl-8-nonadecyl-[1,4]-diazocane-2,5-diketone) (Figure 3) has been found in Chinese fir; it is a highly active allelochemical to be responsible for serious replanting problems in plantations [142]. Benzoxazinoids are a class of well-known nitrogen-containing allelochemicals, among which 2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one (DIMBOA) and 2,4-dihydroxy-(2H)-1,4-benzoxazin-3(4H)-one (DIBOA) (Figure 3) can be released by rye and exert strong suppression of plant growth [143,144]. Cyanogenic glycosides are specialized metabolites derived from amino acids. Sinigrin (Figure 3), as an allelochemical of cyanogenic glycosides from garlic mustard and broccoli (*Brassica oleracea*); it can lead to the poor establishment of North American forests by disrupting the AMF symbionts [145].

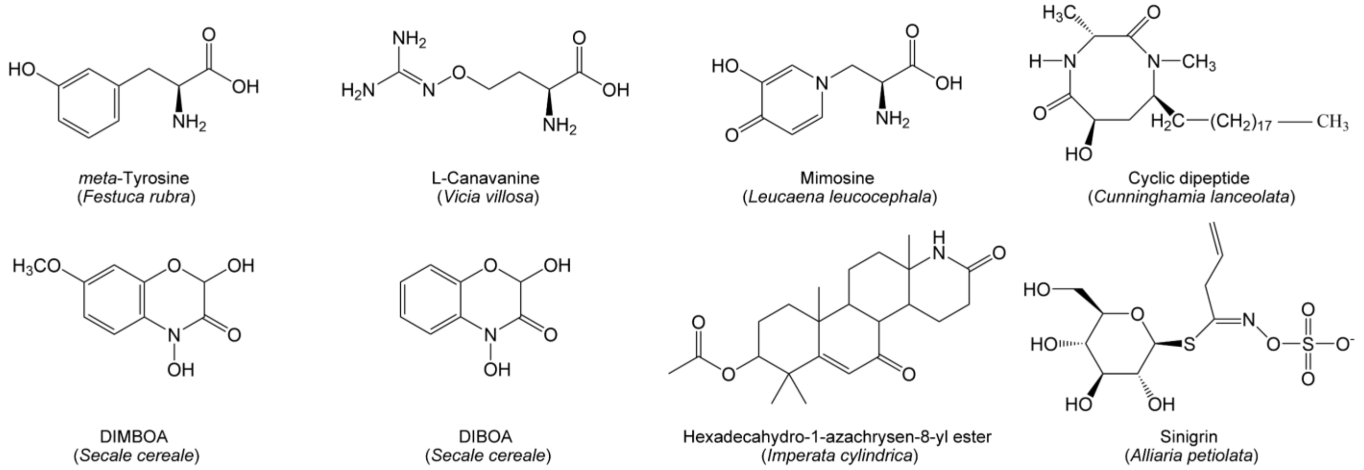
meta-Tyrosine (*Festuca rubra*)
L-Canavanine (*Vicia villosa*)
Mimosine (*Leucaena leucocephala*)
Cyclic dipeptide (*Cunninghamia lanceolata*)
DIMBOA (*Secale cereale*)
DIBOA (*Secale cereale*)
Hexadecahydro-1-azachrysen-8-yl ester (*Imperata cylindrica*)
Sinigrin (*Alliaria petiolata*)

Figure 3. Nitrogen-containing allelochemicals from herbaceous and woody species in grasslands and forests.

4.2. Identification and Detection of Allelochemicals

Allelochemicals can be either unknown or known in plants and their environments. Unknown allelochemicals have to be identified by non-targeted analysis, while known allelochemicals can be detected by targeted analysis. The identification of unknown allelochemicals first isolates pure individuals from sample components, and then the individuals can be determined and analyzed by mass spectrum, infrared spectrum and nuclear magnetic resonance [11]. Such non-targeted analysis may investigate which allelochemicals are responsible for the allelopathic interactions in a given system. Therefore, applying non-targeted analysis for identification of unknown allelochemicals has been key to understanding the ecological role of allelopathy in grasslands and forests.

Compared with the identification of unknown allelochemicals, detection of known allelochemicals is straight forward. Targeted analysis of known allelochemicals is usually conducted by means of gas or liquid chromatography coupled with tandem mass spectrometry (GC-MS/MS, LC-MS/MS). GC-MS/MS is the most preferred technique for qualitative and quantitative assessment of volatile allelochemicals. In contrast, non-volatile allelochemicals with relatively high molecular weight, mainly produced and released from root exudation and plant decomposition, can be analyzed with LC-MS/MS.

Understanding the functional significance of allelopathic plant–plant interactions and processes occurring in grasslands and forests requires accurate information about the quantity, quality and spatiotemporal dynamics of allelochemicals. The best way to trap and detect allelochemicals in vivo, in situ and real time from living plants and their environments remains a problem. Accordingly, it is warranted to develop analytical methods that are more realistic or closer to the actual field situation [146]. Phillips et al. (2008) designed an experimental system employed to trap root exudates from intact tree roots in situ. This method can account for the spatial heterogeneity and temporal dynamics of forest soils and root systems [147]. A recent study has developed quick and in situ detection of allelochemicals in Taxus soil by microdialysis combined with UPLC-MS/MS [148], providing a more finely tuned picture of allelochemical dynamics in grasslands and forests.

4.3. Activity-Concentration Relationship of Allelochemicals

The action of allelochemicals is concentration-dependent. Thus, the activity–concentration relationship is crucial for allelochemical interference, particularly for their presence at the phytotoxic level in the soil. Although soil abiotic factors such as pH, enzyme activities, organic matter and nutrient availability contribute to the change of allelopathic activity, microbial effects are undoubtedly the most crucial factor that affect allelochemicals in the soil. Soil microbes determine the below-ground transportation and intensity of allelochemicals. Accordingly, the fate and dynamics of allelochemicals are mainly attributed to soil biological processes, and potential abiotic controls. For instance, flavonoid allelochemicals have high persistence in soil because they are decomposed very slowly and last a long time in soil, which favors suppression of the emergence and growth of plants and modification of the soil's properties, even at the low levels [149]. However, a recent study has found that soil organic carbon decreases the lifetime of flavonoids underlying plant–microbe interactions. In particular, the dissolved organic carbon in soils can repress flavonoid bioavailability and attenuates the efficacy of flavonoid-based plant–microbe communication [150].

Allelochemicals in grasslands and forests have differential concentrations, activities and categories. Most phenolics at a high concentration show allelopathic activities. Terpenoids and nitrogen-containing allelochemicals may impact plant species at a low concentration (Table 1). Accordingly, the action of phenolics involved in allelopathy requires a considerable amount of them, representing quantitative allelochemicals. In contrast, the act of terpenoids and nitrogen-containing allelochemicals greatly depends on their category rather than their amounts, representing qualitative allelochemicals. In addition, qualitative terpenoids with a diversity of allelochemicals frequently occur in annual grasslands, while quantitative phenolics with a few specialized allelochemicals occur in perennial forests. This is due to the production and release of allelochemicals in perennial forests by large-scale litter decomposition.

Table 1. The phytotoxic level of important allelochemicals in grasslands and forests.

Allelochemicals	Class	Targeted Species	IC50/μM *	Sources
Vanillic acid	Phenolic acids	*Lactuca sativa*	950.2	[151]
Hydroxybenzoic acid	Phenolic acids	*Lactuca sativa*	2470.0	[152]
Coumaric acid	Phenolic acids	*Lepidum sativum*	1120.0	[153]
Ferulic acid	Phenolic acids	*Arabidopsis thaliana*	1099.0	[154]
Juglone	Quinones	*Lactuca sativa*	50.0	[155]
Coumarin	Coumarins	*Lactuca sativa*	23.3	[55]
Umbelliferone	Coumarins	*Lactuca sativa*	430.0	[124]
Daphnoretin	Coumarins	*Lactuca sativa*	1558.3	[124]
Isoliquiritigenin	Flavonoids	*Lactuca sativa*	823.4	[125]
Camphor	Monoterpenes	*Lactuca sativa*	50.0	[156]
(−)-α-Thujone	Monoterpenes	*Taraxacum mongolicum*	140.2	[131]
Betulinic acid	Triterpenes	*Lactuca sativa*	78.8	[136]
Oleanolic acid	Triterpenes	*Lactuca sativa*	94.2	[136]
Ursolic acid	Triterpenes	*Lactuca sativa*	101.6	[136]
Cyclic dipeptide	Nonprotein amino acids	*Cunninghamia lanceolata*	12.5	[141]
meta-Tyrosine	Nonprotein amino acids	*Lactuca sativa*	17.0	[138]
Mimosine	Nonprotein amino acids	*Lactuca sativa*	300.0	[155]
DIMBOA	Benzoxazinoids	*Lepidium sativum*	542.3	[157]
DIBOA	Benzoxazinoids	*Lepidium sativum*	493.1	[157]

* Half-maximal inhibitory concentrations.

In many studies, the applied concentrations of allelochemicals were greater than those detected in the environment. This issue was because the concentrations of allelochemicals detected would be locally much higher in intact soils. Extractions would have diluted the allelochemicals over large soil volumes. Additionally, frequent allelochemicals provided over a long term at low concentrations can have powerful effects. Thus, even if the actual concentration of allelochemicals in the environment was still substantially lower than the necessary concentration to impact neighboring plant species, an effect would still be expected, because in the environment, there would be a constant release of allelochemicals.

5. Allelochemicals Mediate Below-Ground Interactions and Plant–Soil Feedback

5.1. Below-Ground Chemical Interactions

The action of allelochemicals requires their presence in the environment. Environmental factors such as temperature, light, soil nutrients and microorganisms may strengthen or alleviate the allelochemical activity. This adjustment of the action of allelochemicals in response to the environment reflects the adaptability of the allelopathic plants [9]. Most allelochemicals shift from plants into the soil following root exudation, decomposition, volatilization and leaching. These allelochemicals dispersing in the soil inevitably interact with a variety of below-ground components particularly for root placement pattern [158], soil nutrient availability, microbial community structure, mycorrhizal fungi colonization, and subsequent plant–soil feedback [8]. Therefore, the biodiversity, productivity and sustainability of grasslands and forests may be driven by allelochemical-mediated below-ground interactions and plant–soil feedback. Such a conceptual framework is outlined in Figure 4.

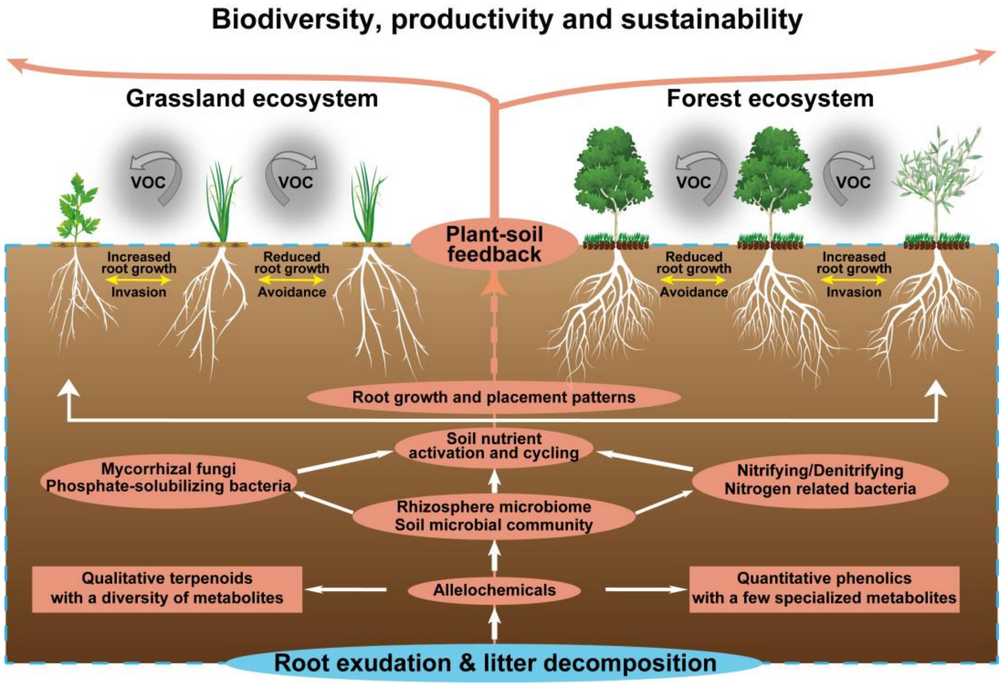

Figure 4. Allelochemical-mediated below-ground interactions and plant–soil feedback.

The root is a vital organ interacted with soil. In response to the soil environment, a plant may place its roots in intrusive (approaching), avoidant (repelling) or unresponsive patterns [159]. Such root placement patterns, particularly for intrusive and avoidant patterns, may be driven by allelochemicals [160,161], altering below-ground ecological interactions and ultimately affecting plant performance and productivity (Figure 4). A recent study has revealed that pairwise allelopathic plant–plant interactions generate all possible combinations of intrusive, avoidant and unresponsive root placement [158]. Allelopathic species showed a general tendency toward root intrusion, while most target species adjusted root placement to avoid root-secreted allelochemicals from allelopathic species [158]. Similar allelochemical-mediated root responses have been observed in forage grass and tree species, such as avoidant response of annual ryegrass (*Lolium rigidum*) roots to neighboring allelopathic canola (*Brassica napus*) [162], and root avoidance in mixed-species plantations of Chinese fir and *Michelia macclurei* [93].

Allelochemical-mediated root placement patterns may contribute to plant–microbe interactions that control vital below-ground processes [158,163]. Allelochemicals are important carbon sources of soil microorganisms that determine the changes in microbial composition and community, and then affect the activation and circulation of soil nutrients (Figure 4). Cinnamic acid can significantly alter soil microbial community functional diversity and genetic diversity [164]. The hyphal branching of AMF is induced and stimulated by flavonoids, and flavonoid-associated microorganisms can colonize the roots of a very wide range of plants in order to increase nutrient uptake, especially that of P, and enhance the plant health [165]. Allelochemicals also directly participate in the activation and cycling of soil nutrients. p-Hydroxybenzoic acid can alter the form of soil N, causing Chinese fir seedlings to shift their N uptake preference from NO_3^- to NH_4^+ [166].

In grassland ecosystems, allelochemicals exuded by toxic weeds may trigger a series of changes in soil enzyme activities, pH, nutrient availability and mycorrhizal fungal colonization [12,13,167]. In particular, the exudate-induced alteration of the soil microbial community heavily promotes the expansion of toxic weeds by supplying higher rhizosphere nutrients [14,45]. Compared with the soil free of toxic weed *Stellera chamaejasme*, the soil infested with *S. chamaejasme* exhibited lower nutrition, organic matter, fungal alpha diversity, and relative abundance of AMF, but a higher abundance of pathogenic fungi [13]. Moreover, *S. chamaejasme* root exudates were alkalescent (pH = 9.28) and had a negative effect on the rate of mycorrhiza infection and spore density of the AMF [167]. Together, allelochemicals exuded from *S. chamaejasme* might increase the soil pH, reduce the soil nutrient availability, damage the AMF of other plants and recruit more pathogenic fungi, thereby posing a great threat to grassland vegetation [167].

In forest ecosystems, the roots of most tree species are extensively infested with obligately soil-borne fungi and mycorrhizas that assist plants in nutrient acquisition, pathogen resistance and carbon transportation [168,169]. Several studies found the critical role of soil microorganisms in the maintenance of *Eucalyptus* plantations, which may mitigate the allelopathic effect of *E. grandisis* leachates [170]. Specifically, a lower content of total phenolics occurred in nonsterile soils than in sterile soils when both were exposed to the *E. grandisis* leachates [171]. In addition, root-associated fungi probably utilize *Eucalyptus* allelochemicals as a carbon source to decompose, ultimately alleviating the allelopathic effect of *Eucalyptus*. AMF colonized in *Eucalyptus* roots could better protect woody species from the allelopathic interference of *Eucalyptus* [172,173]. Allelochemicals of Chinese fir not only exert a direct phytotoxic effect on plant roots but also indirectly disturb the soil microbial community's composition and structure. Compared with the first rotation plantation, allelochemicals of Chinese fir probably suppress beneficial mycorrhizal species while promoting harmful fungi in the second rotation plantation, resulting in the deterioration of the soil microbial community [174]. Interestingly, the hyphal network enables allelochemicals of *Juglans nigra* to extend their bioactive zone and promote the effectiveness of allelopathy, indicating the importance of AMF in the movement of allelochemicals [175,176]. In another example, the leaf litter of nonmycorrhizal willows (*Salix glauca* and *Salix brachycarpa*) cannot reduce AMF colonization of understory herbaceous plants, but transplanted ectomycorrhizal willows can suppress AMF colonization of herbaceous hosts through the interaction of leaf litter and ectomycorrhizal fungi [177]. In addition, some soil fungi function as a 'shield' to protect plant roots from the attack of allelochemicals. *E. urophylla* root-associated fungi have the ability to partly offset the autotoxicity of phenolic acids [172].

On the other hand, allelochemicals are able to either promote or reduce the abundance and diversity of soil microbes. The leachate of *Acacia dealbata* can modify the soil microbial community's assembly, leading particularly to a prominent decline in bacterial richness and diversity in pine forest soil [109]. Likewise, extracts of *Eupatorium adenophorum*, especially from its leaves, can reduce bacterial richness and diversity in soils, [178]. Additionally, root exudates of *V. villosa* can shift the soil microbial community's composition, particularly increasing the abundance of Firmicutes and Actinobacteria while decreasing that of Proteobacteria and Acidobacteria [141]. In contrast, the litter of *P. juliflora* benefits the growth and reproduction of some soil microbes and can stimulate the soil microbial biomass carbon and soil metabolic quotient [179]. Similarly, the litter of *Mikania micrantha* can increase soil bacterial richness, yet decrease fungal richness, which enhances immediate nutrient availability and provides ecological advantages to *M. micrantha* [133]. Plus, allelochemicals may facilitate the reduction of soil pathogens. Aqueous root extracts of *Diplotaxis tenuifolia* can inhibit the activity of *Phytophthora cinnamomi* [180], illustrating that *D. tenuifolia* can be exploited for biological control in pathogen suppression. These studies indicate a shift in bacterial diversity, or a shift from fungal richness toward bacterial richness. However, there is a lack of data on the functional shifts' impact on the affected grasslands and forests, which calls for further studies.

5.2. Below-Ground Chemical Interactions Drive Plant–Soil Feedback

Plant–soil feedbacks (PSFs) are interactions among plants, soil organisms, and abiotic soil conditions that influence plant performance, plant species diversity and community structure, ultimately driving ecosystem processes [8]. Allelochemical-mediated below-ground interactions may alter PSFs and their potential consequences for ecosystem functioning. Allelochemicals influence PSFs through the performance of interacting species and altered community composition resulting from changes in species distributions. Allelochemicals affect plant inputs into the soil subsystem via litter and rhizodeposits. Further, root-exuded and litter-decomposed allelochemicals modulate microbial succession. These interactive effects may cause specific PSFs where the match between the species identity of living roots and litter can modify decomposition and feed back to plant nutrition [7,8].

Allelochemical-mediated below-ground interactions drive plant–soil feedback in grasslands and forests (Figure 4). In grasslands, *S. chamaejasme* exudes allelochemicals that incur the change of soil pH and nutrient availability, which partly contributes to the inhibition of adjacent *L. chinensis* [165]. Similarly, spotted knapweed can reduce the total soil carbon and nitrogen content and alter the soil elemental composition via allelochemicals, subsequently impacting soil ecosystem function and impeding the native plant growth [181]. Allelochemicals of *M. micrantha* can enhance the abundance of soil ammonia-oxidizing bacteria and promote the N cycling process. This plant–soil feedback by which *M. micrantha* improves soil N transformation facilitates its invasion in natural environments [182]. In forests, litter of *Robinia pseudoacacia* through allelopathy decrease understory soil nutrient availability, especially of P, and then hinder the growth of *Phytolacca americana*. This negative plant–soil feedback might underlie the limiting factors in the invasion of exotic plants [183]. Likewise, *Juniperus virginiana* exudes allelochemicals into the soil that allow the collapse or transformation of soil microbial communities, followed by inhibiting the growth of certain grass species through negative plant–soil feedback [184].

Importantly, many of these plant–soil feedback are species-specific and are greatly affected by the identity of co-occurring plant species. The presence of co-occurring plant species can alter the direction of plant–soil feedback as a result of long-lasting effects on below-ground interactions and plant responses to subsequent allelochemicals (Figure 4). In successful mixed-species tree plantations, an appropriate species can enhance autotoxic species growth through below-ground chemical interactions. For example, the presence of larch and *M. macclurei* can improve the establishment and productivity of autotoxic Manchurian walnut and Chinese fir in their mixed-species plantations. This is due to the fact that root exudates of larch and *M. macclurei* can facilitate the growth of autotoxic species and increase the degradation of allelochemicals from autotoxic species [92,93]. Accordingly, the allelochemical context alters the consequences of the below-ground ecological interactions, resulting in positive plant–soil feedback in mixed-species plantations.

6. Challenges and Opportunities

The importance of allelopathy and allelochemicals cannot be overemphasized in grasslands and forests. Recent efforts have made considerable progress toward understanding allelopathy and allelochemicals in grasslands and forests. Nevertheless, the functional consequences of allelopathy for plant communities in natural and managed grasslands and forests remain unsolved.

To confirm whether plant–plant allelopathic interactions occur in a grassland or a forest, there are four steps: (1) to find and select ecologically relevant plant species through field observation and investigation; (2) to determine that the selected plant species can produce and release allelochemicals into the environment through appropriate pathways (volatilization, leaching, root exudation or/and residues decomposition); (3) to qualify and quantify allelochemicals and their migration and transformation in soil; (4) to verify the effect of allelochemicals at effective states and concentrations on neighboring plants. These steps and processes involve multiple biotic and abiotic factors, but the focus and central driver must be allelochemicals. However, identifying when and how plant species produce and release allelochemicals is challenging.

An increasing number of studies have shown that the production of allelochemicals depends on the identity of neighboring plants. Allelopathic plants are capable of discriminating between their neighboring competitors and collaborators, adjusting their production of allelochemicals accordingly [185]. In particular, allelopathic plants may detect competing neighbors and respond by increasing allelochemicals to inhibit them, thereby maximizing their own growth. Accordingly, allelopathic interference involves two inseparable processes of plant neighbor detection and allelochemical response via signaling interactions [185], and even intraspecific kin recognition [186,187]. Particularly intriguing is intraspecific kin recognition's contribution to interspecific allelopathy and improving plant productivity [188]. (–)-Loliolide, jasmonic acid and several chemicals are responsible for these signaling interactions [161,189–191]. Importantly, these signaling chemicals are ubiquitous in plant species. Such plant neighbor detection and allelochemical response, as well as their underlying mechanisms, will provide a wealth of research opportunities in grasslands and forests.

In fact, plant species occurring in grasslands and forests can take advantage of both allelochemicals and signaling chemicals released by neighbors, regulating intraspecific and interspecific interactions. Allelochemicals and signaling chemicals synergistically interact to influence plant coexistence, diversity and community structure in grasslands and forests. Plant neighbor detection and allelochemical response have been found in several mixed-species tree plantations [90,91]. Interestingly, kin recognition could even help forests regenerate. A family of firs may grow faster than unrelated trees by tracing flows of nutrients and chemical signals between trees connected by underground fungi [186,192]. Therefore, revealing the intraspecific and interspecific interactions mediated by allelochemicals and signaling chemicals in grasslands and forests can not only broaden our insight into the key processes and mechanisms of the land surface, but also enhance our ability to predict terrestrial ecosystems' responses to global changes.

Author Contributions: Conceptualization, C.-H.K.; investigation, Y.X. and X.C.; resources, Y.X., X.C. and L.D.; writing—original draft preparation, Y.X. and C.-H.K.; writing—review and editing, C.-H.K.; visualization, Y.X., L.D. and X.C.; supervision, C.-H.K. All authors have read and agreed to the published version of the manuscript.

Funding: This research received no external funding.

Data Availability Statement: Not applicable.

Acknowledgments: The authors sincerely thank the anonymous referees for their constructive comments and suggestions.

Conflicts of Interest: The authors declare no conflict of interest.

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