



# **Advances in Plant–Soil Feedback Driven by Root Exudates in Forest Ecosystems**

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**Abstract:** Plant–soil feedback (PSF) was initially developed in the field of agricultural practices. In recent years, PSF has been extended to various ecosystems. Root exudates, essential for the exchange of materials, energy, and information at the plant–soil interface, significantly influence PSF. However, how PSF is driven by root secretions and the role of these secretions in different PSF pathways still needs to be further explored, particularly in forest ecosystems. Soil nutrients, microbial communities, and nematodes are important research topics in the process of PSF driven by root exudates. Investigating these aspects driven by root exudates provides valuable insights into the complex interactions both above ground and below the surface. This research can offer theoretical support and guidance for building stable, healthy, and sustainable forest ecosystems in the future.

**Keywords:** rhizosphere; in situ determination; soil microorganism; soil nematodes; soil nutrient; ecological stoichiometry

## 1. Introduction

PSF (plant–soil feedback) is a mechanism wherein plants modify the biotic and abiotic properties of rhizosphere soil. The altered soil then affects the growth of either itself or neighboring species [1–3]. PSF achieves this by regulating nutrient uptake, interacting with rhizosphere symbionts, responding to pathogens, et al. [4,5]. Consequently, plant exudates induce changes in the soil environment surrounding the plants, thereby affecting plant growth [6,7]. The impact of these modifications on plant growth can be categorized as either positive or negative feedback, depending on whether the changes in soil properties promote or hinder plant growth [3,8,9].

In 1997, PSF officially appeared in the literature for the first time, introducing the conceptual model and quantitative research approach associated with PSF [2,10]. The keyword "PSF" was searched on Web of Science (WoS), revealing thousands of relevant publications. The volume of literature indicated a clear trend of ongoing expansion, with notable growth observed over the past five years (Figure 1). The research focus on PSF primarily revolves around environmental ecology, agriculture, plant sciences, and biodiversity conservation (Figure 2). So far, in comparison to forest ecosystems, the research on PSF has been more focused on agroecosystems, addressing practical production issues and regional characteristics.



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**Figure 1.** Number of articles published on PSF over the years (the data are from https://webofscience. clarivate.cn/, accessed on 7 March 2024).



**Figure 2.** Comparison of the number of articles published on PSF in different research directions (the data are from https://webofscience.clarivate.cn/, accessed on 7 March 2024).

When the term "TS = (plant soil feedback) AND TS = (forest)" was searched in the WoS, the amount of relevant literature significantly decreased. Related research has been developing consistently since 2003, demonstrating stable growth. At the end of the 20th century, the interaction between tree species and soil was in the initial exploration stage, mainly involving the correlation between soil nutrients and tree growth. In 1990, Matson proposed that differences in soil N among tree species were positively correlated with their growth density, indicating a strong correlation between plant and soil processes [11]. In the early 2000s, scholars initiated a transition in their research focus from soil physicochemical properties to biological properties, with an increasing emphasis on the process of microbial community changes [12–14]. The emergence of climate issues significantly disrupted the stability of forest ecosystem communities. Over the subsequent two decades, research efforts were focused on exploring the potential of PSF in protecting forest species diversity and understanding its role in the invasion of forest plants [15-18]. Furthermore, there has been a more in-depth exploration of both positive and negative PSF involving bacterial and fungal microorganisms within forest ecosystems [19–21]. Particularly, ectomycorrhizal fungi, commonly found in communities dominated by forest trees, have been extensively studied for their significant growth-promoting effects on trees, as well as their notable economic and environmental benefits [19,22,23]. Presently, numerous scholars persist

in their dedication to exploring the utilization of microbial communities (mostly fungi: arbuscular mycorrhizal fungi and ectomycorrhizal fungi) to improve the growth and stress resistance of trees and address ecological challenges including climate degradation and plant invasion [24–27].

Plant roots play a crucial role in PSF. The interest in the rhizosphere was initiated in the 17th century [28]. In the 18th and 19th centuries, it was demonstrated that root exudation could affect the growth of nearby plants either positively or negatively [29,30]. By the early 20th century, scholars including Nutman and Hiltner uncovered the significant impact of root exudates on soil microbes and physicochemical properties [31-33]. Various compounds and ions secreted from different parts of roots, including C-based compounds, inorganic acids, and water, are known as root exudates [34–36]. They act as an internal driver for the vitality and function of the microecological environment within the rhizosphere, exerting a significant influence on PSF [37]. The scientific interests in this relationship are further emphasized by the mutual benefit uncovered between root secretion and nitrogen-fixing bacteria in the 1950s [38]. During the late 20th century, the rapid development of modern instrumental analysis techniques propelled a rapid expansion in the study of rhizosphere microorganisms and the composition of root exudates [39]. Significant progress was observed in the relationship between root exudates and soil microecology [40,41]. Presently, numerous scholars continue to explore the composition, synthesis, and release mechanism of root exudates [42–46]. However, the number of investigations of exudates on trees is lower than those conducted on herbs and shrubs [47,48].

Plant roots release a variety of chemicals, acting as a communication bridge between vegetation and soil [49]. This communication is beneficial in enhancing plants' resistance to threats and ensuring their normal growth. Due to nutrient deficiency caused by weathering in tropical forests, root exudations can react biologically or chemically with soil to release insoluble nutrients for plant growth [49,50]. As a result of species specificity of root secretion, the soil C cycle of different species is different [49]. Root exudates play a vital role in regulating soil microbial composition and soil chemical and physical properties [51–53]. Meanwhile, the growth and development status, along with root secretion patterns of plants, respond to changes in soil. Therefore, root exudates are a significant driving factor in PSF [54]. Research on root exudates primarily focused on agriculture and grassland ecosystems [55]. However, investigations in forest ecosystems have been limited due to the complex root system and long life cycle of forest plants [48].

In this review, the PSF mechanism driven by root exudates was discussed, exploring both biotic and abiotic factors. Subsequently, factors influencing root secretion in forest ecosystems are compared [53]. The current challenges associated with in situ detection of root exudates and relevant progress are discussed. Simultaneously, its future research direction is also proposed. The application potential of ecological stoichiometric characterization and mathematical simulation in PSF driven by root exudates is predicted.

## 2. Mechanism of PSF Driven by Root Exudates

Different ecological niches of woody plants, shrubs, and herbs together constitute the main vegetation of forest ecosystems. At present, there are few articles on root exudates of shrubs and herbs in the forest ecosystem, most of which focus on woody plants [56]. Recent studies have shown differences in root exudations from woody plants, shrubs, and herbaceous plants [57]. The abundance of root exudates of woody plants was significantly higher than that of shrubs and herbs [57]. Compared with woody plants, herbaceous plants tend to give more photosynthesis products to root exudates, forming root exudates with different compositions [58,59]. Root exudates can affect soil microbial activity, regulate microbial composition, and accelerate soil biochemical reactions, forming a specific soil microecological environment [60]. The photosynthetic rate and nutrient uptake rate of woody plants, herbs, and shrubs were different, and the composition of root exudates and rhizosphere microorganisms was distinct [59,61]. Some research results have shown that the rhizosphere effects of the three are significantly different [56]. Plants with different life

forms have varying degrees of impact on forest ecological processes, including regulating soil acidity, litter decomposition, and microbial activity regulation [62–64]. Although different plants regulate ecosystems to varying degrees through root exudates, they all regulate soil biotic and abiotic properties, which in turn feedback on the growth and development of biological communities. The general mechanism of PSF driven by root exudates is shown in Figure 3.



Figure 3. General mechanism of PSF driven by root exudates.

## 2.1. Effects of Root Exudates on Abiotic Factors

## 2.1.1. Soil Property Regulated by Root Exudates

The nutrient basis of plant life activities is minerals, and soil is the primary source of mineral nutrients [65]. An optimal amount of minerals is conducive to plant germination, growth, and protection [66–68]. However, soil nutrients often undergo physical, chemical, and biological changes, causing them to exist in either free or bound states, which leads to changes in soil nutrient availability. Some chemicals in root exudates act as effective activators to enhance the accessibility of inert nutrients in rhizosphere soil through different processes including acidification and reduction; thus, these compounds contribute positively to vegetative development [69]. Consequently, exudates released into the root system are directly correlated with soil nutrients that plants can access [70,71].

#### Effectiveness of Soil Nutrients Regulated by Root Exudates

Minerals are in favor of plant protection; as the main line of defense, they determine the plant's competence to infection and offer anti-pathogen effects [66]. N, P, and K, the main nutrients in the soil, enhance the germination of seeds and the output of plants [68]. However, some soil nutrients need to be transformed before they are absorbed by plant roots. Root secretions comprise intricate chemicals such as sugars, organic acids, phenols, and viscous matter [35]. The majority of cultivated soils have organic acids (OAs) that play a vital role in mineralizing or dissolving insoluble nutrients to increase plant yields [72–74]. When nutrient substances are insufficient to maintain plant growth, plants tend to produce more root exudates to facilitate nutrient uptake [75,76]. Root exudates have the ability to transform the existing form of insoluble nutrients in the soil [77,78]. Many studies have clearly highlighted that root exudates, especially organic acids including oxalic acid, malic acid, and citric acid, play a crucial role in improving the solubility of soil nutrients (K, Fe, and P) through acid hydrolysis and double decomposition [79–81]. A study on subalpine forests and the eastern Tibetan Plateau demonstrated that root exudates, including micromolecule organic acids, predominantly citrate, facilitated the conversion of soil P [82]. This facilitation significantly improved the accessibility of P in subalpine forest rhizosphere soil. The availability of main nutrient N in the soil of mature beech forests was also proposed to be closely linked to root exudates [83]. Intense weathering and leaching results in low nutrient concentrations in tropical forest soils [84]. The high degree of weathering causes P to be oxidized and fixed in the soil, and the content of available P in the soil is very low [85]. P exists mainly in organic and insoluble inorganic forms, which limits the net primary production of tropical forests [85]. However, the aboveground biomass of tropical vegetation in Borneo is still at a high value even if soil P is limited [86]. It has been proven that organic acids exuded from plant roots can dissolve refractory P chelated with metal oxides and can prevent the adsorption of soil on P [87,88]. For woodland plants with highly weathered soil, the root surface area is often gradually increased to enhance root exudation, thus alleviating the purpose of P deficiency.

In addition to organic acids, various substances including riboflavin, coumarins, and others have been identified as contributors to the increased availability of soil nutrients [89,90]. Plant roots exhibit the capacity to secrete not only common compounds but also a variety of enzymes (phosphatase, invertase, and amylase) in abundance to modify the soil [91,92]. *Ailanthus altissima* (Mill.) Swingle significantly increased the activity of Fe reductase in roots under the condition of Fe shortage [93]. Moreover, the exudation of phosphatase has been proposed as an effective mechanism by plant roots to activate soil P [94,95]. Forest plants can also promote soil nutrient cycling by stimulating enzyme activity in soil through root exudations [96]. This process is related to the content of C and N in root exudates. In poor soil, N-containing root exudates can stimulate the activity of N-cycle-related enzymes, while compounds containing only C can cause soil N loss [96]. In fertile soil, on the contrary, root exudates containing only C can stimulate N-cycle enzyme activity [96].

The physical condition of the soil is also influenced by root exudates. Root exudates contain several macromolecular viscous compounds that exert a positive impact on the establishment and stability of soil aggregate [97]. The formation of an aggregate structure enhances the soil porosity, facilitating water and air permeability, which significantly influences root development and nutrient absorption by plants, affecting plant growth.

#### Soil Organic Matter Regulated by Root Exudates

Root exudation is considered an essential plant property for controlling the rhizosphere priming effect (RPE), actively regulating natural soil organic matter (SOM) [98,99]. Among different components of root exudates, primary metabolites also stimulate the activation of soil nutrients [100]. Up to 40% of microorganisms in the soil remain inactive due to lack of energy [101]. Primary metabolites in root secretion serve as C sources for soil microorganisms to stimulate their vitality [102]. The microorganisms can use primary metabolites to synthesize extracellular enzymes to degrade organic matter [96]. The research on subalpine coniferous forests illustrated that C from root exudates of *Picea asperata* Mast can be absorbed by soil heterotrophic microorganisms including *actinomyces* [103]. Consequently, the microbial synthesis of extracellular enzymes (soil urease and phenol oxidase) involved in the decomposition of soil organic N can be enhanced, and N release in SOM can be promoted [104]. Plants can directly increase soil nutrients by acid hydrolysis and complexation or indirectly through microbial enzyme hydrolysis of soil organic matter; thereby, this feedback mechanism ultimately affects plant growth.

### Soil Metal Stress Relieved by Root Exudates

Chemicals derived from root exudates play a vital role in improving plant resistance against heavy metals. Faced with metal stress, plants adapt to environmental changes by adjusting the composition of chemicals in their root exudates [105]. When the metal

concentration in the soil reaches a certain threshold, plant roots respond by releasing a substantial amount of organic acids to alleviate metal stress [106]. An investigation into the influence of heavy metals on root exudates displayed that organic acids produced by roots of heavy-metal-free plants are present only in trace amounts, making detection extremely challenging [107]. However, under conditions of high Cu and Al stress, there is a corresponding increase in the content of organic acids released by plant roots [107]. Plant root exudates modulate the activity of heavy metals through the regulation of the pH of the rhizosphere, the redox state of the rhizosphere, and the precipitation chelating of heavy metals to reduce the stress. Three native grass species of the Atlantic forest have been found to have phytoremediation potential [108]. Paspalum notatum (fork grass), Paspalum plicatulum (mattress grass), and Paspalum urvillei (roça grass) promote carboxylic groups (-COO-) and Cu<sup>+</sup> complexation by releasing root exudates to reduce Cu bioavailability and thus promote plant growth [108]. The availability of metal in soil is significantly influenced by the pH. When plants experience high concentrations of metal stress, they modify the secretion of H<sup>+</sup> to increase the pH to 7 in soil, thus reducing metal activity [109,110]. The activity of Cd has a notable negative correlation with pH in the soil. An effective strategy measure for controlling metal pollution involves increasing the soil pH to achieve a state of weak acidity or weak alkalinity [110]. The activity of free metal ions in the rhizosphere can be reduced by forming stable metal chelates with root exudates. Under Cd stress, Avicennia marina (Forsk.) Vierh. produces low-molecular-weight organic acids, mainly oxalic acid, which have the potential to form complexes with Cd to reduce Cd activity, achieving detoxification in plants. In the case of two cypress species (Juniperus chinensis L. and *Platycladus orientalis* (L.) Franco), root exudates alleviate the toxicity of Cd by chelating with Cd and reducing its inhibitory impact on tree growth [111,112]. An investigation into *Pinus sylvestris* L. Karst. seedlings under the stress of Pb, Cd, and As found that the secretion of amino acids and organic acids in the rhizosphere increased. These chemicals were used as chelating agents to reduce metal toxicity in plants [113]. In the case of certain variable-valence metals, their solubility and phytotoxicity are often influenced by their redox status [114,115]. Therefore, plants have the capacity to oxidize metals including Mn by releasing oxygen and oxides to reduce their toxic effects [116]. Trace elements can be toxic to living organisms at elevated concentrations. However, it was observed that in soil contaminated with elements, plants can exhibit normal growth, which is achieved through the process of root exudation without showing any negative symptoms [117]. The root secretion improved the soil quality to protect its growth. The investigation into how root exudates activate soil nutrients and mitigate the risk of heavy metals primarily focuses on organic acids [118]. The mechanism by which other compounds affect soil nutrients cannot be ignored. However, research on the effects of other chemicals on soil nutrients is more scarce than that of organic acids.

#### 2.1.2. Application of Ecological Stoichiometry in PSF

Ecological stoichiometry is a scientific discipline that investigates the equilibrium between energy and chemical constituents within ecosystems [119]. Its fundamental theory is that the elemental composition of organisms remains relatively stable with the nutrients in the surrounding environment. C, N, and P are the core of nutrient circulation and transformation, regulating and driving the succession of the ecosystem [120]. The stoichiometric ratio of nutrient elements (C:N:P) is one of the important research focuses in the exploration of plant–soil interaction. It has a great impact on individual plant growth, population change, community succession, species diversity, et al. [120]. Light and nutrition can affect energy transfer efficiency. The C:N:P in different regions varies greatly; however, the range of these ratios remains relatively stable within the same community [121]. This implies that environmental factors, including soil conditions, play a significant role in the stoichiometric characteristics of plants [122–124].

Plants possess the self-regulatory ability to adapt to variations in the ratio of C:N:P in their environments, ensuring their survival and optimal growth. A study on Karst primary

forests revealed that factors including altitude, soil acidity, and soil phosphorus affect the ecological stoichiometry characteristics of various plant tissues [125]. The C:N:P ratio of shrub leaves increases rapidly in high-altitude, low-temperature sandy areas [126]. It shows a more significant impact on the stoichiometric characteristics of soil than environmental factors [126]. Therefore, changes in ecological stoichiometric characteristics between plants and soil can reflect their mutual influence.

Based on homeostasis, ecological stoichiometric theory suggests that the element composition ratio of organisms is dynamically stable [127]. Organisms have a relatively stable ratio of C:N:P, and a change in any of these elements modifies that ratio [128]. The element that limits the growth and reproduction of organisms can be inferred by ecological stoichiometric characteristics analysis. The organism can regulate its C:N:P ratio to accommodate variations in growth [129–131]. Therefore, when investigating the regulatory role of root exudates on soil nutrients, utilizing the variations in ecological stoichiometry characteristics to predict and quantify the feedback of soil nutrients on plant growth would be a simple and effective method. Apart from C, N, and P, additional elements significantly influence the physiological processes of organisms. Therefore, there is a need to further expand the investigation of elements in ecological stoichiometry. It contributes to refining the ecological nutrient cycling of soil and the associated biogeochemical cycling processes. Some researchers have extended their exploration of ecological stoichiometry to include additional elements (such as S, Si, Fe, Na, Mn, Al, et al.) [132]. However, the research scope of elements is considerably narrower compared to the diversity of species and ecological environments involved in the ecological stoichiometric characteristics of C, N, and P [133,134]. Thus, further research is required to be conducted on the ecological stoichiometry of other elements.

Traditionally, ecological stoichiometry has primarily been employed in aquatic ecosystems. However, there has been a growing interest in extending this methodology to explore terrestrial ecosystems, including grasslands, forests, and deserts in recent years [135–137]. Root exudates are the product of forest plants responding to environmental changes. However, there have been limited investigations into how the stoichiometric ratio of root exudates affects the ecological stoichiometric characteristics of the surrounding soil environment and how the impact adjusts the ecological stoichiometric characteristics of the plant. The finding revealed a significant decrease in the exudation rate of N with the rise in rainfall and soil N content, leading to a change in C:N ratio [138]. As this ratio increased, plant growth and biomass were promoted and this phenomenon might be attributed to the facilitation of C and N circulation resulting from an increased C:N ratio. However, there is currently limited research on the ecological stoichiometric characteristics of root exudates that promote the efficacy of C and N in soil. Therefore, further investigation is required to support this assertion. Existing studies have demonstrated that the nutrient content of plant leaves can display the distribution of nutritive elements under the influence of different environmental factors [139,140]. In pot experiments conducted under low P conditions, a positive correlation was displayed between trace elements in plant tissues and root sheath carboxylate. According to this observed correlation, the alterations in Mn levels within plant leaves might serve as a quantitative indicator for the exudation of carboxylates [141]. Therefore, alterations in nutrient elements can serve as indicators to infer plant growth and root exudation. This further reinforces the potential of ecological stoichiometry in elucidating root exudate-mediated PSF.

The exploration of nutrient cycling in forest ecosystems often involves analyzing the stoichiometric characteristics of litter and soil, especially in pine–oak and subtropical forests [142,143]. However, investigation on the stoichiometric relationship between root exudates and forest soil nutrients in forest soil is scarce. Plants release root exudates with different C:N:P ratios in response to environmental changes [144]. It is significant to apply the ecological stoichiometric method to further explore the PSF mediated by root exudates. The energy transfer and transformation among plant tissues, root exudates, and soil nutrients can be more easily assessed through the changes in elemental stoichiometric

ratios. Further exploration of plant–soil nutrient cycling in forest ecosystems would provide a theoretical basis for promoting nutrient cycling in forests.

#### 2.2. Effects of Root Exudates on Biological Factors

#### 2.2.1. Response of Microbial Community to Root Exudates

Microorganisms, integral components of the plant rhizosphere, play a pivotal role in facilitating nutrient cycling within forest ecosystems [145]. The resilience of plants to adverse conditions can be enhanced by an optimal soil microbial community [146,147]. These communities stimulated by root exudates have the potential to stimulate plant development and reproduction by activating essential soil minerals including P, N, and K [146].

A study involving 34 mixed tree species revealed that soil pH, organic matter, and the proportion of viscous soil significantly influenced microbial communities [148]. Soil conditions play a pivotal role in modulating microorganisms [149–151]. The exudates secreted by tree roots into the soil undergo constant changes due to dynamic natural environments, shaping the rhizosphere of different trees into unique soil environments [53]. Microorganisms, being essential components of the soil, interact closely with root exudation [152]. The structure of the rhizosphere microbial community can be influenced by root exudates, thereby enhancing nutrient utilization and improving tree resistance to diseases and stress [153,154]. However, the majority of relevant research focuses on the agricultural field. A search in WoS using the keywords 'Root exudate affect microorganisms' and 'forest' yields significantly fewer literature results compared to 'Root exudate affect microorganisms' and 'agriculture'. Recently, there has been a notable increase in exploration focusing on woody plants in forest ecosystems, particularly on *Picea* spp., *Populus* spp., *Quercus* spp., and *Pinus* spp. [155–159].

Root exudates, rich in primary metabolites (sugars and proteins) and some secondary metabolites, provide essential material support for the life activities of rhizospheric microorganisms [160,161]. Glucose secreted by roots as an energy source can significantly improve microbial activity [155]. The finding further supports a correlation between changes in bacterial diversity and variations in rhizosphere secretion concentration [162]. The positive effects of plant root exudates on plant development by affecting microbial growth and metabolism are emphasized [163]. It also explains why the microorganisms in the rhizosphere are consistently more numerous and diverse than those not in the rhizosphere. This phenomenon elucidates the rationale for the richness and diversity of microbial communities in the rhizosphere compared to those inhabiting non-rhizospheric soil.

In addition to providing nutrients, root exudates serve as signaling molecules, regulating microbial composition and distribution. Plants release root exudates as a defense mechanism in response to environmental stress. Certain exudates function as signaling molecules, promoting the proliferation of beneficial bacteria or inhibiting the growth and development of harmful microorganisms, including pathogenic bacteria, thereby regulating plant development. Salicylic acid, a common phytohormone effused by plant roots, has been shown to regulate soil microbial communities in Populus trichocarpa Torr. & Gray [164]. The close relationship between signal molecules and microorganisms has been confirmed in greenhouse and field experiments. Root exudates, acting as signal molecules, can effectively regulate beneficial bacterial communities, thus resulting in positive feedback to plant growth [165]. *Pseudomonas* spp., a common rhizosphere-beneficial bacterium, is attracted and successfully colonized in the plant rhizosphere due to the presence of organic acids and amino acids in plant root exudates [166,167]. It is vital for the process of plant disease control. Malic acid was also proven to be a signal of plant disease stress, inducing the aggregation of Bacillus subtilis (FB17) in the rhizosphere of plants [166]. Following successful colonization in the rhizosphere, these microorganisms provide feedback on plant growth and development through modulation of plant hormone production, facilitation of biofilm formation, enhancement of antioxidant activity, promotion of root nitrogen fixation, et al. [168,169]. Plant growth-promoting bacteria enhance plant growth

and defense by secreting plant hormones, enzymes, membrane transport proteins, and volatile signaling compounds [170–175]. Common rhizosphere growth-promoting bacteria include *Azotobacter*, *Pseudomonas*, *Alcaligenes* (*xylosoxidans*), *Bacillus*, *Gluconacetobacter*, and *Burkholderia* [176]. On the other hand, biocontrol microorganisms suppress the growth of pathogenic bacteria by secreting antimicrobial compounds and competing for nutrients, thereby improving plant growth and development [177–179].

As an indispensable component of the forest ecosystem, symbiotic mycorrhiza plays a crucial role in stress resistance, nutrient mobilization, carbon cycling, and various other processes within the forest milieu. In this mutualistic relationship, plants provide C sources to microorganisms, while microorganisms facilitate plant nutrient uptake. The mutually beneficial relationship between mycorrhizal fungi and plant roots facilitates the formation of beneficial symbionts with different mycelium, mycelial cord, and mycorrhizal branches in the soil rhizosphere [180,181]. In contrast to the prevalence of endophytic fungi in crops, ectomycorrhiza is predominantly found in trees [182]. Studies on forest ectomycorrhiza are more common in European beech and pine, followed by oak, birch, and other conifers [183,184]. Certain fungi display specificity, living symbiotically with particular tree species. Mycorrhizal fungi contribute to plant growth and development, especially arbuscular mycorrhizae (AM), which establish symbiotic associations with the majority of higher plants, facilitating the absorption of soil nutrients by plants. Some beneficial fungi exhibit symbiosis with specific tree species, and their selectivity is related to root exudates of tree species [185]. Root exudates serve as signals that determine the composition of rhizosphere microbes, and certain specific chemicals from root exudates can induce the expression of symbiotic mycorrhizae [186]. The interaction between mycorrhizal fungi and plants depends on root exudates, which act as chemical messengers to stimulate the reaction mechanism [187]. Woody plants, including *Pinus* spp., *Eucalyptus* spp., and *Populus* spp., have been studied, and it has been demonstrated that abietic acid, flavonoids, and strigolactones serve as signaling molecules to trigger mycelial growth, spore germination, and effector protein expression in plant growth [187–190].

In addition to beneficial bacteria, pathogenic bacteria also exist in soil. Deleterious rhizobacteria impede plant growth by inhibiting roots, modulating root metabolic processes, reducing the capacity of roots for nutrient and water uptake, or enhancing plants' susceptibility to parasitic pathogens. Pathogens are also influenced by root exudates within the same habitat [191–193]. Certain root exudates, including antibiotics, can directly impede the activity of pathogenic microorganisms. Root exudates from disease-resistant plant varieties can hinder mycelium growth and spore germination in pathogenic bacteria [194]. Rhizathalenes, a compound secreted by plant roots, exhibit antibacterial activity [191]. This enables plants to maintain resistance even without environmental stress, thereby ensuring a clean rhizosphere soil to help plants avoid interference from pathogenic bacteria.

In summary, root exudates play a vital role in controlling the variety and amount of soil microbial populations by serving as C sources and signal molecules. The preference of certain microorganisms for specific root exudates has contributed to the diversification of microorganism populations in the rhizosphere of trees [6,195–197]. Various research indicates that this specificity is significantly related to the types of compounds, and this relationship can be used to improve the growth of trees [198,199].

Presently, numerous studies mainly focus on specific chemicals or overall root exudates. Certain investigations involve direct supplementation with specific root exudates, including oxalic acid, in *Picea asperata* Mast. [155]. However, these findings lack universality, thus limiting their theoretical implications [155,200]. In response to this limitation, several scholars have recently conducted experiments involving the exogenous addition of chemicals [201]. The specificity of microorganisms influenced by chemicals is demonstrated through single and combined exogenous addition experiments with the representative chemicals in root exudates. *Actinobacteria* were primarily influenced by phenolic acid, while *Bacteroidetes* exhibited sensitivity to organic acids and amino acids. Additionally, it was observed that a high N content in chemicals led to a reduction in plant resistance to disease [201]. The findings regarding *Arabidopsis thaliana* L. are in accordance with the described results [202]. However, it needs to be clarified whether these findings have the same applicability in forests.

#### Potential for Mathematical Models on PSF Driven by Root Exudation

Mathematical models have been widely integrated into various disciplines including the establishment of models for root exudate movement based on the interaction between soil properties and plant root exudations [203]. A microbial activity model has also been employed to simulate the impact of root exudates on soil microbes and enzyme activity [204]. N content in root exudates stimulates microbial activity and extracellular enzyme synthesis, confirming root exudates as the primary driver of rhizosphere microbial activity [204].

In the early 20th century, scientists observed significant differences in the distribution of microorganisms within plants' rhizosphere. And microbial abundance varies in different parts of soil associating with plant roots [205]. The distribution patterns of microorganisms in rhizosphere soils containing soluble organic C were simulated using mathematical models, examining both horizontal and vertical dimensions [206]. The results offered evidence for a strong correlation between the accumulation of microorganisms and plant root exudates. A principal component regression model has been devised to predict the response of microorganisms to plant development. This model was built utilizing the data on the relative abundance of rhizosphere-isolated microorganisms and the preference of microorganisms for the uptake of root exudates [154]. The experiment, however, only explored a large number of compounds in the rhizosphere of plants, and further exploration is required to understand the correlation between some water-soluble compounds and microorganisms. The impact of root exudates on microbial community, soil organic C, and soil organic N was investigated in European beech forests. It was concluded that the addition of exudates promotes the proliferation of fungi, contributing to the formation of large soil aggregates [207]. The model based on the experiment can guide the understanding of soil aggregate stability mechanisms [207]. A quantitative model was developed to simulate and predict the impact of root exudates with varying C:N ratios on plant rhizosphere microorganisms and soil organic matter [208]. This model can also estimate CO<sub>2</sub> emissions and available N resulting from root exudate input in terrestrial ecosystems [208]. Models involving the interaction between root exudates and microbes are more widely used in agriculture compared to forestry [209].

Further research is needed on the specific relationship between root exudates and microorganisms. It would be an effective method to establish an appropriate model to predict the rhizosphere microbial community structure and plant growth by fitting the response values between the compounds in common root exudates of trees and microorganisms. In the initial stages of exploring root exudate-mediated PSF in complex forest ecosystems, it is recommended to utilize the data from small-scale greenhouse experiments to establish an appropriate mathematical model. Selecting common samples is crucial for achieving a good representation, ensuring more convincing and universal results. When selecting root secretions, it is essential to include organic acids such as oxalic acid, a significant component of root secretions in forest environments. This approach allows the model to predict the trends in subsequent large-scale woodland experiments, providing a practical guideline to reduce unnecessary time-consuming experimental steps.

#### 2.2.2. Response of Soil Nematodes Community to Root Exudates

Soil organisms play a crucial role in regulating soil nutrients and ecosystem functions and ensuring the stability of forest ecosystems as vital contributors to biogeochemical cycles [210]. Among soil organisms, soil nematodes are particularly significant members of the plant rhizosphere biota and represent the most abundant species. In 2019, an investigation of different continents' soils demonstrated that soil nematodes exhibit the highest abundance in northern or tropical forests [211]. Nematodes play an important role in regulating forest nutrient dynamics and soil microorganisms [212]. They actively participate in material circulation within soil ecosystems, exhibiting high sensitivity to environmental changes.

Phytophagous nematodes feed on root exudates and fallen leaves. They exhibit a rapid response to changes in aboveground vegetation communities [213]. However, due to their dietary characteristics, excessive feeding on plants by phytophagous nematodes can harm plant growth, elicit negative feedback responses, and ultimately reduce the density of host plants [214,215]. When phytophagous nematodes feed on roots appropriately, the C allocation toward plant roots is enhanced [215]. The leakage of plant root contents caused by feeding can stimulate rhizosphere microorganisms and promote nutrient mineralization, thereby accelerating plant growth [216]. Unstable C sources are key driving factors for soil communities [217,218]. An investigation of coniferous forests indicates that the addition of C reaches an equivalent amount in root exudates, leading to a significant alteration in the abundance of soil nematode communities [219]. Populations of bacteria-feeding nematodes and fungus-feeding nematodes exhibit noteworthy alterations upon introducing a C source. The experiment implies that external energy stimulation increased soil microorganism abundance, indirectly promoting the abundance of microbivorous nematode communities [220]. Microbivorous nematodes can modulate the structure and metabolic activity of microbial communities through selective predation [221,222]. Proper predation by nematodes can result in the rapid growth of microbiota, thereby enhancing its metabolic activity [223]. Simultaneously, the metabolites of nematodes serve as an additional energy source for the microbiota. The inorganic N fixed by fungi can be indirectly released into the soil through nematode metabolism, thereby enriching soil nutrients and promoting plant growth [224].

Based on their interaction with plant roots, nematodes can be divided into plant parasitic nematodes (PPN) and entomopathogenic nematodes (EPN) [225]. Root exudates, serving as C sources and hatching factors, affect the parasitism and hatching of nematodes [226]. Attracted by root exudates, nematodes parasitize different parts of the host plant's roots [227]. The secondary metabolites secreted by plant roots can affect the parasitism trajectory of PPN and may even lead to its growth stasis, thereby mitigating its parasitic rate to safeguard plant growth [228–230]. Meloidogyne, a phytoparasitic nematode, induces the formation of galls in plant roots, impeding plant growth and development, even resulting in plant mortality. The destruction of the life cycle inhibits the activity of soil nematodes, thereby indirectly enhancing the resistance and growth of trees [231]. EPN indirectly promotes plant growth by feeding on herbivores [227]. After insects bite plants, tree roots secrete different compounds, which attract EPN to parasitize the insects [227]. Upon successful parasitism, EPN releases toxins into the insect's body, leading to the insect's death within a few days [232]. The weevil larvae chew on citrus trees, triggering the release of terpene compounds from tree roots. This, in turn, recruits EPN to the damaged parts of plants, inhibiting the reproduction of weevil larvae [233]. EPN plays a crucial biological role in pest and disease control, establishing a positive feedback that supports plant growth [233].

Nematodes, affected by root exudates, play an indispensable role in the PSF of forest plants. The regulatory impacts of root exudates on soil nematodes have primarily been investigated in the agroecosystem, including in potatoes, tomatoes, and peas [234–236]. Nematodes are widely distributed in forest ecosystems, especially among pine plants [237,238]. Further research is imperative to investigate the regulatory mechanism and PSF process of root exudates on nematodes in forest ecosystems.

## 3. Influencing Factors of Root Exudates' Variety and Abundance

Different types of root exudates have the potential to regulate the C cycle, nutrient availability, soil characteristics, and microbial community structure [53,138]. The alteration of the soil environment, in turn, elicits feedback on the growth and metabolism of plants. This ability allows plants to flexibly release appropriate root secretions, facilitating adaptation or defense against environmental changes [239]. The composition and quantity of root

exudates are regulated by internal and external factors [240,241]. Multiple studies have confirmed that plant species, developmental stages, and growing environments have a considerable impact on root secretion [153,242]. Further investigation and analysis are essential in forest ecosystems to understand the relationship between root exudates' content, composition, and various contributing factors.

The internal factors of plants, including species and growth stage, will affect the composition and abundance of their root exudates to varying degrees. The root exudates from six temperate forest tree species have been analyzed and compared, revealing variation in both types and abundance of exudates among different tree species [243]. The pool of root secretion has been found to be species-specific, indicating that the varieties of root exudates in trees were correlated with species similarity [243]. Furthermore, the abundance of root exudates also varied among tree species. The concentration of root exudates is the highest in *Pinus strobus*, while the concentration of root exudates is the lowest in *Quercus rubra* L. (Table 1) [243]. Even within the same genus, the composition of root exudates differs from various species of woody plants. The analysis of root exudation in four species of Populus revealed significant differences in salicylic acid, genetic acid, oleuropein, strigol, chrysin, and linoleic acid among Populus, while the composition of root exudates varied slightly [244]. The composition and abundance of root exudates also vary during different growth phases. The composition of root exudates of Arabidopsis thaliana at different developmental stages was similar, but the concentration was significantly different [245]. The root exudates of slow-growing plants exhibit higher relative abundances of sugars, glycols, and organic acids [245]. However, the prolonged growth period of trees presents challenges for researchers to investigate root exudates at various growth stages.

**Table 1.** Tree species variation in root exudate diversity and abundance [243]. Reprinted/adapted with permission from Ref. [243], 2018, John Wiley and Sons, License Number 5735560623128.

Species	Number of Compounds	Sum of Relative Compound Abundances ( $10^{-3} AU^2 g^{-1}$ root)	Catechin Concentration (µg/g root)
Acer saccharum	$6.6\pm0.7~^{\mathrm{b}}$	$2.1\pm0.5$ c	$19.19\pm5.72~^{\mathrm{b}}$
Alnus rugosa	$28.9\pm1.6~^{\rm a}$	$9.3\pm2.8$ <sup>b</sup>	$4.06\pm1.24$ <sup>c</sup>
Fagus grandifolia	$2.9\pm0.4$ c	$0.8\pm0.2~^{ m c}$	$2.60\pm2.39$ c
Picea abies	$20.0\pm2.0~^{\rm a}$	$7.6\pm1.1$ <sup>b</sup>	$23.54\pm5.15^{\text{ b}}$
Pinus strobus	$26.8\pm1.5~^{a}$	$28.6\pm3.2$ a	$116.06\pm15.65$ $^{\rm a}$
Quercus rubra	$4.12\pm0.5~^{\rm bc}$	$0.2\pm0.0$ d	$1.00\pm0.53$ $^{\rm c}$

(Contrasting letters indicate significant differences (p < 0.05) among tree species within root exudate or tissue samples as determined by Tukey's honest significant difference test).

In addition to internal factors, the external environment also affects the root secretion of plants. The impact of seasonal factors on the abundance of root exudates was proposed by exploring spruce forests and artificial fruit forests [242,246]. Root exudate variation in *Quercus crispula* Blume trees also indicated that solar radiation had a more obvious effect on root exudates than season [247]. The quantity of root exudates showed a positive correlation with daily irradiation. Drought is also one of the environmental factors that significantly affect the composition of root exudates. Under drought conditions, the proportion of root exudates from *Quercus ilex* L associated with aridity stress accounted for 71% of the total root exudates [247]. In comparison to the control group, water-stressed plants exhibited enhanced secretion of lactic acid, pyruvate, abscisic acid, and glucose, resulting in higher accumulation concentrations [247]. When plants lack water for a long time, the content of organic acids, amino acids, and sugars in root exudates, mainly including amino acids, sugars, and secondary compounds, decreased [249]. Through the study of drought stress of four different plants in subtropical forests, it was found that the plants with faster growth

were more sensitive to drought change, and their root exudation changed significantly [250]. This was related to plant root shape and mycorrhizal infection, which also indicated that plant growth strategies had an important effect on root secretion. In addition, investigations of C allocation under drought in temperate tree species have found that a lack of plant water increases C input to the ground, contributing to ecosystem resilience [251].

In addition to natural factors, artificial stimuli affect root exudates [252]. Different degrees of root pruning were carried out, revealing that appropriate root trimming increased the amount of root exudates, with the organic acid content being 31.8% higher than in unpruned poplar species (Figure 4) [253]. The impact of species and environment on the content of root exudates far surpasses any potential influence from moderate pruning, even with optimal pruning extent [253]. It is recommended that a long-term and extensive exploration should be carried out to understand the diverse factors affecting the root secretion of tree species.



**Figure 4.** Effects of root pruning on root exudates contents in rhizosphere soil. Reprinted/adapted from Ref. [253].

## 4. In Situ Determination of Root Exudates

In recent years, ecological research has increasingly focused on the subsurface [254]. Scientists have developed a keen interest in the roots of forest plants, particularly in the context of root exudates. Root exudates are no longer merely seen as intermediates for nutrient absorption. They are recognized for their ability to modulate the soil microenvironment by impacting mycorrhizal symbiosis, physical and chemical properties, and microbial community structure [255–257]. The exudation of roots plays a pivotal role in regulating soil ecology, acting as a signal and energy source for plants, thereby influencing the C cycle within forest ecosystems [258–260].

Due to the intricate "birthplace" of root exudates, finding an effective in situ method for collecting them is challenging [261]. Currently, there are two methods for obtaining root exudates: one involves direct sampling from the rhizosphere soil, while the other requires culturing plants with water or substrate for subsequent sampling. Changes in the soil environment and root damage can greatly affect the composition and content of root exudates. However, most current sampling methods from the plant rhizosphere soil cause damage to plant roots, significantly reducing the accuracy of root exudates' detection due to the sensitivity of root exudates to both root damage and the soil environment [103,262,263]. To avoid the influence of a complex soil environment on root exudates, numerous researchers prefer employing water, vermiculite, sand, and agar as the substrate to collect root exudates [264–266]. However, this method requires the addition of nutrients to the growth medium to maintain plant growth, which can affect the accuracy of root exudates' determination. Recently, it has been suggested that the diameter of fine plant roots plays a vital role in root exudation [180]. A 25 mm diameter glass fiber filter was developed to extract exudates from microscopic fine roots of boreal forest plants in situ for a short time [180]. The device requires careful treatment of the rhizosphere soil to expose living roots for collecting root exudates. This method helps mitigate the effects of soil microbial degradation and adsorption on root exudates. However, the process of sampling living roots demands meticulous measures to prevent potential damage to the roots. This method is more suitable for shallow roots, while extracting secretions from deep roots poses great challenges. A technique combining diffusive gradients in thin films (DGT) with mass spectrometry imaging was developed to reveal the in situ distribution of plant root exudates [267]. The advantage of this method is that it minimizes substrate interference with root exudates, and the sampling method is non-destructive, enhancing the accuracy of determination results [267]. However, the high soil water content (80%) required by DGT can reduce the resolution of compound diffusion at the root–soil interface [267].

The chemicals in root exudates are complex and varied [268,269]. Current analytical methods primarily focus on chemicals with a high content. However, these methods are not well suited for detecting root exudates with low content due to their high sample consumption [269–271]. Certain compounds with low content in root exudates also play a substantial role in plant growth. However, their extraction and detection pose challenges due to their low content. Allelochemicals secreted by plant roots typically exist in soil at low concentrations [272]. These allelochemicals are primarily involved in nutrient cycling, soil remediation, and pesticide degradation through root secretion to affect underground ecosystems and aboveground vegetation communities. They play an important role in the PSF process. Therefore, it is extremely vital to develop an in situ extraction method for allelochemicals with low content in a plant's rhizosphere.

A microextraction sampling device based on capillary interaction has been developed for the in situ extraction of rhizosphere allelochemicals [273]. The device abandons the limitation of solvent extraction and the disadvantage of neglecting soil in aseptic tissue culture and hydroponics. It also addresses issues related to continuous sampling negative pressure including challenges in fixed point sampling and considerable soil disruption. This device enables the sampling of allelochemicals under natural soil conditions. However, it has only been tested on crops, and its effectiveness on forest plants remains uncertain.

Microdialysis is a method employed for dynamic micro-biochemical sampling from living organisms [274]. Widely used in the fields of neurology, pharmacokinetics, and pathology, microdialysis is frequently employed to extract extracellular fluid for monitoring alterations in neurotransmitters' content [275]. In recent years, microdialysis technology has extended its applications to soil sampling within the ecological field [276,277]. Microdialysis enables real-time and dynamic sampling without interfering with the normal life activities of the organism. This technology is particularly effective in minimizing interference from root damage on the composition of root exudates. Considering the low content and the polarity differences of allelochemicals in soil, our group developed microdialysis combined with UPLC-MS/MS technology for in situ dynamic detection of allelochemicals in a plant's rhizosphere (Figure 5) [278,279]. The combination of microdialysis with UPLC-MS/MS has the advantages of high sensitivity and low sample consumption. The in situ real-time detection technique for root exudates is set to significantly advance the development of PSF in forest biology.



**Figure 5.** Experimental flow chart of microdialysis technology combined with UPLC-MS/MS for in situ detection of rhizospheric allelochemicals. Reprinted/adapted from Ref. [279].

## 5. Conclusions and Prospect

Root exudates play a crucial role in the feedback regulation of plant and rhizosphere soil microecology. These exudates have the ability to modify soil nutrients, subsequently influencing plant development and triggering alteration in root secretion. Ecological stoichiometric methods have been employed to examine the forest soil quality, plant growth, and redistribution of nutrients in both soil and plants. It may be an efficient method to investigate the root exudation–soil–plant interaction in forest ecology. However, existing studies mainly focus on the ecological stoichiometric characteristics of plant tissues. Therefore, future exploration is anticipated to delve into PSF driven by root exudates in forest ecosystems through the application of ecological chemometrics. It is valuable for understanding and predicting the influence of root exudates on soil resource availability and vegetation. Moreover, it carries theoretical significance in guiding the establishment of stable and sustainable forest ecosystems.

Soil microorganisms are essential participants in the PSF of forest ecosystems, which are affected by root exudates and impact plant growth in return. It is convenient and effective to use the correlation data between root exudates and microorganisms to establish mathematical models so as to predict tree growth and changes in rhizosphere microbial communities by analyzing the composition of root exudates. Mathematical models in PSF involving root exudates in forest ecosystems are rarely used, requiring further investigation and application across various forest ecosystems.

Root exudates function as signals or energy substances to regulate soil nematode communities, consequently affecting vegetation communities and functions within forest ecosystems. However, the investigation into the impact of root exudates on forest soil nematodes and their feedback is still in its early stages. There is a need to further delve into the regulatory mechanism of nematodes with different chemical compositions or individual root exudates in forest ecosystems. This is conducive to establishing simple and effective biological control technologies, advancing the theory of green prevention and control, and contributing to the development of a healthy and stable forest ecosystem.

Root exudates are influenced by tree species, temperature, light, and external stimuli. However, current studies primarily concentrate on the impact of individual factors on root exudates. There is limited research comparing the effects of multiple factors on root exudates. Therefore, it is recommended that further research explores the changes in root exudates among different species of trees and within the same tree species under the influence of different factors.

Microdialysis combined with UPLC-MS/MS technology has marked a significant breakthrough in achieving minimally invasive and dynamic extraction. It is anticipated that further advancements in combining microdialysis and UPLC-MS/MS or soil column methods can be made to realize the dynamic detection of the migration and degradation process of trace components in the tree's rhizosphere. This progress is expected to promote the research process of root exudates in forest ecosystems.

The root system serves as the crucial interface for the interaction between forest trees and the soil environment, playing an important role in assisting plants to adapt to and resist various adverse environments. Root exudates have a crucial role in regulating rhizosphere microecosystems by driving PSF, ultimately improving plant adaptability and resistance to the environment. Root exudates in diverse forests play a significant role in affecting the growth of themselves and neighboring vegetation by regulating soil nutrients, microorganisms, and nematodes. A comprehensive understanding of the PSF mechanism is beneficial for screening suitable planting species and determining appropriate planting density and other factors. It is necessary to further investigate PSF mediated by root exudates in forest ecosystems using ecological stoichiometric methods and mathematical models. This knowledge can contribute to the effective regulation of root exudates, promoting the growth of forest trees, and thus improving the productivity and sustainability of the forest ecosystem. It also provides a theoretical reference for establishing an excellent, healthy, and sustainable forest plant–soil interaction system.

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