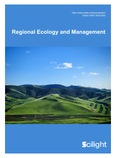
Scilight

Regional Ecology and Management
https://www.sciltp.com/journals/rem



Review

Interspecific Nitrogen Transfer and Nutrient Exchange in Legume-Cereal Intercropping Systems: A Review

Runfu Li [1], Zhixiang Niu [1,2] and Haishan Niu [2,*]

[1] College of Resources and Environment, University of Chinese Academy of Sciences, Beijing 101408, China
[2] Beijing Yanshan Earth Critical Zone National Research Station, University of Chinese Academy of Sciences, Beijing 101408, China
* Correspondence: niuhs@ucas.ac.cn

How To Cite: Li, R.; Niu, Z.; Niu, H. Interspecific Nitrogen Transfer and Nutrient Exchange in Legume-Cereal Intercropping Systems: A Review. *Regional Ecology and Management* **2026**, *1*(1), 4.

Received: 27 January 2026
Revised: 12 February 2026
Accepted: 26 February 2026
Published: 16 March 2026

Abstract: The agronomic advantage of legume-cereal intercropping has been primarily attributed to unidirectional nitrogen (N) transfer. Recent conceptual advances, however, reposition this belowground interaction from a linear, donor-receiver model of N transfer to a dynamic, market-like system of reciprocal N, phosphorus (P), and carbon (C) exchange, mediated by arbuscular mycorrhizal fungi (AMF) and root exudates. This review synthesizes this progression by integrating multiple, temporally distinct pathways of N transfer, spanning rapid root-derived and mycorrhizal pathways to delayed residue-mediated pathways. It further synthesizes their multidimensional regulation and the emergent mechanisms of N-P and C-N exchange into a coherent multi-nutrient network framework. This integrative synthesis moves beyond prior reviews focused on singular processes or nutrients, offering a novel conceptual framework that captures the complexity and reciprocity of belowground interactions. We further evaluate the agronomic outcomes for yield and resource efficiency and outline future research directions. By moving beyond syntheses of singular processes, this work aims to provide an updated ecological foundation for designing sustainable intercropping systems.

Keywords: arbuscular mycorrhizal fungi; root exudates; stable isotope probing; carbon exchange; phosphorus exchange; sustainable intensive agriculture

1. Introduction

The dual pressures of global food security and environmental sustainability have underscored the pivotal need to develop resource-efficient and environmentally friendly cropping systems [1,2]. Intercropping, particularly legume-cereal combinations, is recognized as a cornerstone of ecological intensification for sustainable agriculture and biodiversity conservation [3–6]. A recent global meta-analysis confirms that legume/non-legume intercropping significantly enhances system productivity, increasing non-legume yield by an average of 33% and highlighting its substantial potential to improve resource use efficiency [7]. This practice leverages the engine of symbiotic N_2 fixation, a highly regulated mutualistic process governed by complex signaling, to initiate beneficial interspecific interaction [8,9]. These systems optimize spatiotemporal arrangements and identify optimal species proportions. This strategy enables synergistic productivity gains and reduces dependency on synthetic inputs, thereby contributing to sustainable intensification [10–13]. While foundational reviews have established methodologies for quantifying N transfer [14], recent syntheses have provided deeper mechanistic insights into specific facets, such as the synergistic roles of mycorrhizal networks and N_2-fixers [15], rhizosphere engineering via localized fertilization [16], and the cascading effects framework [17]. Nevertheless, an integrative synthesis that consolidates these advances into a unified multi-nutrient network framework is still lacking.

Conventionally, the agronomic advantage of legume-cereal intercropping was attributed to a unidirectional transfer of fixed N [18–20]. Early isotopic evidence confirmed this transfer [21,22]. Building on this, global syntheses have now quantified that the proportion of N transferred from legumes can range from 0.5% to over 50% and can constitute up to 78% of the non-legume's N uptake, underscoring its potential significance and context-dependent variability [7]. Later sophisticated tracing further quantified its significant contribution to cereal N uptake [22], a process notably suppressed by N fertilizer application [13,23,24]. Contemporary research has fundamentally expanded this linear model, revealing N transfer to be one component within a broader, reciprocal exchange network involving phosphorus (P) [25] and carbon (C) [26]. Crucially, the facilitation within this network is highly context-dependent and species-specific, as evidenced by the positive correlation between interspecific N transfer and AMF colonization [7]. For instance, rhizosphere-driven P facilitation in wheat-faba bean systems emerges only under P-depleted conditions [25], while the magnitude of symbiotic N_2 fixation and transfer varies markedly with specific legume-cereal combinations and is linked to interspecific competitive dynamics [27]. This conceptual progression converges on a new integrative framework: the interspecific nutrient exchange network. This framework is mechanistically founded on belowground interactions mediated by common mycorrhizal networks and root exudates, and is increasingly understood as a dynamic plant-AMF-bacterium continuum [28,29]. This evolution from a linear N transfer model to an integrative network framework represents a significant advancement in agroecological theory.

Accordingly, this review synthesizes the latest evidence underpinning this conceptual shift with three core objectives: to consolidate the mechanistic foundations of interspecific N transfer via both direct and indirect pathways; to elucidate the operational principles and multidimensional regulation of the emergent N-P-C exchange network (Figure 1); and finally, to evaluate the resulting agronomic applications, analyze persisting challenges, and outline future research trajectories aimed at predictive system design. The ultimate aim is to inform the transition of legume-cereal intercropping from an empirically guided practice into a predictable and designable component of next-generation sustainable agroecosystems. Advancing this predictive understanding requires overcoming methodological hurdles. Quantifying the reciprocal, market-like exchanges of nutrients (e.g., N-P, C-N trades) remains challenging, as real-time, *in situ* measurement of these simultaneous fluxes is technically complex. Consequently, much current quantitative evidence stems from controlled single-nutrient experiments, which limits generalizable insights into their context-dependent dynamics.

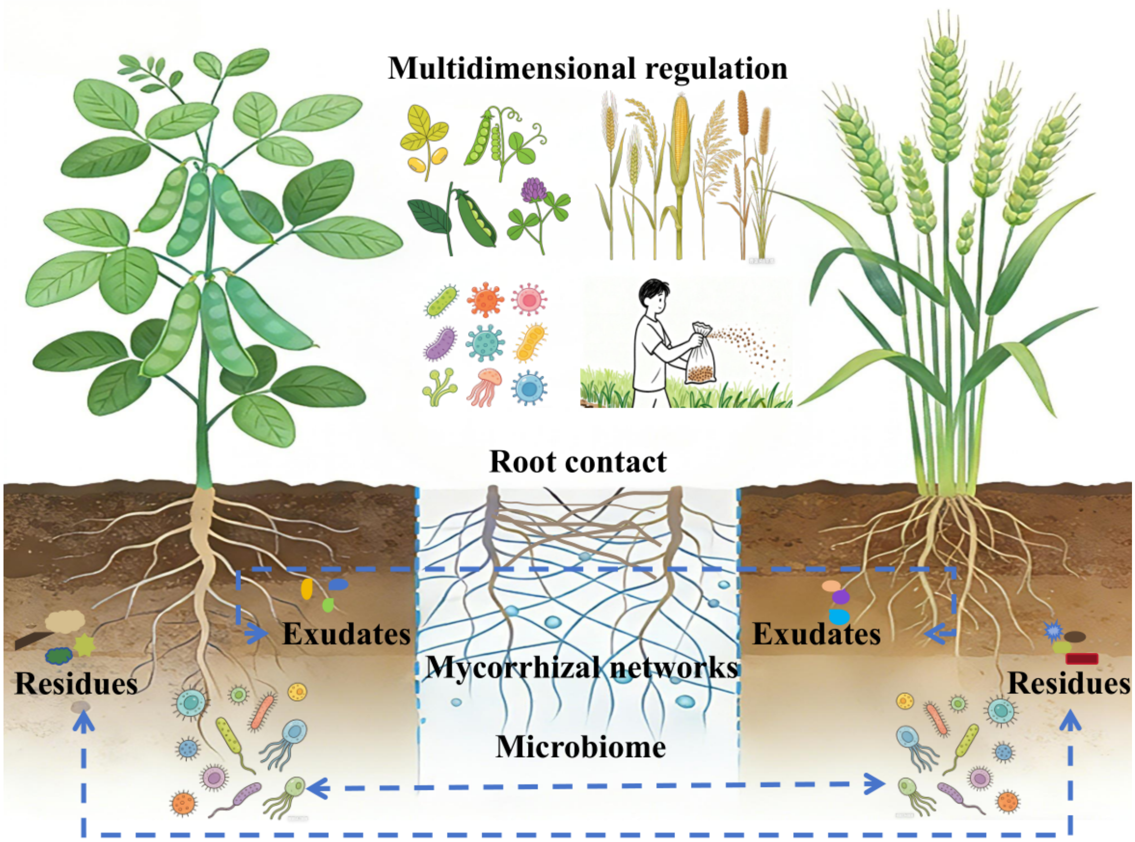


Figure 1. Integration of multiple co-occurring pathways into a multinutrient exchange network between legume and cereal.

2. Mechanistic Basis of Nitrogen Transfer Pathways

The transfer of N from legume to cereals is a pivotal process underpinning the productivity and sustainability of diversified cropping systems [19,30]. Contemporary research elucidates that this transfer is orchestrated through three principal, co-occurring pathways with distinct mechanistic foundations: (1) the root-rhizosphere pathway [31], (2) the mycorrhizal network pathway [32], and (3) the residue decomposition pathway [20,33,34]. The first two pathways operate concurrently and rapidly during the co-growth period, facilitating immediate N sharing. In contrast, the third pathway mediates a delayed but substantial N release, contributing to long-term system fertility. A comprehensive understanding of the interactions and relative contributions of these concurrent routes under field conditions is essential for optimizing intercropping systems and reducing synthetic N inputs.

2.1. The Root-Rhizosphere Pathway

The root-rhizosphere pathway, facilitating near-immediate N sharing, is predominantly driven by rhizosphere interactions and direct root contact between legume and non-legume plants [35]. Legume roots contribute N through both active exudation of low-molecular-weight organic compounds (e.g., amino acids) and passive sloughing of N-rich organic materials (e.g., root cells and mucilage), processes collectively known as rhizodeposition [20,36,37]. These inputs create a localized zone of N enrichment [37,38]. The agronomic efficacy of this enriched zone, however, hinges upon the physical proximity between donor and receiver roots. Specifically, the physical intermingling or close proximity of roots is a key driver of transfer efficiency [39,40]. A study in maize/alfalfa systems show that allowing unrestricted root contact increases N transfer by 1.24 to 1.42 times compared to treatments where roots are separated by barriers, and induces complementary changes in root architecture that facilitate exchange [22]. Similarly, in maize/peanut intercropping, direct root interaction significantly enhances N transfer alongside the activity of rhizosphere enzymes like protease and dehydrogenase, indicating intensified microbial processing [19]. This enhanced microbial activity is crucial, as the legume rhizosphere is a hotspot for N mineralization, with rates shown to be 73.3% to 306.9% higher than in bulk soil [41]. Therefore, this pathway is not merely passive diffusion but an active process where root contact stimulates a biochemical cascade in the rhizosphere, converting legume-derived organic N into inorganic forms readily accessible to neighboring plants. Field evidence confirms the agronomic significance of this pathway; for instance, in soybean-maize intercropping, it can supply 22% to 32% of the total N in maize plants [20].

2.2. The Mycorrhizal Network Pathway

Parallel to the root-mediated process, the mycorrhizal network pathway represents a rapid and direct conduit for N transfer, distinct from soil solution diffusion [42–44]. This pathway is mediated by AMF, whose extraradical hyphae form common mycorrhizal networks that connect the root systems of legume and cereal plants [15,45,46]. And AMF hyphae can absorb ammonium (NH_4^+) from the soil or the legume rhizosphere and transport it internally to the cereal host, effectively bypassing the bulk soil [47]. Quantitative research in an alfalfa and Korla pear intercropping system demonstrated that the N transfer contribution rate was highest (0.92%) under a treatment allowing both hyphal and soil pathways, and was still substantial (0.30%) when relying solely on hyphal channels, compared to complete root isolation (0.28%) [48]. Beyond acting as a direct pipeline, AMF profoundly influence the rhizosphere ecology that governs other transfer pathways. Metagenomic analyses reveal that root interactions in intercrops alter the expression of key N-cycling genes (e.g., *nrfA*, *nirK*), and mycorrhizal associations likely modulate these microbial community functions, thereby indirectly shaping N transfer outcomes [19]. The role of AMF is therefore dual: as a direct transport channel and as a key regulator of the soil N cycle.

2.3. The Residue Decomposition Pathway

In contrast to the immediate pathways, the residue decomposition pathway encompasses the delayed transfer of N mediated by the breakdown of legume-derived organic matter, such as senesced leaves, roots, root nodules, and rhizodeposits [49]. This pathway is vital for system-level N resilience and long-term fertility [37,50,51]. After legume senescence or incorporation as a green manure, this N-rich organic matter is mineralized by soil microbes, releasing plant-available NH_4^+ and nitrate (NO_3^-) for subsequent crops [52,53]. The quantity of N input through this pathway is substantial. Legumes rhizodeposit an average of 83 kg N ha^{-1}, with common grain legumes contributing 25–63 kg N ha^{-1} [33]. A global meta-analysis underscores its power, showing that legumes increase the soil net N mineralization rate by an average of 67% [54]. Subsequent crops can recover a significant portion of this N; for example, wheat has been shown to utilize 13–85% of legume rhizodeposited N, accounting for 4–

20% of the wheat's total N uptake [33]. The efficiency of this transfer is influenced by residue quality (e.g., C:N), soil properties (e.g., temperature, moisture), and the composition of the decomposer community [18,55,56].

2.4. Interactions and Integration of Co-Occurring Pathways

These three pathways are not mutually exclusive but operate simultaneously and synergistically within a cooperative belowground system [57,58]. The root exudation and mycorrhizal network pathways provide swift N supplements to the neighbors during critical co-growth stages [59]. In contrast, the residue decomposition pathway contributes to a more sustained N supply, enhancing soil fertility over time and supporting subsequent crops in a rotation [60,61]. Functional overlap is evident; for instance, root exudates that drive the root-rhizosphere pathway also shape the microbial consortia responsible for residue decomposition [62,63]. Crucially, these pathways are integrated into a complex system orchestrated by chemical communication within the plant-AMF-microbe continuum [28,64]. Arbuscular mycorrhizal fungal hyphae release specific compounds to structure a distinct hyphosphere microbiome, which functionally complements fungal nutrient acquisition [65,66]. Concurrently, plant root exudates drive rhizosphere microbiome assembly, recruiting beneficial microbiota [63]. The collective activity of these exudate-shaped microbial consortia is decisive for system overyielding [67]. Within this continuum, the common mycorrhizal network serves as a core physical and regulatory platform, not only for N transfer but also for the broader exchange of C [28,29] and P [68,69]. This integrated view of belowground facilitation, where multiple specialized nutrient transfer pathways are embedded within a larger biological network, sets the stage for understanding the system as a multi-nutrient exchange economy.

3. Multidimensional Regulation of Transfer Efficiency

The efficiency of N transfer in intercropping systems is dynamically regulated by the complex interplay of biotic [15], abiotic [48,70], and management factors [71], which collectively determine its spatiotemporal variability.

3.1. Biotic Regulation: Plant Traits and Microbial Symbionts

The intrinsic biological traits of donor and recipient plants constitute the foundational biotic control. Phylogenetic relatedness between species is a significant predictor of N transfer patterns, with studies in semi-arid ecosystems demonstrating increased transfer between phylogenetically distant species [72]. Furthermore, differences in root system architecture influence transfer capacity; for example, grasses typically receive more legume-derived N than dicotyledonous herbs in multi-species grasslands [18]. Donor species identity further modulates transfer efficiency. In maize-legume green manure systems, hairy vetch transferred a higher proportion of N to maize (23.3% to 37.0% of maize N uptake) compared to common vetch (5.9% to 32.9%) [73]. Additionally, temporal synchrony of N demand between species, dictated by phenology, critically regulates transfer. Specifically, source-sink gradients driven by phenological asynchrony promote N movement, with evidence showing greater transfer from plants at a low-N-demand stage to those at a high-N-demand stage [74].

Microbial symbionts play a central role in mediating transfer pathways. Although AMF are often proposed as conduits, their direct role is context-dependent. Field experiments in semi-arid ecosystems found that suppressing AMF did not significantly alter the amount of N transferred between plants [72]. However, controlled experiments indicate that soil N availability can modulate the direction and efficiency of N transfer via common mycorrhizal networks. For instance, N addition levels altered AMF colonization, hyphal density, and N transfer rates (16% to 61%) between *Leymus chinensis* and *Cleistogenes squarrosa* [45]. A broader conceptual framework of mycorrhizal networks that includes both direct hyphal connections and indirect rhizosphere interactions is essential. A meta-analysis of ^{15}N labeling studies revealed that mycorrhizal networks and symbiotic N_2-fixing bacteria synergistically enhance interplant N sharing, increasing transfer from N_2-fixing donors to non-fixing receivers by an average of 9.7-fold, with greater transfer to phylogenetically distant plants [15]. This synergy likely arises from functional complementarity between different transfer pathways. Quantitative research in an alfalfa and Korla pear intercropping system showed that the N transfer contribution rate was highest (0.92%) under a no-isolation treatment that allowed both inorganic N ion movement and hyphal channel transfer. This rate was significantly greater than under treatments relying solely on hyphal channels (0.30%) or with complete root isolation (0.28%) [48]. The effectiveness of symbiotic N_2-fixing bacteria (e.g., rhizobia) directly determines the N supply potential of the legume donor [75]. In long-term field experiments, rhizobial inoculation enhanced yield advantages in a faba bean-maize intercrop and increased soil P concentration via strengthened interspecific facilitation [76]. However, this process is highly sensitive to N fertilizer management. In a maize-alfalfa intercropping system, increasing N application from 0 to 224 kg N ha^{-1} reduced the proportion of alfalfa N derived from symbiotic N_2 fixation from 59% to 15%, concurrently decreasing the contribution of fixed N to maize N uptake from 28% to 7% [13]. Intercropping patterns and N management strongly shape the legume rhizosphere microbiome. Maize-soybean intercropping combined with reduced N fertilization significantly altered soybean rhizosphere bacterial and *nifH* communities, enriching beneficial N_2-fixers like *Sinorhizobium* and enhancing microbial network complexity and stability, which in turn predicted higher system yield and N use efficiency [71].

3.2. Abiotic Regulation: Soil Chemical and Physical Factors

Soil chemical properties constitute the fundamental abiotic template governing N transfer processes. Among these, soil pH is a predominant factor, explaining up to 44.04% of the variation in N transfer proportion, with significantly higher efficiency in alkaline than in acidic soils [77]. Soil N availability acts as a master regulator through dual, context-dependent mechanisms. Primarily, low soil N availability stimulates legume nodulation and symbiotic N_2 fixation, thereby enlarging the source pool of transferable N [18]. This is evidenced by ^{15}N studies showing that N transfer from peanut decreases from 12.2% to 6.2% as N fertilizer application increases [78]. Recent research further elucidates that this regulation is mediated by the growth responses of both partners. For instance, the proportion of fixed N transferred is negatively correlated with legume biomass but positively correlated with cereal biomass, indicating that N application affects transfer efficiency by modulating the source-sink dynamics within the intercrop [27]. Ultimately, the legume-derived N source can be substantial, with cover crops in relay intercropping fixing 38–67 kg N ha^{-1} and significantly enhancing the N uptake of subsequent maize [79]. In a contrasting dynamic, under conditions where legume growth and biomass production are limited by N, the application of N-rich amendments can enhance overall system productivity and N flux, potentially increasing the absolute amount of N transferred, particularly to competitive species [18]. A more direct mechanism is that N addition may alter belowground C allocation and root exudation, thereby modifying rhizosphere processes that mediate transfer. Soil P status serves as another key switch; low P availability increases plant dependence on mycorrhizal fungi for nutrient acquisition [18], which can influence hyphal-mediated N transfer. Furthermore, root interactions in intercrops can enhance rhizosphere citric acid exudation and decrease the NO_3^-/NH_4^+, conditions that facilitate N fixation and subsequent transfer [70]. Collectively, the interactive regulation by soil N and P availability underscores that N transfer efficiency is constrained by the stoichiometric balance of the rhizosphere environment, which shapes plant investment in symbiotic partnerships. Therefore, precision management of soil nutrient status is key to unlocking the full N facilitation potential of legume-cereal intercropping systems.

3.3. Management Regulation: Agricultural Practices

Agricultural management interventions can be employed to optimize N transfer. Strategic planting designs, such as combining species with contrasting phenologies to exploit temporal N-demand gradients, are crucial [74]. Root barrier experiments directly quantify the role of belowground interaction in driving this optimization. For instance, allowing root intermingling in soybean-maize systems significantly reduced soil mineral N residue and drove substantial N transfer from soybean to maize (accounting for 22% to 32% of maize N uptake) [20]. This mechanism is key to achieving N-saving benefits, enabling a reduction of the optimal N application rate by approximately 45% (to about 165 kg N ha^{-1}) compared to maize monoculture [20], which serves as a cornerstone for achieving multi-objective agroecosystem balance. Research in a maize-peanut intercropping system demonstrated that a 20% reduction in conventional N application effectively maintained crop productivity while significantly enhancing soil biological health (by 78% in the maize strip and 49% in the peanut strip), achieving an optimal trade-off among productivity, soil health, and soil multifunctionality [11]. Consequently, fertilization management requires a nuanced approach. While N application can enhance overall system productivity and N transfer to strong competitors [18], excessive N suppresses symbiotic N_2 fixation [13]. Beyond targeted nutrient management, the intercropping practice itself modifies soil biotic communities and ecosystem functions. For example, durum wheat-lentil relay intercropping enhanced soil mycorrhizal inoculum potential but variably affected AMF root colonization and community structure compared to sole crops [80]. Similarly, maize-soybean intercropping differentially influenced soil food webs, increasing the complexity and robustness of co-occurrence networks in the maize strip while promoting saprophytic fungi and plant-parasitic nematodes in the soybean strip [81]. On a broader scale, legume-based intercropping systems deliver integrated ecosystem services beyond N transfer. These optimized management practices translate into tangible, multifaceted benefits. Meta-analyses indicate that well-managed legume-cereal intercropping can reduce synthetic N fertilizer requirement by 20–25%, increase main crop equivalent yield by 30–35%, and improve water use efficiency by 20–25% compared to sole cropping [38]. These findings collectively underscore that the optimization of management practices must account for their cascading effects on belowground biotic interactions and ecosystem multifunctionality to maximize the complementary and facilitative processes that underpin efficient and sustainable N cycling in intercropping systems.

4. Multinutrient Exchange Networks Coupled with Nitrogen Transfer

4.1. The Reciprocal Exchange Network of Multiple Nutrients

Research on legume-cereal intercropping has witnessed a fundamental shift in perspective: from a focus on unidirectional N transfer toward recognizing a self-organizing, biological market-like network of multi-nutrient exchange [82–85]. This network, orchestrated within the plant-AMF-bacterium continuum, is the fundamental engine driving system-level advantages in resource use, productivity, and resilience [28,65]. This integrated perspective moves beyond merely listing pathways, instead viewing belowground facilitation as a hierarchical and synergistic system: the common mycorrhizal network acts as the central architectural hub and integrative exchange platform, whose function is initiated by root contact and exudates, executed by recruited microbial consortia, and holistically regulated by soil physicochemical properties [86]. The arbuscular mycorrhizal symbiosis operates as a core dynamic biological market, where reciprocal trading of plant-assimilated C for fungal-acquired P and N is the norm but not an absolute rule [85,87,88]. This market framework posits that cooperation is stabilized through reciprocal reward mechanisms. However, a empirical study revealed prevalent asymmetric exchanges, where C investment and nutrient return are unevenly distributed among connected plants [89]. This suggests the market is driven by a complex interplay of reciprocity, competition for surplus resources, and the functional diversity of partners [90]. Notably, these dynamics function at a community scale, with C and nutrient flows dynamically regulated by neighboring plants, highlighting the network's role as a resilient, multi-host platform rather than a series of isolated pairwise trades [91].

4.2. Exchange Mechanisms, Network Dynamics, and Agroecological Implications

The stability and efficiency of this network arise from the functional complementarity of the intercrop partners. Legumes possess a high metabolic demand for P) to support energy-intensive symbiotic N_2 fixation, a process tightly regulated by nodule-specific energy sensors that modulate C allocation [92,93]. Cereals, in contrast, often exhibit stronger mycorrhizal dependence and are proficient at acquiring soil P through extensive root systems and symbiotic associations with AMF [94,95]. This niche differentiation creates a natural synergy: cereals may supply acquired P (or C) in return for legume-derived N [96]. Importantly, these exchanges are not simple bilateral trades but are regulated by the entire plant community, exhibiting emergent network properties. For instance, the presence of a legume can non-additively enhance the transfer of C and N from a grass to a third, non-leguminous species, demonstrating that network function transcends pairwise interactions [26,91]. Empirical evidence reveals a critical functional specialization within this network: C transfer is strongly dependent on direct root contact, whereas N moves predominantly via the mycorrhizal pathway [26]. This logistical divergence indicates that different nutrients follow distinct transport rules within the belowground economy. Furthermore, these dynamic nutrient flows generate positive belowground feedbacks by modifying soil structure, specifically increasing the volume of protective 8–30 μm pores, which enhances soil organic C stabilization and directly links short-term nutrient dynamics to long-term soil health [26]. This integrated network framework converges on a powerful agroecological insight: the productivity and resilience advantage of legume-cereal intercropping is increasingly attributed to enhanced soil ecosystem multifunctionality. This multifunctionality is driven by the network's ability to simultaneously increase nutrient availability, stimulate key microbial processes, and improve soil physical structure [97]. This mechanistic understanding of the belowground economy provides a foundational framework for the predictive management and design of next-generation sustainable agroecosystems.

5. Conclusions and Prospective

Research on legume-cereal intercropping now recognizes a reciprocal exchange network of C, N, and P, moving beyond the earlier focus on unidirectional N transfer. This network is understood as a self-organized, market-like system operating within the plant-AMF-bacterium continuum. Its operation relies on specialized pathways: C transfer depends strongly on direct root contact, N is predominantly channeled through mycorrhizal hyphae, and cereals facilitate P acquisition in a trade for legume-derived N. These exchanges generate emergent system properties, where community-level synergies enhance overall efficiency, and nutrient flows create positive feedbacks by improving soil structure and C stabilization.

Key questions remain regarding how to scale individual traits to system-level performance and how to elucidate the precise regulatory mechanisms of hyphosphere microbiota. Addressing these questions necessitates integrating advanced methodologies, such as *in situ* multi-isotope tracing, high-resolution imaging, and meta-omics, to quantitatively map the interactions between nutrient fluxes, microbial networks, and soil architecture. The integration of these data into process-based models or digital twins is crucial for developing predictive frameworks. The insights generated by these advanced methodologies will directly inform practical design decisions. Ultimately, this knowledge should guide the design of next-generation practices. This includes selecting cooperative crop phenotypes and engineering synthetic microbial consortia, a promising yet challenging approach currently limited by persistence, context-dependency, and scaling from lab to field, to stabilize and enhance the belowground economy. Advancing this predictive understanding is essential for scaling legume-cereal intercropping into a more efficient and sustainable pillar of agricultural intensification.

Author Contributions

R.L.: Conceptualization, Writing-original draft. Z.N.: Writing—review & editing. H.N.: Writing—review & editing, Supervision, Funding acquisition, Conceptualization. All authors have read and agreed to the published version of the manuscript.

Funding

This work was supported by the project titled "Assessment of the Ecological and Environmental Effects of the Main Afforestation Measures in the Northern and Southern Mountains of Lhasa City", funded by the Lhasa Municipal Forestry and Grassland Bureau, and Fundamental Research Funds for the Central Universities.

Data Availability Statement

Data will be made available on request.

Conflicts of Interest

The authors declare no conflict of interest.

Use of AI and AI-Assisted Technologies

No AI tools were utilized for this paper.

References

1. Ullah, F.; Saqib, S.; Qin-Zheng, H.; et al. Intercropping for sustainable agroecosystems: Enhancing biodiversity, resource efficiency, and mitigating greenhouse gas emissions. *Mitig. Adapt. Strateg. Glob. Chang.* **2025**, *30*, 62. https://doi.org/10.1007/s11027-025-10263-4.
2. Wang, Y.; Wu, L.; Zhao, J.; et al. Navigating the sustainability challenges of food systems: A review of life cycle-based environmental footprints and future directions. *J. Environ. Manag.* **2025**, *392*, 126794. https://doi.org/10.1016/j.jenvman.2025.126794.
3. Ruillé, M.; Beillouin, D.; Prudhomme, R. Ecological drivers of intercropping performance for enhanced global crop production. *NPJ Sustain. Agric.* **2026**, *4*, 8. https://doi.org/10.1038/s44264-025-00110-z.
4. Kamran, M.; Zhang, M.; Jia, Q.; et al. Legume-grass intercropping at low nitrogen input: Achieving the dual goals of lower greenhouse gas emissions and high quality forage productivity in the arid region. *Agric. Ecosyst. Environ.* **2025**, *393*, 109859. https://doi.org/10.1016/j.agee.2025.109859.
5. Ebbisa, A. Mechanisms underlying cereal/legume intercropping as nature-based biofortification: A review. *Food Prod. Process. Nutr.* **2022**, *4*, 19. https://doi.org/10.1186/s43014-022-00096-y.
6. Yu, R.P.; Yang, H.; Xing, Y.; et al. Belowground processes and sustainability in agroecosystems with intercropping. *Plant Soil* **2022**, *476*, 263–288. https://doi.org/10.1007/s11104-022-05487-1.
7. Chen, C.; Li, L.; Wu, S.; et al. Nitrogen transfer in legume/non-legume intercropping systems: A global meta-analysis. *Agric. Ecosyst. Environ.* **2026**, *401*, 110295. https://doi.org/10.1016/j.agee.2026.110295.
8. Chiurazzi, M.; Frugis, G.; Navazio, L. Symbiotic nitrogen fixation: A launchpad for investigating old and new challenges. *J. Exp. Bot.* **2025**, *76*, 1473–1477. https://doi.org/10.1093/jxb/erae510.
9. Ouyang, S.; Tian, Y.; Liu, Q.; et al. Symbiotic nitrogen fixation and interspecific transfer by *Caragana microphylla* in a temperate grassland with ^{15}N dilution technique. *Appl. Soil Ecol.* **2016**, *108*, 221–227. https://doi.org/10.1016/j.apsoil.2016.08.011.
10. Luo, C.L.; Duan, H.X.; Wang, Y.L.; et al. Complementarity and competitive trade-offs enhance forage productivity, nutritive balance, land and water use, and economics in legume-grass intercropping. *Field Crops Res.* **2024**, *319*, 109642. https://doi.org/10.1016/j.fcr.2024.109642.

11. Wang, X.; Li, Y.; Yang, M.; et al. Intercropping with appropriate nitrogen reduction achieves the trade-off among soil biological health, soil multifunctionality, and crop productivity. *Field Crops Res*. **2025**, *333*, 110085. https://doi.org/10.1016/j.fcr.2025.110085.
12. Salinas-Roco, S.; Morales-González, A.; Espinoza, S.; et al. N_2 Fixation, N transfer, and land equivalent ratio (LER) in grain legume-wheat intercropping: Impact of N supply and plant density. *Plants* **2024**, *13*, 991. https://doi.org/10.3390/plants13070991.
13. Osterholz, W.; Ruark, M.; Renz, M.; Grabber, J. Interseeded alfalfa N_2 fixation and transfer to maize are reduced by N fertilizer. *Nutr. Cycl. Agroecosyst.* **2023**, *126*, 67–79. 10.1007/s10705-023-10276-y.
14. Chalk, P.M.; Peoples, M.B.; McNeill, A.M.; et al. Methodologies for estimating nitrogen transfer between legumes and companion species in agro-ecosystems: A review of ^{15}N-enriched techniques. *Soil Biol. Biochem.* **2014**, *73*, 10–21. https://doi.org/10.1016/j.soilbio.2014.02.005.
15. Gao, Y.; Wu, Y.; Chang, P.; et al. Mycorrhizal network and symbiotic N-fixer jointly enhance the interplant nitrogen sharing. *Ecol. Lett.* **2025**, *28*, e70204. https://doi.org/10.1111/ele.70204.
16. Wang, L.; Liao, D.; Rengel, Z.; et al. Soil–plant–microbe interactions in the rhizosphere: Incremental amplification induced by localized fertilization. *Front. Agric. Sci. Eng.* **2025**, *12*, 57 -68. https://doi.org/10.15302/J-FASE-2024575.
17. Li, C.; Lambers, H.; Jing, J.; et al. Belowground cascading biotic interactions trigger crop diversity benefits. *Trends Plant Sci.* **2024**, *29*, 1191–1202. https://doi.org/10.1016/j.tplants.2024.04.010.
18. Pirhofer-Walzl, K.; Rasmussen, J.; Høgh-Jensen, H.; et al. Nitrogen transfer from forage legumes to nine neighbouring plants in a multi-species grassland. *Plant Soil* **2012**, *350*, 71–84. https://doi.org/10.1007/s11104-011-0882-z.
19. Dong, Q.; Su, H.; Sun, Y.; et al. Metagenomic insights into nitrogen cycling functional gene responses to nitrogen fixation and transfer in maize–peanut intercropping. *Plant Cell Environ.* **2024**, *47*, 4557-4571. https://doi.org/10.1111/pce.15034.
20. Jing, B.; Shi, W.; Chen, T.; et al. Underground interaction saves nitrogen input by driving nitrogen fixation and transfer in maize-soybean intercropping. *Field Crops Res*. **2025**, *334*, 110150. https://doi.org/10.1016/j.fcr.2025.110150.
21. Shen, Q.; Chu, G. Bi-directional nitrogen transfer in an intercropping system of peanut with rice cultivated in aerobic soil. *Biol. Fertil. Soils* **2004**, *40*, 81–87. https://doi.org/10.1007/s00374-004-0737-3.
22. Shao, Z.; Zheng, C.; Postma, J.A.; et al. Nitrogen acquisition, fixation and transfer in maize/alfalfa intercrops are increased through root contact and morphological responses to interspecies competition. *J. Integr. Agric.* **2021**, *20*, 2240–2254. https://doi.org/10.1016/S2095-3119(20)63330-5.
23. Zhang, H.; Wang, X.; Gao, Y.; et al. Short-term N transfer from alfalfa to maize is dependent more on arbuscular mycorrhizal fungi than root exudates in N deficient soil. *Plant Soil* **2020**, *446*, 23–41. https://doi.org/10.1007/s11104-019-04333-1.
24. Zhou, M.; Li, Y.; Yao, X.L.; et al. Inorganic nitrogen inhibits symbiotic nitrogen fixation through blocking NRAMP2-mediated iron delivery in soybean nodules. *Nat. Commun*. **2024**, *15*, 8946. https://doi.org/10.1038/s41467-024-53325-y.
25. Li, C.; Dong, Y.; Li, H.; et al. Shift from complementarity to facilitation on P uptake by intercropped wheat neighboring with faba bean when available soil P is depleted. *Sci. Rep.* **2016**, *6*, 18663. https://doi.org/10.1038/srep18663.
26. Lee, J.H.; Ulbrich, T.C.; Oerther, M.; et al. Belowground plant carbon and nitrogen exchange: Plant-derived carbon inputs and pore structure formation. *Soil. Biol. Biochem*. **2025**, *207*, 109833. https://doi.org/10.1016/j.soilbio.2025.109833.
27. Zhao, Y.; Tian, Y.; Li, X.; et al. Nitrogen fixation and transfer between legumes and cereals under various cropping regimes. *Rhizosphere* **2022**, *22*, 100546. https://doi.org/10.1016/j.rhisph.2022.100546.
28. Duan, S.; Feng, G.; Limpens, E.; et al. Cross-kingdom nutrient exchange in the plant–arbuscular mycorrhizal fungus-bacterium continuum. *Nat. Rev. Microbiol.* **2024**, *22*, 773–790. https://doi.org/10.1038/s41579-024-01073-7.
29. Duan, S.; Jin, Z.; Zhang, L.; et al. Mechanisms of cooperation in the plants-arbuscular mycorrhizal fungi-bacteria continuum. *ISME J.* **2025**, *19*, wraf023. https://doi.org/10.1093/ismejo/wraf023.
30. Zhang, W.; Wei, Y.-X.; Khan, A.; et al. Intercropped soybean boosts nitrogen benefits and amends nitrogen use pattern under plastic film mulching in the semiarid maize field. *Field Crops Res.* **2023**, *295*, 108881. https://doi.org/10.1016/j.fcr.2023.108881.
31. Hupe, A.; Naether, F.; Haase, T.; et al. Evidence of considerable C and N transfer from peas to cereals via direct root contact but not via mycorrhiza. *Sci. Rep*. **2021**, *11*, 11424. https://doi.org/10.1038/s41598-021-90436-8.
32. Zhang, T.; Yu, L.; Shao, Y.; et al. Root and hyphal interactions influence N transfer by arbuscular mycorrhizal fungi in soybean/maize intercropping systems. *Fungal Ecol.* **2023**, *64*, 101240. https://doi.org/10.1016/j.funeco.2023.101240.
33. Wang, X.; Yang, Y.; Pei, K.; et al. Nitrogen rhizodeposition by legumes and its fate in agroecosystems: A field study and literature review. *Land Degrad. Dev.* **2021**, *32*, 410–419. https://doi.org/10.1002/ldr.3729.
34. Thilakarathna, M.S.; McElroy, M.S.; Chapagain, T.; et al. Belowground nitrogen transfer from legumes to non-legumes under managed herbaceous cropping systems. A review. *Agron. Sustain. Dev.* **2016**, *36*, 58. https://doi.org/10.1007/s13593-016-0396-4.
35. Xiao, Y.; Li, L.; Zhang, F. Effect of root contact on interspecific competition and N transfer between wheat and fababean using direct and indirect ^{15}N techniques. *Plant Soil* **2004**, *262*, 45–54. https://doi.org/10.1023/B:PLSO.0000037019.34719.0d.

36. Yin, X.; Yang, H.; Yu, R.; et al. Interspecific below-ground interactions driven by root exudates in agroecosystems with diverse crops. *Chin. J. Eco-Agric.* **2022**, *30*, 1215–1227. https://doi.org/10.12357/cjea.20220150.
37. Qiao, M.; Sun, R.; Wang, Z.; et al. Legume rhizodeposition promotes nitrogen fixation by soil microbiota under crop diversification. *Nat. Commun.* **2024**, *15*, 2924. https://doi.org/10.1038/s41467-024-47159-x.
38. Akchaya, K.; Parasuraman, P.; Pandian, K.; et al. Boosting resource use efficiency, soil fertility, food security, ecosystem services, and climate resilience with legume intercropping: A review. *Front. Sustain. Food Syst.* **2025**, *9*, 2025. https://doi.org/10.3389/fsufs.2025.1527256.
39. Zhang, H.; Zeng, F.; Zou, Z.; et al. Nitrogen uptake and transfer in a soybean/maize intercropping system in the karst region of southwest China. *Ecol. Evol.* **2017**, *7*, 8419–8426. https://doi.org/10.1002/ece3.3295.
40. Arafat, Y.; Shah, A.; Din, I.U.; et al. Root interactions in wheat/fababean intercropping system enhanced growth performance and yield. *Rhizosphere*, **2021**, *33*, 101007. https://doi.org/10.1016/j.rhisph.2024.101007.
41. Dong, Y.; Shen, G.; Jiao, Y.; et al. The rhizosphere: A key hotspot for gross nitrogen transformations and nitrous oxide emissions in legume cropping systems. *Geoderma* **2025**, *463*, 117567. https://doi.org/10.1016/j.geoderma.2025.117567.
42. Ingraffia, R.; Giambalvo, D.; Frenda, A.S.; et al. Mycorrhizae differentially influence the transfer of nitrogen among associated plants and their competitive relationships. *Appl. Soil. Ecol.* **2021**, *168*, 104127. https://doi.org/10.1016/j.apsoil.2021.104127.
43. Fall, F.; Ndoye, D.; Galiana, A.; et al. Arbuscular mycorrhizal fungi-mediated biologically fixed N transfer from *Vachellia seyal* to *Sporobolus robustus*. *Symbiosis* **2022**, *86*, 205–214. https://doi.org/10.1007/s13199-022-00833-4.
44. He, Y.; Cornelissen, J.H.C.; Wang, P.; et al. Nitrogen transfer from one plant to another depends on plant biomass production between conspecific and heterospecific species via a common arbuscular mycorrhizal network. *Environ. Sci. Pollut. R.* **2019**, *26*, 8828–8837. https://doi.org/10.1007/s11356-019-04385-x.
45. Muneer, M.A.; Chen, X.; Munir, M.Z.; et al. Interplant transfer of nitrogen between C_3 and C_4 plants through common mycorrhizal networks under different nitrogen availability. *J. Plant Ecol.* **2023**, *16*, rtac058. https://doi.org/10.1093/jpe/rtac058.
46. Xu, P.; Wang, E. Diversity and regulation of symbiotic nitrogen fixation in plants. *Curr. Biol.* **2023**, *33*, R543–R559. https://doi.org/10.1016/j.cub.2023.04.053.
47. He, X.; Critchley, C.; Ng, H.; Bledsoe, C. Nodulated N_2-fixing Casuarina cunninghamiana is the sink for net N transfer from non-N_2-fixing *Eucalyptus maculata* via an ectomycorrhizal fungus *Pisolithus* sp. using $^{15}NH_4^+$ or $^{15}NO_3^-$ supplied as ammonium nitrate. *New Phytol.* **2005**, *167*, 897–912. https://doi.org/10.1111/j.1469-8137.2005.01437.x.
48. Ming, Y.; Dou, Z.; Zheng, W; et al. Quantitative analysis of nitrogen transfer pathways in intercropping systems between alfalfa and Korla pear. *Acta Pratacult. Sin.* **2025**, *34*, 51–61. https://doi.org/10.11686/cyxb2024469. (In Chinese)
49. Sierra, J.; Nygren, P. Transfer of N fixed by a legume tree to the associated grass in a tropical silvopastoral system. *Soil. Biol. Biochem.* **2006**, *38*, 1893–1903. https://doi.org/10.1016/j.soilbio.2005.12.012.
50. Mayer, J.; Buegger, F.; Jensen, E.S.; et al. Turnover of grain legume N rhizodeposits and effect of rhizodeposition on the turnover of crop residues. *Biol. Fertil. Soils* **2004**, *39*, 153–164. https://doi.org/10.1007/s00374-003-0694-2.
51. Geng, S.; Li, L.; Miao, Y.; et al. Nitrogen rhizodeposition from corn and soybean, and its contribution to the subsequent wheat crops. *J. Integr. Agric.* **2024**, *23*, 2446–2457. https://doi.org/10.1016/j.jia.2023.11.018.
52. Gan, H.; Drinkwater, L.E. Leguminous green manure promotes N accrual in labile and persistent soil organic matter pools. *Plant Soil* **2025**, *507*, 763–781. https://doi.org/10.1007/s11104-024-06764-x.
53. Liu, C.; Wei, S.; Li, M.; et al. Nitrogen reduction via cultivation of green manures in drylands: A microbial perspective on enhancing soil nitrogen availability to increase wheat yield. *Agric. Ecosyst. Environ*. **2026**, *400*, 110208. https://doi.org/10.1016/j.agee.2025.110208.
54. Gou, X.; Reich, P.B.; Qiu, L.; et al. Leguminous plants significantly increase soil nitrogen cycling across global climates and ecosystem types. *Glob. Chang. Biol*. **2023**, *29*, 4028–4043. https://doi.org/10.1111/gcb.16742.
55. Chaves, B.; Redin, M.; Giacomini, S.J.; et al. The combination of residue quality, residue placement and soil mineral N content drives C and N dynamics by modifying N availability to microbial decomposers. *Soil. Biol. Biochem.* **2021**, *163*, 108434. https://doi.org/10.1016/j.soilbio.2021.108434.
56. Surigaoge, S.; Yang, H.; Fornara, D.; et al. Litter functional dissimilarity accelerates carbon and nitrogen release from the decomposition of straw but not root in maize/legume intercropping. *Plant Soil* **2025**, *506*, 487–502. https://doi.org/10.1007/s11104-024-06616-8.
57. Reay, M.K.; Pears, K.A.; Kuhl, A.; et al. Mechanisms of nitrogen transfer in a model clover-ryegrass pasture: A ^{15}N-tracer approach. *Plant Soil* **2022**, *480*, 369–389. https://doi.org/10.1007/s11104-022-05585-0.
58. San-nai, J.; Ming-pu, Z. Nitrogen transfer between N_2-fixing plant and non-N_2-fixing plant. *J. For. Res.* **2000**, *11*, 75–80. https://doi.org/10.1007/BF02856678.
59. Jalonen, R.; Nygren, P.; Sierra, J. Transfer of nitrogen from a tropical legume tree to an associated fodder grass via root exudation and common mycelial networks. *Plant Cell Environ*. **2009**, *32*, 1366–1376. https://doi.org/10.1111/j.1365-3040.2009.02004.x.

60. Liu, C.; Feng, X.; Xu, Y.; et al. Legume-based rotation enhances subsequent wheat yield and maintains soil carbon storage. *Agron. Sustain. Dev.* **2023**, *43*, 64. https://doi.org/10.1007/s13593-023-00918-4.
61. Sunil Kumar, T.; Virdia, H.M.; Patel, K.G.; et al. Residual effect of summer legumes incorporation on soil nutrient status and nutrient use efficiency of kharif rice. *Front. Sustain. Food Syst.* **2025**, *9*, 2025. https://doi.org/10.3389/fsufs.2025.1535162.
62. Shafi, Z.; Shahid, M. Root exudates as molecular architects shaping the rhizobacterial community: A review. *Rhizosphere* **2025**, *36*, 101212. https://doi.org/10.1016/j.rhisph.2025.101212.
63. Yang, C.X.; Chen, S.J.; Hong, X.Y.; et al. Plant exudates-driven microbiome recruitment and assembly facilitates plant health management. *FEMS Microbiol. Rev.* **2025**, 49, fuaf008. https://doi.org/10.1093/femsre/fuaf008.
64. Kothamasi, D. Much ado about communicating: Plant-AMF chemical crosstalk and structuring of the rhizospheric microbiome. *Appl. Soil Ecol.* **2026**, *218*, 106759. https://doi.org/10.1016/j.apsoil.2025.106759.
65. Zhang, L.; Zhou, J.; George, T.S.; et al. Arbuscular mycorrhizal fungi conducting the hyphosphere bacterial orchestra. *Trends Plant Sci.* **2022**, *27*, 402–411. https://doi.org/10.1016/j.tplants.2021.10.008.
66. Wang, L.; Zhang, L.; George, T.S.; et al. Hyphosphere core taxa link plant-arbuscular mycorrhizal fungi combinations to soil organic phosphorus mineralization. *Soil. Biol. Biochem.* **2025**, *201*, 109647. https://doi.org/10.1016/j.soilbio.2024.109647.
67. Qiao, X.; Bei, S.; Wang, G.; et al. Soil biota is decisive for overyielding in intercropping under low phosphorus conditions. *J. Appl. Ecol.* **2022**, *59*, 1804–1814. https://doi.org/10.1111/1365-2664.14187.
68. Duan, S.; Zhang, L.; Declerck, S. Early-stage reciprocal cooperation between the arbuscular mycorrhizal fungus Rhizophagus irregularis and the phosphate-solubilizing bacterium *Rahnella aquatilis* is dependent on external phosphorus availability. *Commun. Biol.* **2025**, *8*, 1075. https://doi.org/10.1038/s42003-025-08501-1.
69. Lekberg, Y.; Jansa, J.; McLeod, M.; et al. Carbon and phosphorus exchange rates in arbuscular mycorrhizas depend on environmental context and differ among co-occurring plants. *New Phytol.* **2024**, *242*, 1576–1588. https://doi.org/10.1111/nph.19501.
70. Wang, X.; Gao, Y.; Zhang, H.; et al. Enhancement of rhizosphere citric acid and decrease of NO_3^-/NH_4^+ ratio by root interactions facilitate N fixation and transfer. *Plant Soil* **2020**, *447*, 169–182. https://doi.org/10.1007/s11104-018-03918-6.
71. Dang, P.; Lu, C.; Huang, T.; et al. Enhancing intercropping sustainability: Manipulating soybean rhizosphere microbiome through cropping patterns. *Sci. Total Environ.* **2024**, *931*, 172714. https://doi.org/10.1016/j.scitotenv.2024.172714.
72. Montesinos-Navarro, A.; Collins, S.; Dumitru, C.; et al. Phylogenetic relatedness predicts plant–plant nitrogen transfer better than the duration of water scarcity periods. *New Phytol.* **2025**, *246*, 1848–1860. https://doi.org/10.1111/nph.70116.
73. Liu, R.; Zhou, G.; Chang, D.; et al. Transfer characteristics of nitrogen fixed by leguminous green manure crops when intercropped with maize in northwestern China. *J. Integr. Agric.* **2022**, *21*, 1177–1187. https://doi.org/10.1016/S2095-3119(21)63674-2.
74. Montesinos-Navarro, A. Nitrogen transfer between plant species with different temporal N-demand. *Ecol. Lett.* **2023**, *26*, 1676–1686. https://doi.org/10.1111/ele.14279.
75. Li, X.; Li, Z. What determines symbiotic nitrogen fixation efficiency in rhizobium: Recent insights into Rhizobium leguminosarum. *Arch. Microbiol.* **2023**, *205*, 300. https://doi.org/10.1007/s00203-023-03640-7.
76. Mao, J.; Wang, P.; Xiao, C.L.; et al. Rhizobium inoculation improves yield advantages and soil Olsen phosphorus by enhancing interspecific facilitation in intercropping. *Plant Soil* **2025**, *506*, 359–373. https://doi.org/10.1007/s11104-023-06425-5.
77. Wang, L.; Yu, W.Q.; Lu, D.X.; et al. Soil pH modulates nitrogen transfer from nitrogen-fixing plants to non-nitrogen-fixing plants. *Chin. J. Plant Ecol.* **2022**, *46*, 1–17. https://doi.org/10.17521/cjpe.2021.0283. (In Chinese)
78. Chu, G.X.; Shen, Q.R.; Cao, J.L. Nitrogen fixation and N transfer from peanut to rice cultivated in aerobic soil in an intercropping system and its effect on soil N fertility. *Plant Soil* **2004**, *263*, 17–27. https://doi.org/10.1023/B:PLSO.0000047722.49160.9e.
79. Amossé, C.; Jeuffroy, M.H.; Mary, B.; et al. Contribution of relay intercropping with legume cover crops on nitrogen dynamics in organic grain systems. *Nutr. Cycl. Agroecosyst.* **2014**, *98*, 1–14. https://doi.org/10.1007/s10705-013-9591-8.
80. Koskey, G.; Avio, L.; Turrini, A.; et al. Durum wheat-lentil relay intercropping enhances soil mycorrhizal activity but does not alter structure of arbuscular mycorrhizal fungal community within roots. *Agric. Ecosyst. Environ.* **2023**, *357*, 108696. https://doi.org/10.1016/j.agee.2023.108696.
81. Zhang, G.; Yang, H.; Zhang, W.; et al. Interspecific interactions between crops influence soil functional groups and networks in a maize/soybean intercropping system. *Agric. Ecosyst. Environ.* **2023**, *355*, 108595. https://doi.org/10.1016/j.agee.2023.108595.
82. Liu, H.; Gao, X.; Fan, W.; et al. Optimizing carbon and nitrogen metabolism in plants: From fundamental principles to practical applications. *J. Integr. Plant Biol.* **2025**, *67*, 1447–1466. https://doi.org/10.1111/jipb.13919.
83. Wang, W.; Chen, D.; Sun, H.; et al. Genetic improvement of nitrogen- and phosphorus-use efficiency in crops: Old goals with new aspirations. *Mol. Plant* **2026**, *in press*. https://doi.org/10.1016/j.molp.2025.12.030.
84. Govindarajulu, M.; Pfeffer, P.E.; Jin, H.; et al. Nitrogen transfer in the arbuscular mycorrhizal symbiosis. *Nature* **2005**, *435*, 819–823. https://doi.org/10.1038/nature03610.

85. Kiers, E.T.; Duhamel, M.; Beesetty, Y.; et al. Reciprocal rewards stabilize cooperation in the mycorrhizal symbiosis. *Science* **2011**, *333*, 880–882. https://doi.org/10.1126/science.1208473.
86. Van Der Heijden, M.G. A.; Horton, T.R. Socialism in soil? The importance of mycorrhizal fungal networks for facilitation in natural ecosystems. *J. Ecol.* **2009**, *97*, 1139–1150. https://doi.org/10.1111/j.1365-2745.2009.01570.x.
87. Shi, J.; Wang, X.; Wang, E. Mycorrhizal symbiosis in plant growth and stress adaptation: From genes to ecosystems. *Annu. Rev. Plant Biol.* **2023**, *74*, 569–607. https://doi.org/10.1146/annurev-arplant-061722-090342.
88. Wipf, D.; Krajinski, F.; van Tuinen, D.; et al. Trading on the arbuscular mycorrhiza market: From arbuscules to common mycorrhizal networks. *New Phytol.* **2019**, *223*, 1127–1142. https://doi.org/10.1111/nph.15775.
89. Walder, F.; Niemann, H.; Natarajan, M.; et al. Mycorrhizal networks: Common goods of plants shared under unequal terms of trade. *Plant Physiol.* **2012**, *159*, 789–797. https://doi.org/10.1104/pp.112.195727.
90. Walder, F.; van der Heijden, M.G.A. Regulation of resource exchange in the arbuscular mycorrhizal symbiosis. *Nat. Plants* **2015**, *1*, 15159. https://doi.org/10.1038/nplants.2015.159.
91. Durant, E.; Hoysted, G.A.; Howard, N.; et al. Herbivore-driven disruption of arbuscular mycorrhizal carbon-for-nutrient exchange is ameliorated by neighboring plants. *Curr. Biol.* **2023**, *33*, 2566–2573.e4. https://doi.org/10.1016/j.cub.2023.05.033.
92. Ke, X.; Wang, X. Energy sensors: Emerging regulators of symbiotic nitrogen fixation. *Trends Plant Sci.* **2024**, *29*, 730–732. https://doi.org/10.1016/j.tplants.2024.01.010.
93. Zhong, Y.; Tian, J.; Li, X.; et al. Cooperative interactions between nitrogen fixation and phosphorus nutrition in legumes. *New Phytol.* **2023**, *237*, 734–745. https://doi.org/10.1111/nph.18593.
94. Sawers, R.J.H.; Gutjahr, C.; Paszkowski, U. Cereal mycorrhiza: An ancient symbiosis in modern agriculture. *Trends Plant Sci.* **2008**, *13*, 93–97. https://doi.org/10.1016/j.tplants.2007.11.006.
95. Li, M.; Perez-Limón, S.; Ramírez-Flores, M.R.; et al. Mycorrhizal status and host genotype interact to shape plant nutrition in field grown maize (*Zea mays* ssp. *mays*). *Mycorrhiza* **2023**, *33*, 345–358. https://doi.org/10.1007/s00572-023-01127-3.
96. Picone, R.; Pietramellara, G.; Guggenberger, G.; et al. The contemporary plant-soil feedback in legume-cereal intercropping systems: A review of carbon, nutrient, and microbial dynamics. *Plant Soil* **2025**. https://doi.org/10.1007/s11104-025-07723-w.
97. Ma, H.; Zhou, J.; Ge, J.; et al. Intercropping improves soil ecosystem multifunctionality through enhanced available nutrients but depends on regional factors. *Plant Soil* **2022**, *480*, 71–84. https://doi.org/10.1007/s11104-022-05554-7.