

Review

Roots to Riches: Unearthing the Synergy of Intercropping, Microbial Interactions, and Symbiotic Systems for Sustainable Agriculture: A Review

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Abstract

Intercropping, especially legume-cereal systems, is a mixed farming approach that can improve agricultural resilience by addressing challenges such as soil degradation, biodiversity loss, and global change, all while promoting the sustainable production of protein-rich and nutritious food. However, its adoption in industrialized countries remains limited due to economic and technical challenges, as well as a fragmented understanding of soil-plant-microbe interactions, which hinders its complete optimization. This article provides an overview of the current situation and future perspectives on the importance of legume-cereal intercropping, with examples such as common bean-maize, soybean-maize, alfalfa-corn-rye, and legumes-pulses-little millet systems. These combinations highlight how intercropping can improve nutrient cycling, increase root growth, forage and grain yield, suppress soil-borne diseases, and promote soil microbial population and enzymatic activity. While it offers environmental benefits, practical challenges such as system design, management complexity, and cost-effectiveness must be addressed to encourage wider adoption. In preparing this review, we synthesized studies published between 2000 and 2025, with a particular emphasis on recent research from China and Southeast Asia. We also considered broader intercropping contexts, including energy crops, agroforestry systems, rice paddy co-cultures, and phytoremediation approaches. The review also highlights legume-cereal as a solution to sustainable soil management, ecosystem health, and the potential for increased nutritional food production in developed countries.

Keywords: climate resilience; legume-cereal intercropping; agroforestry; phytoremediation; soil-plant-microbe interactions; sustainable agriculture



Academic Editor: Huashou Li

Received: 21 July 2025

Revised: 28 August 2025

Accepted: 11 September 2025

Published: 22 September 2025

Citation: Sisodia, P.; Gryta, A.; Pathan, S.I.; Pietramellara, G.; Frąc, M. Roots to Riches: Unearthing the Synergy of Intercropping, Microbial Interactions, and Symbiotic Systems for Sustainable Agriculture: A Review. *Agronomy* **2025**, *15*, 2243. <https://doi.org/10.3390/agronomy15092243>

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1. Introduction

One of the most significant concerns in agriculture today is achieving food and nutritional security for an expanding population in the face of challenging global change. The United Nations' Millennium Development Goals Report 2015 [1] estimates that approximately one in nine people worldwide are undernourished or at risk, which equates to 795 million people out of a global population size of 7.6 billion. However, the global population is expected to rise to 8.6 billion by 2030 and 11.2 billion by 2100 [2]. Thus, food demand will rise, intensifying food insecurity. As a result, agriculture has enormous challenges in addressing three critical imperatives: (1) ensuring food and nutritional security

for an expanding population, (2) mitigating the adverse effects of climate change, and (3) enhancing soil health, climate resilience and the utilization of natural resources [3,4]. However, the demand for higher productivity through intensive agricultural practices has increased yields but has also accelerated biodiversity loss, soil degradation, and greenhouse gas emissions [5,6]. These trade-offs underscore the critical need to implement sustainable farming systems that maintain productivity while reducing ecological costs. Intercropping, crop rotation, cover crops, reduced tillage, and agroforestry are promoted as agroecological techniques for enhancing soil quality, improving nutrient cycling, and increasing system resilience [7–9].

Intercropping, defined as the simultaneous cultivation of two or more crops in the same field, has been practiced historically in diverse regions, including ancient Mediterranean and Asian systems, where farmers recognized its benefits for yield stability and soil fertility [10]. Its increased importance today arises from growing evidence that spatial and temporal complementarity among crops improves the capture of light, water, and nutrients, increases soil microbial diversity, and reduces pest and disease pressure [11].

Recent experimental and modeling studies demonstrate that intercropping contributes to multiple ecosystem services, such as carbon sequestration, nitrogen fixation, improved soil structure, and increased resistance to climatic stressors [12]. These ecological and agronomic benefits provide a solid scientific basis for promoting intercropping as a key component of sustainable agriculture, beyond its traditional role in subsistence farming.

Intercropping also suppresses weeds and enhances biodiversity, resulting in a resilient and sustainable ecosystem (Figure 1). These benefits stem from the complementary use of growth resources, such as light, water, and nutrients, showcasing variations in the morphology, phenology, and physiology of the component crops [13,14]. These outcomes align with the ecological principles, whereby biodiversity enhances productivity through complementary and facilitative interactions among species.

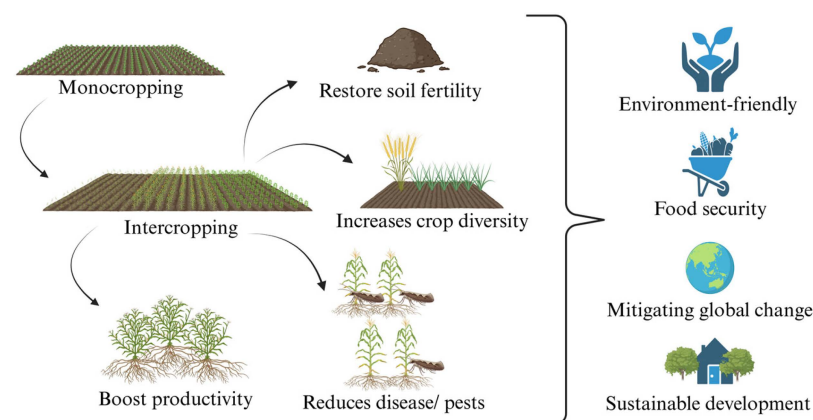


Figure 1. Benefits of intercropping over monocropping.

The adoption of intercropping and related agroecological practices is gaining popularity worldwide as evidence of their potential to boost production and improve environmental outcomes continues to grow. While traditional farming systems in developing countries are more likely to adopt such methods quickly, their incorporation into industrialized nations often requires technological advancements such as precision agriculture and multi-purpose machinery [15].

Policy incentives, farmer education, and collaborative efforts across research, advisory, and production sectors are essential for wider adoption [16]. Encouraging such integrated approaches is critical for ensuring global food security, strengthening ecosystem resilience, and addressing the challenges posed by climate change.

Search strategy and scope. To prepare this review, we systematically surveyed the Web of Science and Scopus databases (2000–2025, with emphasis on 2020–2025) using search terms including “intercropping”, “legume-cereal systems”, “agroforestry mixed cropping”, “rice co-culture”, and “phytoremediation intercropping”. We prioritized peer-reviewed field and mesocosm studies, meta-analyses, and region-focused syntheses, with particular attention to research conducted in China and Southeast Asia, where intercropping practices are historically widespread and well-documented scientifically. Studies that addressed agronomic performance, soil health, microbial communities, or ecosystem services within intercropping systems were included.

Building on this evidence, the next section focuses on legume–cereal intercropping as a model system, while briefly situating related intercropping contexts (bioenergy, agroforestry, and rice paddy co-cultures).

2. Legume–Cereal Intercropping

Although intercropping includes a variety of systems, including energy crops, agroforestry, rice paddy co-cultures, and phytoremediation, this review focuses on legume–cereal systems, which have been thoroughly studied and are ecologically significant. Legume–cereal intercropping has long been recognized as a model system due to the complementary nature of nitrogen-fixing legumes and high-demand cereals, providing well-documented benefits for the nutrient cycle, soil fertility, and yield stability (Figure 2). While legume–cereal systems are our primary focus, we briefly note other intercropping contexts of regional and thematic importance.

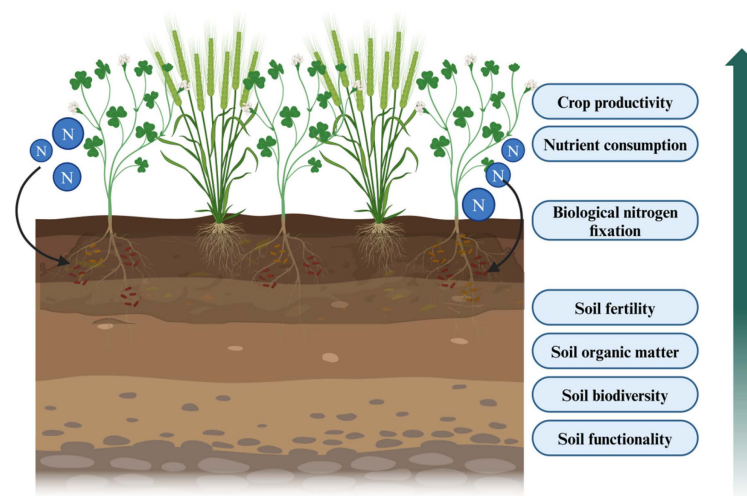


Figure 2. Schematic representation of beneficial effects of legume–cereal intercropping.

In a pigeon pea-maize intercropped system, the direct interaction of roots within the rhizosphere and associated biochemical processes significantly enhanced soil structure and nutrient retention in soils with high P-sorption capacity [17]. Consequently, the soil’s macroaggregates increased by 52% and microaggregates by 111%, compared to maize monocropping, and the fraction of biologically fixed nitrogen increased from 89% with pigeon pea monocropping to 96% in the intercropped system [17].

Intercropping with legumes enhances soil fertility by fixing atmospheric nitrogen through symbiotic nitrogen fixation, reducing reliance on synthetic fertilizers [18]. Alvey et al. [19] demonstrated that intercropping cereals with legumes led to yield increases ranging from 15% to 79%, frequently resulting in superior yield and enhanced nutrient availability, particularly greater quantities of mineral nitrogen and phosphorus. Similarly, a study conducted by Tsubo et al. [20] found that intercropping with legumes increased

the efficiency of nutrient resource utilization, thereby enhancing the growth of both crops, especially in low-input agricultural systems. Comparable results have been observed by Latati et al. [21] when cowpea was intercropped with maize, demonstrating the ability to improve soil phosphorus (P) availability and increase maize yields in alkaline soils.

2.1. Intercropping with Bioenergy Crops

Intercropping can also be utilized for biomass feedstocks (like sugarcane, sweet sorghum, and Miscanthus), where legumes or service crop companions help maintain biomass, reduce weeds, and improve nitrogen availability on marginal land. The effect on yield varies by species and their arrangement, but recent studies show that gains in resource-use efficiency and soil quality can outweigh slight production losses in some situations [22,23].

2.2. Agroforestry Mixed Cropping

Tree-crop combinations (alley cropping and multistrata systems) are common in China and Southeast Asia, contributing significantly to diversification, microclimate buffering, and nutrient cycling. Recent analyses have underscored the significance of intercropping/agroforestry as effective climate-adaptation strategies (e.g., shade trees with tea or fruit trees with annuals), emphasizing the importance of site-specific designs and economic evaluation. Landscape evaluations conducted at the regional level highlight the importance of native tree species in Southeast Asia's dietary diversity and farm resilience [24].

2.3. Rice Paddy Intercropping

(a) Aquatic plant/animal co-cultures: Rice–Azolla and rice–duckweed systems improve nitrogen availability, suppress weeds, and increase soil organic carbon and microbial activity in paddy systems [25]. The rice–fish–duck system, recognized as a GIAHS site in China, efficiently combines aquaculture and agriculture with documented ecological and productivity benefits [26,27].

(b) High/low heavy-metal accumulator pairings: Pairing high- and low-Cd rice cultivars through intercropping has been shown to both reduce grain Cd concentration (e.g., from 0.30 mg kg^{−1} to safer levels around 0.16 mg kg^{−1}) and promote soil remediation via enhanced Cd uptake, effectively repairing contaminated paddy fields while producing rice [28,29].

Table 1. Benefits of legume–cereal intercropping in different countries.

Country	Crops Mixture	Benefits/Results	References
Algeria	Common bean–Maize	The rhizosphere microbial biomass is enhanced through the facilitation of C and N partitioning between root nodules and the rhizosphere microbial community	Latati et al., 2017 [30]
China	Soybean–Maize	Prevented the emergence of soybean red crown rot	Gao et al., 2014 [31]
	Alfalfa–Corn–Rye	The intercropping system provided higher forage production performance	Zhang et al., 2015 [32]
	Soybean–Maize	Enhanced root length density (RLD) in both intercrops compared to the corresponding monocrop	Ren et al., 2017 [33]

Table 1. Cont.

Country	Crops Mixture	Benefits/Results	References
China	Soybean–Maize	Selecting the optimal planting arrangement (2Maize–2Soybean) can enhance light interception and influence its distribution between maize and soybean rows under relay-intercropping conditions	Feng et al., 2019 [34]
	Peanut–Maize–Millet	Applying seedling defoliation in intercropped corn could increase peanut yield without compromising corn yield	Huang et al., 2022 [35]
	Alfalfa–Spring wheat	Intercropped alfalfa and spring wheat could reduce soil salinity, improve soil structure and ionic balance	Su et al., 2024 [36]
Ethiopia	Faba bean–Barley	Intercropping faba bean with barley produced a higher yield than monocropping of each crop species	Agegnehu et al., 2006 [37]
	Bean–Maize	Intercropping reduced weeds, it was more productive and cost-effective than single-crop farming	Workayehu and Wortmann, 2011 [38]
France	Pea–Durum wheat	Crude protein content in grain dry matter of durum wheat was significantly higher in intercrops than in monocrops (14% on average)	Bedoussac and Justes, 2010 [39]
India	Legumes–Pulses–Little millet	Soil microbial population and enzymatic activity were higher in little millet-based legume intercropping compared to the monocropping	Keerthanapriya et al., 2019 [40]
Iran	Legumes–Cereals	Acceptable feed production and quality can be produced due to the low dry matter content of legumes	Eskandari et al., 2009 [41]
	Sword bean–White Bean–Maize	Population density of the two-spotted spider, <i>Tetranychus urticae</i> , was significantly reduced (62–83%)	Ziaie-Juybari et al., 2021 [42]
	Vetch–Barley	Intercropped barley and vetch at a ratio of 80:20 improved the grain yield, its components, and forage quality compared to other intercropping ratios	Kahrarian et al., 2021 [43]
	Clover–Sorghum	The intercropping system under 75% soil moisture deficit irrigation regime is recommended for semi-arid regions due to saving water while producing desired forage yield and quality	Pourali et al., 2023 [44]

Table 1. Cont.

Country	Crops Mixture	Benefits/Results	References
Italy	Pea–Faba bean–Barley	Pea–barley intercropping enhanced the overall sustainability of the rotation by promoting greater complementarity in N resource utilization	Monti et al., 2019 [45]
Kenya	Bean–Maize	Greater weed control increased overall yields, and the highest Land Equivalent Ratio (LER)	Maina et al., 1997 [46]
Lithuania	Field pea–Barley–Wheat–Oat–Triticale	The number of weeds was significantly lower in peas–cereals stands than with peas alone	Deveikyte et al., 2009 [47]
Northwest China	Faba Bean–Wheat–Maize	The top 20 cm of soil organic C and N content was $4\% \pm 1\%$ and $11\% \pm 1\%$ higher in intercrops than in monocrops, respectively	Cong et al., 2015 [48]
Pakistan	Soybean–Maize	Strip intercropping systems can conserve 20–50% of water and land	Raza et al., 2022 [49]
Poland	Soybean–Winter barley	Crop protein yields protection under unfavorable weather conditions	Świtek et al., 2024 [50]
	Field pea–Maize	Intercropping for forage increases protein production	Sowiński, 2024 [51]
South Africa	Cowpea–Sorghum	LER increased productivity by 46% across all intercrop systems	Chimonyo et al., 2016 [52]
Spain	Faba bean–Pea–Oat	<i>Orobanche crenata</i> infection on faba bean and pea is reduced when these host crops are intercropped with oat	Fernandez-Aparicio et al., 2007 [53]
Türkiye	Runner bean–Corn	The ammonia-N levels linearly increase from 0.90% to 2.218% in intercropping areas mixed with beans	Bildirici et al., 2009 [54]

Recent studies and case analyses emphasize intercropping systems' practical applications and advantages (Table 1). For instance, studies have shown that strip-intercropping maize with legumes can significantly increase biomass production and grain yields through improved light utilization and reduced pest pressure, with maize-cowpea and maize-crotalaria systems reporting yield increases of 24.5% and 32%, respectively, compared to sole maize [55]. Similarly, alternate intercropping systems have improved soil structure and yield stability over time [14]. These systems affect not only the physical and chemical characteristics of soil but also the structure of the soil microbial community. The diverse root structures absorb nutrients and moisture from different soil layers, thereby increasing overall resource use efficiency [56], while also altering the physiology of crops and root exudate profiles. These factors indirectly affect the soil microbial community and enzyme activities, ultimately enhancing soil fertility [57]. To understand why legume–cereal intercropping delivers these benefits, the next sections examine the belowground mechanisms that drive soil health, pest suppression, yield stability, forage quality, and water management.

3. Outlook and Legume Production in Industrialized Nations

The scientific concepts outlined in Section 2 highlight the agronomic and ecological benefits of intercropping. The next step is to examine how these in-sights are applied in practice within industrialized nations, where legume adoption remains constrained by economic, technical, and policy barriers.

The increased use of legumes in developed countries provides a practical solution to contemporary agricultural and ecological challenges. Current trends in replacing animal-based foods have brought legumes into focus [58,59].

Legumes play a significant role in biodiversity conservation. The intensification of agriculture has led to the widespread adoption of high-profit crops, resulting in the loss of landscape diversity and the degradation of the natural habitats of many species [60]. One major driver is excessive nitrogen inputs from synthetic fertilizers, causing soil acidification, toxicity, and other negative consequences [61]. Ecosystems are losing their capacity to provide essential services [62]. Introducing legumes into intensive, cereal-dominated farming systems has increased habitat heterogeneity and maintained the persistence of multi-annual habitats on which arthropods, birds, and small mammals depend [63]. Legumes also offer floral resources that support pollinator populations, which benefits food production and plant breeding [64].

Grain legumes provide a unique combination of high protein food and feed (23–40% seed protein), biological nitrogen fixation (BNF), and system-level benefits including pest and disease suppression, soil quality improvement, reduced greenhouse gas emissions, and greater biodiversity [65–68]. Their inclusion in crop rotations also supports wild flora, fauna, and soil microorganisms [69–71]. Despite growing recognition of legumes in national dietary and sustainability agendas, policy support for legume adoption remains inconsistent across industrialized nations [72].

In Europe, grain legumes represented 67% of the total annual production area in the 1960s but declined to only 27% by 2013, primarily due to cheaper imports (mainly from Canada) and reduced dietary demand [73–75]. Today, soybeans, peas, and broad beans are the leading crops, with soybean cultivation rising from 943,000 hectares in 2018/2019 to 1.3 million hectares by 2030 (+44%) [61]. In 2018, field peas and broad beans yielded 4.4 million tons, with two-thirds used for animal feed and 20% for human consumption [61]. Conversely, lentils, chickpeas, and lupins are minor crops, primarily used for food or livestock feed [61]. Despite these uses, legumes occupy only 1.5% of EU arable land compared to 14.5% globally [76,77], and they represented just 1.4% of Europe's total crop area in 2018 [61]. Only 43% of the food legumes consumed were produced domestically, forcing the EU to import almost 70% of its protein-rich feed, with soybeans and soymeal accounting for 87% of the imports [73]. This reliance persists as cereals dominate European agriculture, occupying 31% of arable land [61]. As illustrated in Figure 3, global output of grain legumes, particularly soybeans, has increased significantly since the 1960s, whereas production in Europe has remained relatively low [78].

In summary, legumes have great potential to enhance agricultural sustainability. but their adoption in industrialized nations remains constrained by economic and structural barriers. Targeted investments and consistent policies are required to unlock this potential. Intercropping legumes and cereals is a particularly promising approach combining ecological benefits with practical strategies for creating more diversified, resilient, and resource-efficient agroecosystems.

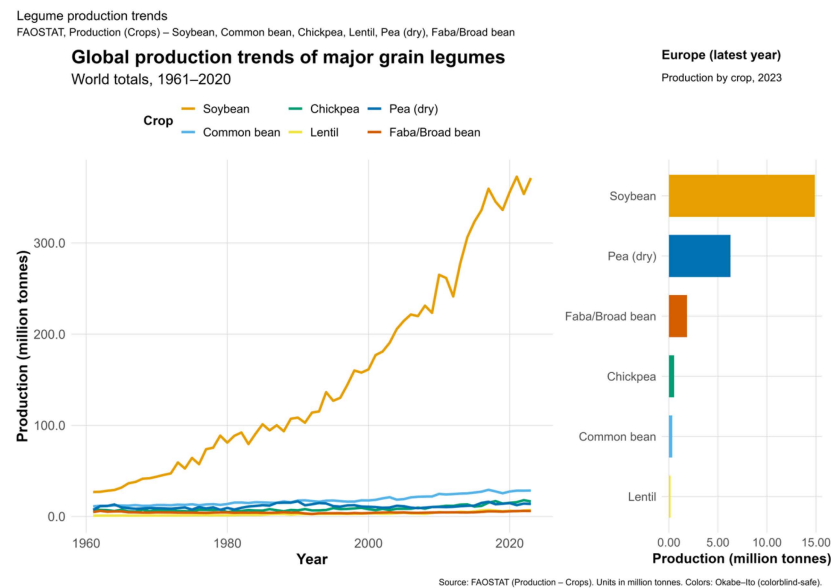


Figure 3. Global production trends of major grain legumes (1961–2020) and European production snapshot (2023). The line chart shows global production of soybean, common bean, chickpea, lentil, dry pea, and faba/broad bean, highlighting the dominance of soybean over other legumes. The bar chart presents European production for the same crops in 2023, underscoring the region’s comparatively limited output and dependence on imports. Source: FAOSTAT (Production-Crops).

4. Interactions Between Soil–Plant–Microbes in an Intercropping System

The success of intercropping systems also depends on belowground bio-logical processes. Beyond the economic and policy aspects discussed above, soil microorganisms are key components contributing to the soil’s ecological functions. They play a crucial role in processes such as organic matter decomposition [79], mineral nutrient cycling, nitrification, mobilization, mineralization, and soil structure formation—all of which are important to plant growth [80]. The composition of soil microbial communities is influenced by several factors, such as environmental conditions, fertilization, pesticide use, agricultural practice [81,82], and plant species or varieties [83]. Modifications to the composition and abundance of these communities can impact crop performance, including growth, nutrient uptake, yield, and pest management.

Root exudates attract a diverse range of microorganisms, shaping rhizosphere interactions [84–87], and these can lead to outcomes that are either beneficial or detrimental [88]. Legume intercropping consistently alters microbial community structure and function, raising diversity, biomass, and activity, while intensifying rhizosphere processes such as nutrient cycling and carbon fluxes [21,89–98]. Understanding how these belowground processes operate requires a closer look at the dynamics of soil–plant–microbe interactions.

4.1. Dynamics of Soil–Plant–Microbe Interaction

Soil–plant–microbe interactions drive nutrient cycling by converting minerals into plant-available forms (N, P, K) via oxidation, dissolution, chelation, and organic-acid release [99,100]. Incorporating legumes into cropping systems further enhances these dynamics by stimulating facilitative and complementary interactions in intercropping, as reported by Fridley [101], Hinsinger et al. [102], and Tang et al. [97]. Complementarity minimizes competition by sharing resources among crops when grown together and occurs when crops utilize the same resource differently in time, space, or form [101]. Facilitation occurs when a plant species directly or indirectly benefits another species by altering the biotic or abiotic environment of the intercropped species, thereby improving resource availability [103].

A characteristic of legumes is their ability to form symbiotic relationships with rhizobia facilitating atmospheric nitrogen fixation in nodules [104]. This allows for reduced external nitrogen input in fields, ultimately resulting in lower carbon content in food products and lower CO₂ emissions [105–108]. Representative rhizobial genera include *Rhizobium*, *Bradyrhizobium*, *Mesorhizobium*, and *Ensifer*, which develop nodules on a wide range of legumes, including *Trifolium* (clovers), *Vicia* (vetches), and *Glycine max* (soybean) [104,106]. *Bradyrhizobium japonicum* is a notable strain known for its large genome and distinct nodulation processes. Another example is *Azorhizobium caulinodans*, which is capable of both symbiotic and free-living nitrogen fixation with the ability to nodulate stems, illustrating the variety of adaptations found in rhizobia [104]. Furthermore, nitrogen-fixing *Burkholderia* strains also play a role in legume symbioses [104].

Legumes exude flavonoids, which have the potential to modulate root-associated bacterial activity under low-nitrogen scenarios in intercropped systems [109]. Free-living nitrogen-fixing bacteria such as *Azospirillum* can colonize the rhizosphere of grasses, thereby supporting intercropping practices [105]. The intermingling of legume and cereal roots promotes the amalgamation of microbial communities from both plants, fostering the cross-migration of bacteria within 28 days of sowing [110]. The resulting increase in root mass and asynchronous nutrient demands of component crops further enhance nutrient acquisition over time and space [111]. Legume–cereal intercropping often increases microbial diversity and activity [112], as discussed further in Section 4.2.1. In addition to altering nutrient dynamics, legume residues and their associated root exudates, rich in organic acids and phenolics, can reshape soil microbial populations. For instance, in rotational strip intercropping of maize and peanut, these inputs promoted the growth of beneficial groups such as Actinobacteria and Ascomycota [113]. Researchers found that intercropping soybean and wheat increased root microbial diversity, root biomass allocation, and P-hydrolyzing acid phosphatase activity under phosphorus-deficient conditions, resulting in increased phosphorus and nitrogen uptake [114]. These intercropping systems can also decrease nitrate leaching by promoting synergistic nitrogen utilization between cereals and legumes [115]. Additionally, intercropping can modulate plant gene expression related to stress tolerance and nutrient uptake, improving resource-use efficiency [14,116,117]. Plant-to-plant signaling (including volatile organic compound-mediated cues) can prime defenses and lower pest damage in specific species combinations [118–120].

Legume–cereal intercropping and rotation systems also contribute to phytoremediation. This strategy utilizes plants and soil microbes to reclaim various heavy metals and radionuclides from contaminated soil through phytoextraction, rhizofiltration, phytostabilization, photodegradation, and phytovolatilization [121–124]. For example, mixed cultures of white lupin with oats enhanced the mobilization of Pb, La, Nd, Sc, Th, and U, facilitating both phytoremediation and phytomining of elements such as Sc and Ge [124,125]. Similarly, intercropping ryegrass and alfalfa restricted Pb transfer from soil to plants, highlighting the potential of intercropping for phytostabilization [124,126].

Recent studies extend these insights beyond traditional legume–cereal combinations: intercropping the Cd-hyperaccumulating plant (*Sedum alfredii*) with oilseed rape increased Cd removal and biomass across contaminated soil types [127,128]. At the same time, field-scale experiments indicate that intercropping can accelerate Cd remediation by altering rhizosphere pH and Cd translocation [129]. Additionally, intercropping the arsenic hyperaccumulator (*Pteris vittata*) with legumes (*Sesbania cannabina*) has been shown to increase arsenic uptake by 19–54% and reduce grain arsenic in the companion crop, with rhizosphere acidification playing a key mechanistic role [130]. These approaches are increasingly being field-tested in East and Southeast Asia, where intercropping has historically been widespread [127–130].

Collectively, these examples show that intercropping promotes both agricultural output and bioremediation, positioning it as a practical multifunctional approach for sustainable soil management.

4.2. Rhizospheric Interactions in Legume–Cereal Intercropping System

The rhizosphere is a dynamic interface where host plants and microorganisms engage in complex interactions [131,132], influencing the availability and cycling of nutrients. These interactions form a feedback loop, as plants exude a considerable part of their photosynthates as rhizodeposits, attracting a microbial community adapted to the rhizosphere environment. These microorganisms influence plant growth, nutrition, and health by interacting with one another and with the host plant [133,134]. In legume–cereal intercropping, cereals compete more aggressively for nutrient absorption than legumes [135] because of a higher root growth rate and wider root distribution that lowers the nitrogen concentration in the rhizosphere [136]. This competition often stimulates legume's nitrogen fixation potential. The absorption of legume-fixed nitrogen by cereal crops is mainly via transfer through root and mycorrhizal networks [137]. Researchers have reported a significant variability in nitrogen transfer from intercropped legumes to cereals, ranging from 0 to 73%, depending on the species and planting method used [138]. For instance, Tripathi et al. [139] observed nitrogen savings of up to 25% for maize + legume–wheat intercropping for subsequent wheat crops. Cereal root exudates can significantly promote nodulation in legumes, thereby increasing the rate of symbiotic nitrogen fixation in legume–cereal intercropping. The mutualistic interaction between legumes and rhizobia increases the nitrogen pool in soil, thereby aiding in mutual growth benefits [140]. Li et al. [141] observed that maize–faba bean intercropping increased maize yield by 7.8–32.9% and faba bean yield by 23.7–63.8% compared with sole cropping. This advantage was attributed to the intermingling of root systems, which led to reduced nitrogen repression of legume nodules and facilitated mutual growth benefits.

Nitrogen transfer through roots is key to improving nitrogen use efficiency in intercropping systems. Yong et al. [142] used ^{15}N isotope-labeling and leaf-labeling techniques to study nitrogen transfer in wheat–maize–soybean rotation. The findings showed that nitrogen transfer and percentage (%NT) decreased with increased soil fertilization. Additionally, the results underscore the significance of bidirectional nitrogen transfer in improving crop-based nitrogen use efficiency. Comparable results were observed by Ledgard et al. [143] when studying nitrogen transfer using the leaf feeding method N^{15} in a clover–ryegrass intercropping system. He reported a direct nitrogen transfer of 2.2% from clover to ryegrass. Similarly, Shao et al. [144] evaluated the influence of root contact on nitrogen transfer in the maize–alfalfa intercropping system, finding that transfer primarily occurred from alfalfa to maize. When root contact was unrestricted, nitrogen transfer was higher, ranging from 7.02% to 15.05%, contributing 2.36% to 4.72% of the total nitrogen uptake. This highlights the importance of root interactions on nitrogen transfer, ultimately increasing total biomass, total N uptake, and utilization in maize.

Soil–plant–microbe interactions in the rhizosphere play a key role in driving the success of legume–cereal intercropping. These systems reduce nutrient loss through symbiotic nitrogen fixation, bidirectional nutrient transfer, and increased root–microbial interactions, resulting in improved nutrient use efficiency and sustainability. The importance of rhizosphere organisms in these processes highlights the need to explore the composition and functioning of rhizospheric microbial communities.

4.2.1. Rhizosphere Microbial Community and the Role of Exudates in Shaping These Communities

Root exudates are composed of low-molecular-weight compounds, including organic acids, sugars, phenolic acids, proteins, and flavonoids, which play a crucial role in microbial interactions [145,146]. For instance, in the legume–rhizobium interaction, plants synthesize and secrete flavonoids to attract compatible rhizobia, which, in turn, respond by producing lipochitooligosaccharides (Nod factors). This chemical interaction initiates symbiosis, resulting in the production of nitrogen-fixing nodules on legume roots [147–150]. In addition, photosynthate-derived exudates make a significant contribution to rhizosphere carbon fluxes [151,152] and serve as an energetic substrate that fuels microbial abundance and activity [153].

Liu et al. [154] examined a broad bean–wheat intercropping system, where wheat roots stimulated the production of flavonoids such as flavonols, isoflavones, chalcone, and hesperetin in legume root exudates, leading to increased nodulation biomass and nitrogen availability in the soil. These higher nitrogen levels were consumed by cereal crops, demonstrating a finely attuned nutrient cycling mechanism. Because numerous plant species coexist in intercropping, root exudates with variable chemical compositions are released at different stages of plant growth, imposing considerable selection pressures on rhizosphere communities [155–157]. Recent multi-omics research confirms this, showing that intercropping increases network complexity while enriching core abundant taxa. Notably, bacterial groups such as Actinomycetales and Rhodocyclaceae, fungi such as *Tausonia* and *Curvularia*, and eukaryotes like Leptophyryidae and Ochromonadaceae were found to be closely associated with improved nutrient cycling and maize productivity [156]. Pivato et al. [134] also found that pea–wheat intercropping altered rhizosphere bacterial networks, revealing interaction patterns not observed in monocultures. In legume–cereal intercropping, this restructuring has been associated with the enrichment of nitrogen-fixing microbes, thereby increasing the functional capacity of the soil microbiome [79,158].

Intercropping systems can also help with the resilience of intercropped crops. A recent study found that interspecific plant interactions during the cultivation of peanut–wheat intercropping triggered the secretion of defense hormones (salicylic acid, jasmonic acid, and methyl jasmonate), which regulated peanut root endophytes in intercropped peanut tissues, thereby improving their ability to withstand environmental stress [159]. Triggering of these hormones favors crop growth and significantly alters the Fe, Zn, and phytate contents in grains, contributing to nutritional quality [124,160].

4.2.2. Plant-Microbe Interactions

Plant growth-promoting rhizobacteria (PGPR) are free-living beneficial microorganisms that colonize the rhizosphere and shape its microbiome, thus establishing a dynamic interaction and altering plant roots and microbial activity [161]. Together with arbuscular mycorrhizal fungi (AMF), they reshape the rhizosphere by supplying nutrients and phytohormones, as well as enhancing root development and plant growth [162–167].

PGPRs can reduce the usage of chemical fertilizers by 25% [168] and improve plant growth and yield in legume–cereal intercropping systems [169,170]. The combination of biofertilization using PGPR (*Pseudomonas* and *Bradyrhizobium*) with AMF has been shown to boost the growth of finger millet when intercropped with pigeon pea, a finding corroborated under field conditions [171,172]. In addition, legume root compounds, such as lectins, isoflavones, and N-AHL mimics, facilitate microbial colonization and communication, thereby enhancing these benefits [173–175]. Legume residues also “prime” microbial mineralization, resulting in faster nutrient release for both crops [176–179].

These microbial interactions collectively enhance soil processes and resource flows, establishing the basis for the nutrient cycling benefits outlined in the next section.

4.3. *The Role of Soil Organisms in Nutrient Cycling in Legume–Cereal Intercropping*

Legume–cereal intercropping is well known for efficiently optimizing nutrient cycling through complex biological interactions. Legumes can fix 75–150 kg of nitrogen per year, adding up to 300 kg per hectare under optimal conditions. The nitrogen from this process can fulfill >50% of the nutrient needs of legumes and intercropped cereal crops [135,180].

In addition to nitrogen cycling, phosphorus mobilization is another key area contributing to the success of legume–cereal intercropping systems. Although most soils contain abundant total phosphorus (P), a significant portion is present in insoluble forms, making it inaccessible to plants [181,182]. Legumes possess a higher proton-releasing ability and acidify the rhizosphere considerably, which enables the activation and uptake of soil-insoluble phosphorus, supporting N fixation and maintaining N:P balance in intercrops [183].

Francisquini et al. [184] demonstrated that legumes can partially substitute for nitrogen fertilizer inputs, even under conditions of low phosphorus availability, thereby sustaining crop performance without additional chemical nitrogen application. Similarly, Brahimi et al. [185] highlighted the efficient nutrient uptake and improved productivity in low-P soil under faba bean–barley intercropping, where crop growth increased by 18% and nodulation by 32% compared with monocropping. Beyond macronutrients, intercropping can also improve the micronutrient status of crops; for example, sorghum–cowpea intercropping enhanced the calcium, magnesium, copper, manganese, and iron contents of sorghum seeds [124,186].

Legume–cereal intercropping also promotes microbial activity in the rhizosphere, especially in interaction with phosphate-solubilizing bacteria (PSBs). These bacteria secrete organic acids that solubilize unavailable phosphorus, stimulating soil phosphatase activity and increasing phosphorus availability to the plant [96,182]. Arbuscular mycorrhizal fungi (AMF) are indispensable partners in the legume–cereal cropping system and contribute to the uptake of multiple nutrients, such as nitrogen, phosphorus, potassium, sulfur, calcium, iron, zinc, manganese, and copper. In many cropping systems, AMF can supply the majority of plant phosphorus needs (up to approx. 90%), a substantial proportion of nitrogen (around 60%), and a smaller share of carbon inputs (about 20%) [187–192]. They also facilitate interspecific relationships within legume systems by promoting phosphate ion production through alkaline phosphatase activity, thus increasing phosphorus availability [193,194]. This role is reinforced by interactions with phosphate-solubilizing bacteria (PSB), which not only promote AMF activity but also improve hyphal development and fungal viability while reducing soil-borne pathogens [195,196]. A practical example of these synergistic effects is shown through the inoculation of AMF in intercropping systems of coix and faba bean, which led to increased solubilization of inorganic phosphorus and mineralization of organic phosphorus, ultimately enhancing nutrient absorption and productivity [197]. Beyond their role in nutrient acquisition, AMF also supports environmental sustainability. For instance, when associated with maize in a maize–soybean intercropping system, AMF lowered nitrous oxide emissions by altering the abundance and community composition of denitrifying bacteria, thereby improving nitrogen use efficiency [136,198].

The significant impact that AMF and PSB activity have on nutrient cycling and broader ecosystem services makes it clear that they play an essential role in legume–cereal intercropping. These belowground interactions provide the functional foundation for addressing broader ecological challenges, which are considered in the next section.

5. Ecological Challenges and the Role of Legume–Cereal Intercropping in the Development of Sustainable Agriculture: Opportunities and Limitations

Agriculture faces several ecological challenges, including degraded soil, polluted water, biodiversity loss, and greenhouse gas emissions. Such issues risk compromising soil fertility, depleting natural resources, and exacerbating climate change, creating an urgent need for sustainable farming methods that address these challenges while meeting the rising demand for food [199]. Among diversification options, cereal-legume intercropping offers consistently documented biophysical benefits and context-dependent economic outcomes.

5.1. Analytical Framework for Synthesis

To evaluate the opportunities and constraints of cereal-legume intercropping, this review synthesizes outcomes using standard agroecological metrics. The most extensively used is the Land Equivalent Ratio (LER), indicating land productivity advantages compared to sole crops [200,201]. Nitrogen Use Efficiency (NUE) serves as a nutrient-focused metric that assesses the effectiveness of systems in utilizing soil-derived and biologically fixed nitrogen [202]. Additional indicators include soil enzyme activity and microbial diversity indices, which provide insights into soil health and functional capacity [97,203,204]; biodiversity measures, such as predator and parasitoid abundance [205,206]; and greenhouse gas emissions, including nitrous oxide (N₂O) [207,208]. Methodological factors, including design type (relay, additive, or replacement), strip width, fertilizer input, and surrounding landscape context, significantly influence these metrics and help explain the variability observed across studies. These indicators provide the basis for assessing the environmental and economic outcomes of legume–cereal intercropping, which are examined in detail in the following subsections.

5.2. The Environmental and Economic Potential of Legume–Cereal Intercropping

Intercropping exploits ecological complementarity. In legume–cereal combinations, cereals are significant consumers of nitrogen while legumes supply nitrogen via rhizobia, reducing the need for fertilizers and improving nutrient-use efficiency [209,210]. The Land Equivalent Ratio (LER) indicates the overall productivity advantages of land, with a mean LER of 1.22 for intercropping versus sole crops, indicating around 22% land savings at equal output. Economic gains result from resource efficiency and yield stability, though realized profits vary depending on management and market conditions [200,201]. Furthermore, increased crop diversification provides additional market stability by allowing farmers to market multiple products from the same field [211–213].

While these benefits illustrate the environmental and economic promise of legume–cereal systems, their wider role must also be understood in terms of how they address major ecological challenges.

5.3. Addressing Ecological Challenges

Intercropping as a mixed farming system addresses several ecological challenges relevant for upcoming decades, resilience agriculture and climate, including the following:

- **Climate Change**

Intercropping, especially with legumes, can maintain or improve yields while enhancing soil carbon (C) and reducing N-related emissions in low-input systems. Long-term research suggests that diverse systems reduce N₂O when N inputs are moderated and residues are returned [207,208].

- **Soil Degradation**

Soil health lies at the core of sustainable agriculture, and intercropping addresses the adverse impacts of soil degradation. Legumes enrich the soil with organic matter, thereby improving soil structure and microbial activity, which ultimately contributes to enhanced water retention and reduced erosion. With cereal roots extracting nutrients from deep in the soil and legumes fixing nitrogen into the soil, the complementary relationship ensures that soil fertility is preserved over time, thereby reducing the risk of nutrient depletion and the need for chemical inputs [214,215].

Legume–cereal systems enhance phosphorus mobilization and nitrogen capture through rhizosphere processes, thereby improving soil function under reduced inputs [216].

- **Loss of Biodiversity**

Meta-analyses indicate that intercropping reduces herbivores and increases predators/parasitoids; the effects depend on the design and landscape context (e.g., spatial arrangement, distance from floral strips) [205,206].

- **Water Pollution**

Monoculture farming requires large quantities of chemical fertilizers, which accelerate the leaching of nutrients and pollute the water [217]. Cereal-legume intercropping reduces this risk by enhancing nutrient cycling and reducing the need for synthetic inputs. The excess nitrogen fixed by leguminous plants can be utilized by cereal crops, resulting in less nitrogen being lost to runoff, which leads to lower water contamination and a reduced likelihood of harmful algal blooms, preserving aquatic ecosystems [218].

Reduced fertilizer inputs and tighter nitrogen (N) cycling in legume–cereal pairs lower the risk of nitrate loss to water, consistent with findings on Nitrogen Use Efficiency (NUE) across systems [202].

Taken together, these ecological dimensions highlight both the opportunities and the systemic pressures shaping intercropping performance. The following subsection considers how these insights can inform the scaling up of intercropping practices for sustainable agriculture.

5.4. Future of Sustainable Agriculture: Scaling up Intercropping Practices

Cereal-legume intercropping offers a promising approach to meet the increasing food demand while reducing the environmental costs of intensive agriculture. Evidence suggests that diversified systems can simultaneously address climate change, soil degradation, biodiversity loss, and water pollution through improved nutrient-use efficiency, soil health, and ecosystem services [15,202]. Supportive policies and advisory systems are crucial for encouraging adoption, along with farmer-led innovation, in regions where institutional frameworks are robust [16]. Technological advancements such as precision seeding, guidance systems, and modified harvest equipment also improve feasibility at larger scales [16].

Scaling intercropping, therefore, requires integration of governance, farmer training, and automation tailored to regional conditions. Although the potential is substantial, outcomes remain context-dependent, making it essential to consider the limitations, trade-offs, and cases where intercropping does not provide consistent advantages.

5.5. Limitations, Trade-Offs, and Conflicting Results

Meta-analyses indicate that in approximately 20–40% of intercropping comparisons, productivity gains are negligible (total LER ≤ 1.0), or the costs associated with management outweigh the advantages, highlighting that results are not consistently positive [200,219,220]. These findings illustrate that legume–cereal intercropping can involve trade-offs and variable results.

- Neutral or negative yield outcome

Some combinations show neutral or even negative yield outcomes. For example, Pinto et al. [221] reported that intercropping intermediate wheatgrass (*Kernza*[®]) with legumes like alfalfa or red clover increased forage yield and quality. However, it also reduced the grain yield of *Kernza* compared to monoculture systems. In another study, intercropping occasionally failed to increase the stability of biomass or grain yields compared to monocultures, particularly when competitive effects were strong [222].

- Management complexity and cost

Intercropping introduces logistical challenges. Machines designed for monocultures may not work well in mixed cropping systems, necessitating labor-intensive operations or equipment modifications. Furthermore, the current study indicates a lack of detailed economic assessments. Gkalitsas et al. [223] emphasize that even when intercropping improves productivity and resource-use efficiency, limited cost–benefit evaluations hinder the understanding of adoption potential.

- Variable pest and disease dynamics

While intercropping often increases the abundance of beneficial arthropods and reduces pests, its effectiveness varies depending on the circumstances. For example, meta-analysis shows cereal-legume intercropping generally enhances predator populations and reduces pests, but the benefits rely substantially on management intensity and field context [224].

Collectively, these contradictory findings underscore that legume cereal intercropping is context-specific with benefits limitations that must be carefully weighed. The following conclusion summarizes these findings and highlights future possibilities for incorporating intercropping into sustainable agricultural practice.

6. Conclusions

Legume–cereal intercropping provides a possible approach to sustainable agriculture by boosting resource-use efficiency, reducing dependency on fertilizers, and improving ecosystem services. However, outcomes are not consistently positive; yield gains are influenced by combination of species, soil fertility, and management practices, and trade-offs such as competition for water or increased management complexity can limit attainment in some systems. Addressing these limitations requires developing context-specific techniques, encouraging farmer-led innovation, and providing supportive institutional frameworks.

In the future, integration of information from molecular and omics analysis of root exudates and microbiomes will enable us to identify key interactions that determine when and where intercropping performs best. In parallel to this, microbial biostimulants such as PGPR and AMF offer practical tools to assist beneficial interactions in the field. Policies that encourage crop diversification, combined with education of farmers and precision-agriculture technology, will be key to upscale. These approaches together place legume–cereal intercropping at the center of future agroecological systems compatible with both productivity and environmental sustainability.

Author Contributions: Conceptualization, M.F. and P.S.; software, P.S. and M.F.; formal analysis, P.S.; writing—original draft preparation, P.S.; writing—review and editing, P.S., A.G., S.I.P., G.P. and M.F.; visualization, P.S.; supervision, M.F.; funding acquisition, G.P., S.I.P. and M.F. All authors have read and agreed to the published version of the manuscript.

Funding: The paper was supported by the project entitled “Legume-cereal intercropping for sustainable agriculture across Europe” within the framework of Horizon Europe Program, funded by the European Commission, agreement no. Project 101082289—LEGUMINOSE.

Data Availability Statement: This is review paper and research data were not included.

Acknowledgments: We express our gratitude to Stefanie Vink (<https://greenfinchresearch.com/>) for her assisting with the English language correction.

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

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