Intercropping for Enhanced Agroecosystem Services: Research Advances and Application Prospects (Postprint)

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Abstract

Intercropping represents the quintessence of traditional Chinese agriculture. Its existence for over 2,000 years inevitably embodies important scientific principles. Previous research has demonstrated that intercropping can not only substantially increase crop yields, but also fully utilize aboveground light and heat resources, and thoroughly exploit and utilize belowground water and nutrient resources, thereby enhancing farmland ecosystem service functions. In recent years, significant progress has been achieved in research on efficient resource utilization in intercropping systems both domestically and internationally, particularly regarding belowground resources. This paper first reviews relevant research progress: intercropping, as an important measure for increasing biodiversity in farmland ecosystems, possesses significant ecological functions, such as improving crop yields, enhancing the stability of crop productivity, and fully utilizing aboveground light and heat resources, soil water, nitrogen and phosphorus in soils and fertilizers, and micronutrients. Subsequently, the mechanisms through which intercropping improves resource use efficiency are analyzed, including temporal and spatial niche complementarity in water demand; complementarity and facilitation between legume biological nitrogen fixation and cereal utilization of soil nitrogen in legume/cereal intercropping systems; promotion of crops with weak phosphorus mobilization capacity by those with strong capacity in intercropping systems combining such varieties; and improvement of micronutrient content (e.g., Fe, Zn) in dicotyledonous plants through dicotyledonous/monocotyledonous plant combinations. Finally, perspectives and directions for future research and application of intercropping are proposed. Research aspects include crop diversity and sustainable agricultural development, belowground interspecific signaling among crops, mutual feedback regulation mechanisms between above- and belowground diversity, and crop growth models. Application aspects include incorporating legume crops into agricultural production systems to develop ecological intensification agriculture, utilizing intercropping to develop organic agriculture, and exploiting interspecific interactions to improve phosphorus fertilizer use efficiency and increase micronutrient content in crop edible parts. It is also suggested that solving issues such as mechanization and breeding in intercropping will facilitate its further development.

Full Text

Preamble

Intercropping Enhances Agroecosystem Services and Functioning: Current Knowledge and Perspectives

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Abstract: Intercropping represents the essence of traditional Chinese agriculture. Having persisted for over 2,000 years, it must embody important scientific principles. Previous research has demonstrated that intercropping not only substantially increases crop yields but also enables efficient utilization of aboveground light and thermal resources while tapping into soil water and nutrient resources, thereby strengthening agroecosystem services. Recent advances, particularly in belowground resource utilization, have yielded significant progress. This paper first reviews relevant research developments: intercropping serves as a crucial measure for enhancing biodiversity in agroecosystems, delivering important ecological functions such as increased crop yields, improved stability of crop productivity, and efficient utilization of aboveground light and thermal resources, soil water, nitrogen and phosphorus from both soil and fertilizer sources, and micronutrients. Subsequently, we analyze the mechanisms underlying improved resource use efficiency in intercropping systems, including temporal and spatial niche complementarity in water demand, complementary and facilitative nitrogen use between legumes and cereals through biological nitrogen fixation and soil nitrogen uptake, and facilitation of phosphorus-immobilizing species by phosphorus-mobilizing species in appropriate intercropping combinations. Additionally, dicot-monocot combinations can improve micronutrient content in dicotyledonous crops. Finally, we propose perspectives and directions for future research and application of intercropping. Research directions include crop diversity and agricultural sustainability, belowground interspecific signaling, feedback mechanisms linking aboveground and belowground diversity, and crop growth modeling. Application prospects encompass integrating legumes into farming systems for ecologically intensive agriculture, developing organic agriculture through intercropping, improving phosphorus fertilizer use efficiency via interspecific interactions, and increasing micronutrient content in edible crop parts. We conclude that solving mechanization and breeding challenges will facilitate further development of intercropping systems.

Keywords: Intercropping; Crop diversity; Efficient resource utilization; Productivity; Symbiotic N_2 fixation; Phosphorus mobilization; Microelement

1. Intercropping and Modern Agriculture

Intercropping and relay cropping represent the essence of traditional Chinese agriculture. Historical records date back to the Western Han Dynasty’ s *Fan Shengzhi Shu* (1st century BCE), with further documentation in the 6th century *Qimin Yaoshu* describing intercropping of legumes (mung bean, adzuki bean) and non-legumes (foxtail millet) in mulberry orchards. The Ming Dynasty’ s *Nongzheng Quanshu* detailed relay cropping of barley/naked barley with cotton, and wheat with faba bean. The Qing Dynasty’ s *Nongcanjing* recorded wheat-soybean relay systems. By the pre-1949 period, maize-legume intercropping had become widespread nationwide. Over two millennia, intercropping has evolved from low-input/low-output systems to high-input/high-output modern agricultural models, maintaining relevance in contemporary farming.

Intercropping patterns in modern Chinese agriculture exhibit remarkable diversity. During the 1980s, relay cropping on dryland reached 17 million hectares, with intercropping covering 25-28 million hectares distributed across all regions except Tibet and Qinghai. In northern cotton regions, wheat-cotton relay systems expanded from 130,000 hectares in 1972 to 3.4 million hectares by 1981, reaching 33 million hectares nationally by the 1990s. Statistical analysis of Chinese journal publications reveals intercropping practices in every province, with greater diversity in eastern and southern regions compared to western and northern areas.

Although official statistics on intercropping area are unavailable, fragmentary reports illustrate its continued significance. In 1980, wheat-maize relay systems in Beijing-Tianjin-Hebei-Shandong-Henan-Shanxi covered 4.197 million hectares, representing 57.1% of maize area and 74.4% of wheat-maize double-cropping systems. During the 1970s, responding to population and food pressures, agricultural scientists developed high-yielding gramineous/gramineous intercropping systems, exemplified by wheat/maize strip systems in northwestern China achieving “ton-grain fields” (1,000 kg per 667 m^2). By 1996, such systems exceeded 100,000 hectares in Gansu Province, contributing 43.3% of Ningxia’ s total grain production and 53.8% of grain output in Ningxia’ s Yellow River irrigation district. However, water scarcity has since reduced wheat/maize intercropping, replaced by lower-water-use pea/maize strip systems recently promoted in the Hexi Corridor.

Southern China’ s favorable thermal conditions support extensive intercropping. Southwestern diversified planting patterns such as "wheat-maize-potato" and "rapeseed-maize-potato" cover over 3.5 million hectares annually. With rising soybean profitability, "wheat-maize-soybean" systems expanded rapidly, exceeding 400,000 hectares in Sichuan Province by 2013. Southern intercropped soybean area reached 1.47 million hectares in 2008, primarily in multi-cropping systems like "rapeseed-soybean-rice." Guangxi' s intercropping area expanded to over 1.2 million hectares between 2008-2010, while Yunnan utilizes intercropping to enhance yields, increase farmer income, and reduce chemical fertilizer and pesticide use.

2.1 Enhancing Agrobiodiversity

Intensive agricultural systems typically prioritize optimizing productivity of monoculture systems, reducing crop diversity to a single genetically uniform species requiring substantial external inputs of chemical fertilizers and pesticides. These systems face criticism for environmental impacts including soil erosion, degradation, chemical pollution, biodiversity loss, and excessive fossil fuel consumption.

Intercropping inherently increases crop biodiversity by cultivating at least two crop species simultaneously in the same field. Legume-cereal intercropping represents a common configuration globally, including soybean/maize, soybean/wheat, faba bean/maize, peanut/maize, millet/peanut, and pea/maize. Non-legume/non-legume systems such as potato/maize and wheat/maize are also widely applied. These systems fundamentally alter the uniform appearance and internal structure of intensive farmland, modifying canopy architecture and root spatial distribution to enhance crop diversity.

Altered crop diversity changes root exudate composition and root components, consequently affecting soil biota diversity, including earthworms (Lumbricus spp.) and microbial community structure.

2.2 Increasing Productivity

Biodiversity enhances ecosystem productivity. Over 150 years ago, Darwin proposed that communities with higher plant species richness exhibit greater primary productivity—a concept referenced for nearly a century. Studies in both artificially constructed micro-ecosystems and semi-natural grasslands demonstrate that biodiversity improves ecosystem functions, particularly productivity. A meta-analysis of 44 grassland studies by Cardinale et al. revealed that 79% of experiments showed high-diversity communities produced 1.7 times more biomass than monocultures. Recent research indicates that high biodiversity suppresses soil-borne pathogens, thereby increasing ecosystem productivity. In grasslands, biodiversity loss driven by human activities, particularly functional group loss, reduces ecosystem productivity.

In agroecosystems, numerous studies confirm that crop diversity through intercropping enhances system productivity. In northern Europe, pea/barley intercropping achieved grain yields of 4.6 $t \cdot hm^{-2}$, significantly higher than monocultures, with intercropped pea nitrogen accumulation reaching 73 $kg(N) \cdot hm^{-2}$ versus 15 $kg(N) \cdot hm^{-2}$ in monoculture. Long-term pea/barley intercropping may deplete soil nitrogen, but more slowly than barley monoculture. In East Africa, maize/Desmodium intercropping increased maize grain yield by 511.1% compared to monoculture. In India, direct-seeded rice intercropped with peanut or pigeonpea outperformed monoculture rice, with rice/peanut systems achieving maximum yields of 2,815 $kg \cdot hm^{-2}$. Soybean/pigeonpea intercropping yielded 60% higher than soybean monoculture. Our research demonstrates that on fertile soils with high nitrogen and low phosphorus, four-year intercropped maize grain yields increased by 43% and faba bean yields by 26% compared to monocultures. In wheat/maize and wheat/soybean systems, wheat grain yields increased by 40-70% and 28-30%, respectively, while maize yields increased 19-32% and soybean yields 0-12%. Rapeseed/maize, faba bean/maize, chickpea/maize, and soybean/maize intercropping increased total grain yields by 30.7%, 24.4%, 44.6%, and 39.1%, respectively, over corresponding monocultures. On newly reclaimed infertile soils, faba bean/maize intercropping with rhizobial inoculation increased maize grain yields by 30-197% and faba bean yields by 0-31%.

2.3 Enhancing Productivity Stability

The relationship between diversity and ecosystem stability has been debated theoretically for over half a century, but recent field and controlled experiments provide substantial evidence that high diversity enhances productivity stability. In natural ecosystems, significant correlations exist between biodiversity and ecosystem stability, with higher biodiversity reducing coefficient of variation in grassland biomass and increasing system stability. Biodiversity enhances temporal stability across trophic levels, particularly for aboveground productivity.

Research on yield stability in intercropped agroecosystems remains limited. In India, analysis of 94 sorghum/pigeonpea intercropping trials revealed greater yield stability than monocultures: under stress conditions, monoculture pigeonpea yields declined in 1 of 5 years, monoculture sorghum in 1 of 8 years, while intercropped yields declined in only 1 of 36 years. European wheat/faba bean intercropping showed more stable yields than corresponding monocultures. In Ghana, cassava/maize, cassava/soybean, and cassava/cowpea intercropping exhibited higher stability than monoculture crops. In four African locations at different altitudes, maize/perennial crop intercropping and annual legume/maize rotation showed the lowest coefficient of variation for maize grain yield (9-16%)

compared to unfertilized maize monoculture (17-30%). However, these studies primarily focus on spatial stability across environments and locations, rarely addressing temporal stability. Whether species diversity can maintain long-term stability under continuous high yields and nutrient removal warrants investigation, as it bears both theoretical implications for understanding biodiversity-stability relationships and practical significance for the long-term sustainability of intercropping systems.

2.4 Improving Forage Protein Content

Legume/non-legume intercropping represents an important direction for high-quality forage production in developed countries. In Europe's temperate regions, cereal forages are valued for high yield and energy content, but low protein reduces forage quality. Intercropping legumes with cereals produces high-yielding, nutritionally balanced mixed forage. Annual legume forage berseem clover (Trifolium alexandrinum), widely cultivated in Mediterranean and Central Asian countries and recently popularized in the United States, has traditionally been grown as monoculture hay. In the UK, berseem clover is now mixed with annual grasses like Italian ryegrass (Lolium multiflorum) and oats (Avena sativa) to produce high-yielding, nutritionally balanced forage. Pea, a high-protein forage crop, suffers from lodging and leaf diseases in cool, humid northern European conditions, complicating mechanical harvest. Pea-oat intercropping effectively addresses these challenges. Recent research on white lupin (Lupinus albus) intercropped with wheat or ryegrass demonstrated dry forage yields of 20 $\mathrm{t} \cdot \mathrm{hm}^{-2}$, with intercropping outperforming monocultures in land use efficiency, yield, and nutritional value.

2.5 Weed Control

Legume/non-legume intercropping controls weeds through allelopathic effects. In Denmark during the 1980s-1990s, silage maize area expanded dramatically from near-zero to 40,000 hectares by 1999, accompanied by severe weed problems in southern Nordic countries. Herbicide use increased production costs and environmental impacts. Comparative studies identified faba bean as having strong weed competitiveness with minimal competition against maize, making faba bean/maize intercropping effective for weed control in maize production.

Striga spp., parasitic plants widespread in Africa, threaten staple crops like maize. Striga germination requires hydroquinone and sesquiterpene lactones (particularly strigolactones) from host root exudates, enabling parasitism and nutrient extraction that severely impacts host growth. Intercropping maize with the leguminous forage Desmodium uncinatum prevents Striga hermonthica parasitism, offering important insights for weed management.

2.6 Pest and Disease Control

1) Rice genetic diversity for disease control: Research by Zhu Youyong’ s group at Yunnan Agricultural University systematically demonstrated that rice genetic diversity (intercropping blast-susceptible and resistant varieties) significantly controls blast disease in susceptible glutinous rice, reducing disease index by 94% and increasing yield by 89%. Mechanisms include pathogen dilution, barrier effects, and improved canopy ventilation, light penetration, and humidity conditions that enhance disease resistance.

2) Crop species diversity for disease control: Yunnan Agricultural University leads research and application in this area. Studies show maize/tobacco (Nicotiana alata) intercropping reduces maize leaf blight by 17.0-19.7%; maize/sugarcane (Saccharum officinarum) intercropping reduces maize leaf blight by 55.9-49.6% without affecting companion crops. Notably, maize/potato intercropping reduces maize leaf blight by 30.4-23.1% while also reducing potato late blight by 32.9-39.4%. These results have been widely applied in Yunnan with significant ecological and social benefits.

3.1.1 Niche Separation

Differential water requirements among crops create temporal niche differentiation in system-wide water demand, reducing competition and enhancing water acquisition. In the widely promoted pea/maize strip intercropping system in the Hexi Corridor, intercropped peas obtain more water during early growth (April-May) when they exhibit higher water use efficiency (dry matter per unit water). Intercropped maize, with relatively lower water demand during this period, experiences no water acquisition reduction. During later growth stages, intercropped maize obtains more water than monoculture, enabling the intercropping system to acquire significantly more water than the weighted average of monocultures while maximizing water use efficiency. Pea/maize intercropping differentiates peak water demand periods, optimizing system water utilization.

3.1.2 Hydraulic Lift

Some plant roots penetrate dry soil layers to reach moist subsoil, absorb water, and transport it along water potential gradients to roots in dry layers, releasing water and moistening surrounding soil—termed hydraulic lift. Due to heterogeneous soil moisture distribution, this “hydraulic lift” can occur in multiple directions, with the broader concept being hydraulic redistribution. Intercropping systems with different root characteristics enable compensatory water use.

3.2 Efficient Nitrogen Utilization

3.2.1 Nitrogen Inhibition

"Nitrogen inhibition" refers to the suppression of biological nitrogen fixation under high soil fertility or nitrogen fertilizer input. Salvagiotti et al. analyzed over 630 datasets from 1966-2006, revealing a significant exponential negative correlation between soybean biological nitrogen fixation and chemical nitrogen application, demonstrating clear inhibition of legume nitrogen fixation by nitrogen fertilizer.

Our research confirmed nitrogen inhibition effects: compared to no nitrogen, applications of 150, 225, and 300 $\mathrm{kg(N) \cdot hm^{-2}}$ reduced faba bean nodule numbers by 6.6%, 16.6%, and 21.8%, respectively, while 75 $\mathrm{kg(N) \cdot hm^{-2}}$ increased nodule numbers by 7.6%. Nodule weight decreased by 8.8%, 32.5%, 42.3%, and 53.8% under 75, 150, 225, and 300 $\mathrm{kg(N) \cdot hm^{-2}}$, respectively, confirming nitrogen inhibition.

Legume-cereal intercropping alleviates nitrogen inhibition of legume biological nitrogen fixation. Field sampling across growth stages revealed that faba bean/maize root interactions significantly increased nodule weight per plant by 22.5% and individual nodule weight by 14.6% compared to monoculture faba bean. Nodule weight increases ranged from 7-58% at initial flowering, 8-72% at full flowering, 4-73% at pod filling, and 7-62% at maturity.

Enhanced nodulation through faba bean/maize interspecific interactions significantly increased nitrogen fixation. Using the δ^{15}N natural abundance method, intercropped faba bean nitrogen fixation increased by 8-33% (initial flowering), 54-61% (full flowering), 18-50% (pod filling), and -7-72% (maturity) compared to monoculture.

Calculated from total nitrogen accumulation and fixation proportion, nitrogen fertilizer application significantly reduced nitrogen fixation across three planting patterns: faba bean/maize, monoculture faba bean, and faba bean/wheat decreased by 36%, 43%, and 34%, respectively. Without nitrogen fertilizer, faba bean/maize fixation was 87% higher than monoculture, while faba bean/wheat was 29% lower. At 120 $\mathrm{kg(N) \cdot hm^{-2}}$, faba bean/maize fixation was 109% higher than monoculture, while faba bean/wheat was 18% lower.

In summary, cereal-legume intercropping mitigates nitrogen inhibition: as nitrogen application increases, monoculture faba bean nodulation and nitrogen fixation decline significantly, while intercropped faba bean shows smaller reductions, demonstrating that cereals alleviate nitrogen inhibition of legume biological nitrogen fixation.

3.2.2 Cereal Competition for Soil Nitrogen

Using ^{15}N isotopic labeling and a root separation apparatus, we investigated facilitation mechanisms. ^{15}N fertilizer was applied to soil with three root interaction treatments: no separation (complete interaction), nylon mesh separation (rhizosphere effects only), and plastic film separation (no interaction). Results showed wheat’ s stronger competitive ability for soil and fertilizer nitrogen reduced faba bean ^{15}N uptake by 80.1%, yet total faba bean nitrogen uptake did not decline significantly, indicating increased atmospheric nitrogen acquisition. Intercropped wheat obtained more soil nitrogen, with ^{15}N uptake increasing by 79.2% compared to monoculture. Niche differentiation in nitrogen use represents the primary mechanism for nitrogen compensation in legume/non-legume intercropping systems.

3.2.3 Interspecific Nitrogen Transfer

Using high-enrichment ^{15}N (99%) solution injected into faba bean petioles, we confirmed that 4% of legume nitrogen transfers to intercropped non-legume crops, though direct transfer is not the primary pathway for efficient nitrogen utilization. Studies in upland rice/peanut intercropping revealed bidirectional nitrogen transfer: at nitrogen application rates of 15, 75, and 150 $\mathrm{kg(N)} \cdot \mathrm{hm}^{-2}$, rice derived 11.9%, 6.4%, and 5.5% of its nitrogen from peanut transfer, respectively, indicating substantive contributions only at very low nitrogen rates.

In summary, cereals in legume/gramineous intercropping systems absorb more soil nitrogen, reducing soil nitrogen concentration. This provides adequate nitrogen nutrition for cereals with significant yield benefits while lowering soil nitrogen levels to promote legume nodulation and nitrogen fixation, thereby achieving niche differentiation that reduces interspecific competition and enables high yields for both crops [Figure 1: see original paper].

3.3.1 Mechanisms for Mobilizing Sparingly Soluble Inorganic Phosphorus

Given increasingly scarce global phosphate rock resources, soil phosphorus deficiency has become a worldwide challenge. Biological approaches to enhance crop utilization of sparingly soluble soil phosphorus have become a research priority. Four-year field trials in Wuwei, Gansu, demonstrated that intercropped maize yields increased by 43% and faba bean yields by 26% compared to monocultures, confirming significant mutualistic effects. Root separation techniques revealed that faba bean improved maize phosphorus nutrition under both field and pot conditions through both spatial complementarity of root occupation and rhizosphere effects. Mechanisms include faba bean’ s stronger proton release capacity acidifying the rhizosphere, facilitating mobilization of sparingly soluble inorganic phosphorus (Fe-P and Al-P) for uptake by both species. Additionally, faba bean root exudation of organic acids promotes phosphorus mobilization, benefiting both crops.

3.3.2 Mechanisms for Organic Phosphorus Mobilization in Chickpea/Wheat and Chickpea/Maize Systems

Soil phosphorus exists not only as inorganic forms but also substantially as organic phosphorus that must be mineralized before plant uptake. Plant species differ significantly in organic phosphorus mobilization capacity. When species with strong mobilization capacity are grown with weak mobilizers, interspecific facilitation may occur. Under simulated organic phosphorus supply in controlled conditions, chickpea rhizosphere effects improved wheat phosphorus nutrition through rhizosphere acidification and, more importantly, through greater secretion of acid phosphatase [Figure 2a: see original paper], with chickpea rhizosphere acid phosphatase activity 1-2 times higher than that of maize.

These findings reveal interspecific rhizosphere facilitation mechanisms with important implications for improving nutrient use efficiency through intercropping and for applying biodiversity principles to enhance ecosystem productivity and stability.

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3.4 Efficient Micronutrient Utilization

Iron and zinc are essential micronutrients for both crops and humans. In calcareous upland soils, iron primarily exists as sparingly soluble ferric iron. Dicotyledonous plants absorb ferrous iron depending on root membrane reductases to convert ferric to ferrous iron. Limited mobility of ferric iron restricts iron acquisition unless roots approach iron compounds, making dicots prone to iron deficiency chlorosis in calcareous soils. Dicot-gramineous monocot intercropping significantly improves dicot iron nutrition. For example, peanut/maize intercropping markedly alleviates peanut iron deficiency chlorosis and increases seed iron content. The primary mechanism involves gramineous monocots secreting phytosiderophores that chelate soil ferric iron, increasing its mobility to approach peanut roots and facilitating peanut iron nutrition [Figure 2b: see original paper]. Recent advances confirm peanuts can absorb phytosiderophore-chelated iron, improving their iron nutrition. Studies further demonstrate that legumes like chickpea and soybean intercropped with cereals can improve their iron, zinc, and copper nutrition.

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3.5 Crop Root Distribution

Our long-term intercropping root interaction research reveals that intercropping advantages correlate closely with root distribution. During co-growth, wheat and maize exhibit aboveground interspecific competition, with wheat as the dominant competitor and maize as the subordinate species. Belowground, wheat roots grow laterally into maize strips, occupying larger soil volumes. Compared to monoculture maize root distribution, intercropped maize roots occupy smaller soil volumes, and interestingly, maize root growth struggles to penetrate wheat root zones [Figure 3: see original paper]. In contrast, faba bean/maize intercropping shows aboveground facilitation, with maize roots growing laterally into faba bean root zones and intermingling [Figure 3: see original paper]. These differences in root distribution between competitive (wheat/maize) and facilitative (faba bean/maize) systems suggest that belowground root interactions may underlie interspecific interactions.

4.1 Diversified Planting and Agricultural Sustainability

Intensive monoculture has degraded soil properties, yet research on its impacts on soil biodiversity remains limited. Conversely, whether crop diversification can reverse these trends and the underlying mechanisms represent important future research directions. Numerous studies demonstrate that intercropping increases crop yields while removing substantial amounts of nitrogen, phosphorus, potassium, and micronutrients from soil. Whether excessive nutrient removal degrades soil fertility, or whether increased root inputs and belowground biodiversity from aboveground plant diversity provide positive feedback to soil fertility, are crucial scientific questions closely related to agricultural sustainability.

4.2 Belowground Interspecific Signaling

Understanding whether plants can perceive neighboring plants through signaling and respond accordingly is essential for comprehending the nature of plant interactions and has important practical implications for managing agroecosystems. Gersani et al. used split-root experiments with soybean to demonstrate that plants sharing resources developed 85% more root dry weight than those with exclusive resources, with corresponding reductions in shoot and grain yield, proving plants can sense neighbors and modify root growth, development, and morphology. Falik et al. confirmed this recognition effect in peas. However, these studies focused on conspecific interactions, with limited research on interspecific signaling, primarily in natural ecosystems and biological invasion contexts, and mostly addressing aboveground volatile signaling after herbivore attack. Systematic research at the agroecosystem level remains lacking. Investigating belowground signaling in intercropping systems will provide theoretical insights into the nature of interspecific interactions and practical prospects for regulating these interactions to optimize intercropping systems.

4.3 Feedback Regulation Between Crop and Soil Biodiversity

Previous research has focused more on aboveground diversity, while how aboveground diversity influences belowground biodiversity and how belowground biodiversity feeds back to regulate aboveground ecological processes—such as mechanisms controlling interspecific competition and facilitation—can reveal agrobiodiversity processes at higher hierarchical levels. In natural ecosystems, different plant species inputs of organic matter with varying quality and quantity profoundly affect soil fauna and microbes, altering belowground biodiversity, as validated in grassland and forest ecosystems. Conversely, altered belowground biodiversity can feedback to regulate aboveground plant diversity, productivity, and stability through multiple pathways. However, research in this area remains limited and should constitute an important future direction.

4.4 Intercropping Crop Growth Models

Intercropping systems, with at least two crop species, exhibit complex, heterogeneous aboveground canopies and belowground root distributions with dynamic changes. Modeling provides the most effective tool for understanding these complex relationships and quantifying efficient resource use. Current intercropping models include INTERCOM and wheat/cotton models. Functional-structural plant models (FSPM), emerging in the 1990s, effectively integrate physiological process-based crop models with plant virtualization, emphasizing structure-function linkages. A recent FSPM for wheat/maize intercropping quantified community-level light interception, showing 23% higher light interception than monoculture weighted averages, with 36% attributed to community structural changes and 64% to crop plasticity responses. Developing intercropping models based on climate, soil, and crop genotypes will enable evaluation of resource use efficiency across larger spatial and temporal scales, which is crucial for assessing productivity, sustainability, climate risks, and resource use efficiency. For example, under water-limited conditions with high seasonal and interannual precipitation variability, adjusting planting time, strip width, and cultivar selection is critical for yield improvement and climate risk reduction. Models like APSIM applied to intercropping can quantify yield and resource use advantages at farm and regional scales for large-area assessment.

5. Directions for Intercropping Application and Key Challenges

National policy emphasizes intercropping as an efficient resource use practice. The *State Council Opinion on Accelerating Transformation of Agricultural Development Methods* (Guobanfa [2015] No. 59) specifically advocates “vigorously promoting rotation and intercropping, supporting ecological compound planting adapted to local conditions, rational utilization of arable land resources, and integrating crop cultivation with soil conservation.” Thus, intercropping development enjoys strong policy support.

5.1 Integrating Legumes into Farming Systems for Ecologically Intensive Agriculture

Legume-rhizobia symbiotic nitrogen fixation represents a crucial natural pathway for converting inert nitrogen to reactive forms. Modern agriculture’ s heavy nitrogen fertilizer use suppresses legume biological nitrogen fixation, while limited arable land and staple crop demand pressure have reduced legume planting area. Large-scale legume monoculture faces severe land competition constraints. Consequently, this cost-effective green nitrogen fixation method has been underutilized. Legume-cereal intercropping can coordinate staple food and legume production while fully utilizing symbiotic nitrogen fixation for ecologically intensive agriculture.

Successful integration models include maize/pea, potato/pea, maize/faba bean, and wheat/soybean intercropping in the Hexi Corridor; maize/peanut intercropping in northeast and north China; millet/peanut intercropping in the northeast; maize/soybean intercropping in northeast and south China; “wheat-maize-soybean” systems in the southwest; and wheat/faba bean intercropping on the Yunnan-Guizhou Plateau. Optimizing and standardizing these models for high-yield, high-efficiency production while building soil fertility, harnessing biodiversity for pest control, and developing supporting machinery represents an important application direction.

In some regions, short-duration green manure crops are relay-cropped into staple crops. For example, spring wheat relay-cropped with sweet clover (Melilotus suaveolens), hairy vetch (Vicia villosa), or common vetch (Vicia sativa) in Gansu historically provided livestock feed while building soil fertility. Mixed cropping of non-legume forages with legumes can improve forage protein content and utilize legume nitrogen fixation to reduce chemical nitrogen requirements.

5.2 Intercropping and Organic Agriculture

Organic agriculture eliminates or minimizes synthetic fertilizers, pesticides, growth regulators, and feed additives, relying on organic fertilizers and feeds while emphasizing biological cycling, soil health, and biodiversity protection. Intercropping’ s resource-use efficiency enables mobilization of sparingly available soil phosphorus, maximizes legume biological nitrogen fixation potential, and improves micronutrient utilization, meeting requirements for reduced or eliminated chemical fertilizer use. Additionally, strategic crop configuration controls pests and diseases, reducing or eliminating chemical pesticide needs. Thus, intercropping will play a crucial role in organic agriculture.

5.3 Enhancing Phosphorus Fertilizer Use Efficiency Through Intercropping

Phosphorus fertilizer rapidly converts to sparingly soluble forms in soil, resulting in low use efficiency. Appropriate intercropping combinations can substantially improve phosphorus fertilizer recovery. Trials on newly reclaimed infertile soils showed intercropping significantly improved phosphorus fertilizer apparent recovery efficiency. In fertile irrigation desert soils, three-year studies of faba bean/maize, chickpea/maize, soybean/maize, and rapeseed/maize intercropping systems demonstrated average phosphorus recovery improvements of over 10 percentage points compared to corresponding monocultures.

5.4 Enhancing Grain Micronutrient Content Through Intercropping

As previously discussed, dicot-gramineous monocot intercropping improves dicot iron nutrition due to different iron acquisition pathways. Improved crop iron nutrition not only increases yield but also enhances human nutrition, as iron is an essential human micronutrient. Agronomic biofortification through intercropping represents an important approach for improving human iron nutrition. In peanut/maize intercropping, peanut seed iron concentration was 1.43 times higher than monoculture; in wheat/chickpea intercropping, chickpea seed zinc concentration was 2.82 times higher than monoculture. Our field trials in Wuwei, Gansu, demonstrated that chickpea/maize intercropping increased chickpea seed iron, zinc, and copper concentrations by 26.3%, 12.8%, and 15.4%, respectively, while faba bean/maize intercropping increased faba bean seed zinc and copper concentrations by 10.6% and 7.5%.

5.5 Mechanization Challenges

Mechanization represents the key constraint for large-scale intercropping adoption. Rising labor costs and rural labor shortages intensify this challenge. Achieving mechanization requires standardized, high-yielding interspecific configurations and row spacing on the agronomic side, and corresponding machinery for planting, fertilization, pesticide application, and harvesting. Research teams at South China Agricultural University and Sichuan Agricultural University have developed micro, small, and medium-sized machinery for the “100-100” strip pattern of wheat-maize-soybean relay intercropping in southwestern hilly regions, achieving mechanized operations for tillage, planting, management, and harvesting with high efficiency and quality, proving mechanized intercropping feasible. Further development requires testing and prototyping across more intercropping patterns and regions for broader application.

5.6 Cultivar Selection and Breeding for Intercropping

Appropriate crop combinations and cultivar selection are critical for intercropping success but receive limited attention. Suitable combinations can enhance positive interspecific interactions while reducing competition, increasing productivity. Breeding crops with traits favoring facilitation and reducing competition warrants attention, achievable through directed breeding for appropriate growth duration, root size and depth, and canopy height.

In conclusion, intercropping represents the essence of traditional Chinese agriculture and crystallizes empirical knowledge gained through long-term practice. Rational intercropping embodies rich ecological principles. Unearthing these scientific principles to enrich ecological theory while continuously improving this planting pattern represents an important mission for agricultural ecologists. This traditional approach will serve as a crucial measure for developing ecologically intensive agriculture and play an increasingly important role in modern farming.

References

[1] Liu X H. Farming System[M]. Beijing: China Agriculture Press, 1994

[2] Zou C Y, Li Z J. Crop intercropping[M]//Shi Y C, Zhang X Q. Chinese Academy Ceremony: Agricultural Sciences. Fuzhou: Fujian Education Press, 2002: 49-51

[3] Li L. The Ecological Principles and Applications of Biological N_2 Fixation in Legumes-Based Intercropping Systems[M]. Beijing: China Agricultural University Press, 2013

[4] Li L, Zhang L Z, Zhang F S. Crop mixtures and the mechanisms of overyielding[M]//Levin S A. Encyclopedia of Biodiversity. 2nd ed. Waltham, MA: Academic Press, 2013

[5] Wu W X, Luo X W, Yang W Y, et al. Research progress on mechanization of wheat-maize-soybean strip compound planting system[J]. Transactions of the CSAE, 2015, 31(Supp. 1): 1-7

[6] Zhou X A, Nian H, Yang W Y, et al. Developmental situation and countermeasure of intercropped soybean ( )[J]. Soybean Science and Technology, 2010(5): 1-2

[7] Zhang M P. Relay Intercropping[M]. Nanning: Guangxi People' s Publishing House, 2011

[8] Li C Y, He X H, Zhu S S, et al. Crop diversity for yield increase[J]. PLoS One, 2009, 4(11): e8049

[9] Giller K E, Beare M H, Lavelle P, et al. Agricultural intensification, soil biodiversity and agroecosystem function[J]. Applied Soil Ecology, 1997, 6(1): 3-16

[10] Tilman D, Cassman K G, Matson P A, et al. Agricultural sustainability and intensive production practices[J]. Nature, 2002, 418(6898): 671-677

[11] Li Y. Earthworm diversity as affected by intercropping systems[D]. Beijing: China Agricultural University, 2006

[12] Song Y N, Marschner P, Li L, et al. Community composition of ammonia-oxidizing bacteria in rhizosphere of intercropped wheat (Triticum aestivum L.), maize (Zea mays L.), and faba bean (Vicia faba L.)[J]. Biology and Fertility of Soils, 2007, 44(2): 307-314

[13] Naeem S, Thompson L J, Lawler S P, et al. Declining biodiversity can alter the performance of ecosystems[J]. Nature, 1994, 368(6473): 734-737

[14] Tilman D, Wedin D, Knops J. Productivity and sustainability influenced by biodiversity in grassland ecosystems[J]. Nature, 1996, 379(6567): 718-720

[15] Hector A, Schmid B, Beierkuhnlein C, et al. Plant diversity and productivity experiments in European grasslands[J]. Science, 1999, 286(5442): 1123-1127

[16] Loreau M. Biodiversity and ecosystem functioning: A mechanistic model[J]. Proceedings of the National Academy of Sciences of the United States of America, 1998, 95(10): 5632-5636

[17] Cardinale B J, Wright J P, Cadotte M W, et al. Impacts of plant diversity on biomass production increase through time because of species complementarity[J]. Proceedings of the National Academy of Sciences of the United States of America, 2007, 104(46): 18123-18128

[18] Eisenhauer N, Reich P B, Scheu S. Increasing plant diversity effects on productivity with time due to delayed soil biota effects on plants[J]. Basic and Applied Ecology, 2012, 13(7): 571-578

[19] Hauggaard-Nielsen H, Ambus P, Jensen E S. Interspecific competition, N use and interference with weeds in pea-barley intercropping[J]. Field Crops Research, 2001, 70(2): 101-109

[20] Hauggaard-Nielsen H, Ambus P, Jensen E S. The comparison of nitrogen use and leaching in sole cropped versus intercropped pea and barley[J]. Nutrient Cycling in Agroecosystems, 2003, 65(3): 289-300

[21] Khan Z R, Pickett J A, Wadhams L J, et al. Combined control of Striga hermonthica and stemborers by maize-Desmodium spp. intercrops[J]. Crop Protection, 2006, 25(9): 989-995

[22] Sarkar R K, Pal P K. Effect of intercropping rice (Oryza sativa) with groundnut (Arachis hypogaea) and pigeonpea (Cajanus cajan) under different

row orientations on rainfed uplands[J]. Indian Journal of Agronomy, 2004, 49: 147-150

[23] Ghosh P K, Mohanty M, Bandyopadhyay K K, et al. Growth, competition, yield advantage and economics in soybean/pigeonpea intercropping system in semi-arid tropics of India: I. Effect of subsoiling[J]. Field Crops Research, 2006, 96(1): 80-89

[24] Li L, Li S M, Sun J H, et al. Diversity enhances agricultural productivity via rhizosphere phosphorus facilitation on phosphorus-deficient soils[J]. Proceedings of the National Academy of Sciences of the United States of America, 2007, 104(27): 11192-11196

[25] Li L, Sun J H, Zhang F S, et al. Wheat/maize or wheat/soybean strip intercropping: I. Yield advantage and interspecific interactions on nutrients[J]. Field Crops Research, 2001, 71(2): 123-137

[26] Xia H Y, Wang Z G, Zhao J H, et al. Contribution of interspecific interactions and phosphorus application to sustainable and productive intercropping systems[J]. Field Crops Research, 2013, 154: 53-64

[27] Mei P P, Gui L G, Wang P, et al. Maize/faba bean intercropping with rhizobia inoculation enhances productivity and recovery of fertilizer P in a reclaimed desert soil[J]. Field Crops Research, 2012, 130: 19-27

[28] Tilman D, Reich P B, Knops J M H. Biodiversity and ecosystem stability in a decade-long grassland experiment[J]. Nature, 2006, 441(7093): 629-632

[29] Proulx R, Wirth C, Voigt W, et al. Diversity promotes temporal stability across levels of ecosystem organization in experimental grasslands[J]. PLoS One, 2010, 5(10): e13382

[30] Rao M R, Willey R W. Evaluation of yield stability in intercropping: Studies on sorghum/pigeonpea[J]. Experimental Agriculture, 1980, 16(2): 105-116

[31] Jensen E S. Intercropping field bean with spring wheat[J]. Vorträge für Pflanzenzüchtung, 1986, 11: 67-75

[32] Dapaah H K, Asafu-Agyei J N, Ennin S A, et al. Yield stability of cassava, maize, soya bean and cowpea intercrops[J]. The Journal of Agricultural Science, 2003, 140(1): 73-82

[33] Snapp S S, Blackie M J, Gilbert R A, et al. Biodiversity can support a greener revolution in Africa[J]. Proceedings of the National Academy of Sciences of the United States of America, 2010, 107(48): 20840-20845

[34] Giambalvo D, Ruisi P, Di Miceli G, et al. Forage production, N uptake, N_2 fixation, and N recovery of berseem clover grown in pure stand and in mixture with annual ryegrass under different managements[J]. Plant and Soil, 2011, 342(1/2): 379-391

[35] Kontturi M, Laine A, Niskanen M, et al. Pea-oat intercrops to sustain lodging resistance and yield formation in northern European conditions[J]. Acta Agriculturae Scandinavica, Section B-Soil & Plant Science, 2011, 61(7): 612-621

[36] Azo W M, Lane G P F, Davies W P, et al. Bi-cropping white lupins (Lupinus albus L.) with cereals for wholecrop forage in organic farming: The effect of seed rate and harvest dates on crop yield and quality[J]. Biological Agriculture & Horticulture, 2012, 28(2): 86-100

[37] Jorgensen V, Moller E. Intercropping of different secondary crops in maize[J]. Acta Agriculturae Scandinavica, Section B-Soil & Plant Science, 2000, 50(2): 82-88

[38] Hooper A M, Hassanali A, Chamberlain K, et al. New genetic opportunities from legume intercrops for controlling Striga spp. parasitic weeds[J]. Pest Management Science, 2009, 65(5): 546-552

[39] Zhu Y Y, Chen H R, Fan J H, et al. Genetic diversity and disease control in rice[J]. Nature, 2000, 406(6797): 718-722

[40] Mao L L, Zhang L Z, Li W Q, et al. Yield advantage and water saving in maize/pea intercrop[J]. Field Crops Research, 2012, 138: 11-20

[41] Sekiya N, Araki H, Yano K. Applying hydraulic lift in an agroecosystem: Forage plants with shoots removed supply water to neighboring vegetable crops[J]. Plant and Soil, 2011, 341(1/2): 39-50

[42] Salvagiotti F, Cassman K G, Specht J E, et al. Nitrogen uptake, fixation and response to fertilizer n in soybeans: A review[J]. Field Crops Research, 2008, 108(1): 1-13

[43] Li Y Y, Yu C B, Cheng X, et al. Intercropping alleviates the inhibitory effect of N fertilization on nodulation and symbiotic N_2 fixation of faba bean[J]. Plant and Soil, 2009, 323(1/2): 295-308

[44] Fan F L, Zhang F S, Song Y N, et al. Nitrogen fixation of faba bean (Vicia faba L.) interacting with a non-legume in two contrasting intercropping systems[J]. Plant and Soil, 2006, 283(1/2): 275-286

[45] Xiao Y B, Li L, Zhang F S. Effect of root contact on interspecific competition and N transfer between wheat and fababean using direct and indirect ^{15}N techniques[J]. Plant and Soil, 2004, 262(1/2): 45-54

[46] 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[J]. Plant and Soil, 2004, 263(1/2): 17-27

[47] Zhou L L, Cao J, Zhang F S, et al. Rhizosphere acidification of faba bean, soybean and maize[J]. Science of the Total Environment, 2009, 407(14): 4356-4362

[48] Li L, Tang C X, Rengel Z, et al. Chickpea facilitates phosphorus uptake by intercropped wheat from an organic phosphorus source[J]. Plant and Soil, 2003, 248(1/2): 297-303

[49] Li S M, Li L, Zhang F S, et al. Acid phosphatase role in chickpea/maize intercropping[J]. Annals of Botany, 2004, 94(2): 297-303

[50] Li L, Tilman D, Lambers H, et al. Plant diversity and overyielding: Insights from belowground facilitation of intercropping in agriculture[J]. New Phytologist, 2014, 203(1): 63-69

[51] Zuo Y M, Zhang F S, Li X L, et al. Studies on the improvement in iron nutrition of peanut by intercropping with maize on a calcareous soil[J]. Plant and Soil, 2000, 220(1/2): 13-25

[52] Zuo Y M, Zhang F S. Effect of peanut mixed cropping with gramineous species on micronutrient concentrations and iron chlorosis of peanut plants grown in a calcareous soil[J]. Plant and Soil, 2008, 306(1/2): 23-36

[53] Zuo Y, Zhang F. Iron and zinc biofortification strategies in dicot plants by intercropping with gramineous species. A review[J]. Agronomy for Sustainable Development, 2009, 29(1): 63-71

[54] Xiong H C, Kakei Y, Kobayashi T, et al. Molecular evidence for phytosiderophore-induced improvement of iron nutrition of peanut intercropped with maize in calcareous soil[J]. Plant, Cell & Environment, 2013, 36(10): 1888-1902

[55] Wang Y. Effect of species allocation on productivity and microelement uptake of crop intercropping system under different phosphorus levels[D]. Beijing: China Agricultural University, 2015

[56] Li L, Sun J H, Zhang F S, et al. Root distribution and interactions between intercropped species[J]. Oecologia, 2006, 147(2): 280-290

[57] Callaway R M. The detection of neighbors by plants[J]. Trends in Ecology & Evolution, 2002, 17(3): 104-105

[58] Gersani M, Brown J S, O' Brien E E, et al. Tragedy of the commons as a result of root competition[J]. Journal of Ecology, 2001, 89(4): 660-669

[59] Falik O, Reides P, Gersani M, et al. Self/non-self discrimination in roots[J]. Journal of Ecology, 2003, 91(4): 525-531

[60] Aphalo P J, Balaré C, Scopel A L. Plant-plant signaling, the shade-avoidance response and competition[J]. Journal of Experimental Botany, 1999, 50(340): 1629-1634

[61] Walker T S, Bais H P, Grotewold E, et al. Root exudation and rhizosphere biology[J]. Plant Physiology, 2003, 132(1): 44-51

[62] Dicke M, Agrawal A A, Bruin J. Plant talks, but are they deaf?[J]. Trends in Plant Science, 2003, 8(9): 403-405

[63] Bais H P, Park S W, Weir T L, et al. How plants communicate using the underground information superhighway?[J]. Trends in Plant Science, 2004, 9(1): 26-32

[64] Wardle D A, Bardgett R D, Klironomos J N, et al. Ecological linkages between aboveground and belowground biota[J]. Science, 2004, 304(5677): 1629-1634

[65] Zhang L, Spiertz J H J, Zhang S P, et al. Nitrogen economy in relay intercropping system of wheat and cotton[J]. Plant and Soil, 2008, 303(1/2): 55-68

[66] Zhang L, van der Werf W, Bastiaans L, et al. Light interception and radiation use efficiency in relay intercrops of wheat and cotton[J]. Field Crops Research, 2008, 107(1): 29-42

[67] Sievänen R, Mäkelä A, Nikinmaa E, et al. Special issue on functional-structural tree models: Preface[J]. Silva Fennica, 1997, 31: 237-238

[68] Sievänen R, Nikinmaa E, Nygren P, et al. Components of functional-structural tree models[J]. Annals of Forest Science, 2000, 57(5): 399-412

[69] Zhu J Q, van der Werf W, Anten N P R, et al. The contribution of phenotypic plasticity to complementary light capture in plant mixtures[J]. New Phytologist, 2015, 207(4): 1213-1222

[70] Meinke H, Sivakumar M V K, Motha R P, et al. Preface: Climate predictions for better agricultural risk management[J]. Australian Journal of Agricultural Research, 2007, 58(10): 935-936

[71] Whitbread A M, Robertson M J, Carberry P S, et al. Applying farming systems simulation to the development of more sustainable smallholder farming systems in Southern Africa[J]. European Journal of Agronomy, 2010, 32(1): 51-58

[72] Brooker R W, Bennett A E, Cong W F, et al. Improving intercropping: A synthesis of research in agronomy, plant physiology and ecology[J]. New Phytologist, 2015, 206(1): 107-117

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