

Integration of legume intercropping into sustainable farming systems for nitrogen fixation, soil health, and climate resilience

Edited by

Libert Brice Tonfack, Keston Njira and
Sudhir Kumar Rajpoot

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Integration of legume intercropping into sustainable farming systems for nitrogen fixation, soil health, and climate resilience

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Editorial: Integration of legume intercropping into sustainable farming systems for nitrogen fixation, soil health, and climate resilience

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legume intercropping, nitrogen fixation, soil health, land degradation, food security

Editorial on the Research Topic

Integration of legume intercropping into sustainable farming systems for nitrogen fixation, soil health, and climate resilience

1 Introduction

Soil health describes a soil's capacity to function within its ecological boundaries—supporting plant growth, sustaining water and air quality, and maintaining robust microbial and animal life. It's critical to ecosystem's ability to deliver services such as food production, nutrient cycling, carbon storage, and biodiversity support (Pinto et al., 2017). Unfortunately, converting native landscapes into monocultures and relying heavily on synthetic fertilizers depletes soil organic matter, damages microbial communities, and lowers water retention, weakening these essential services.

The incorporation of legumes in various cropping systems holds immense potential for addressing numerous challenges in modern agriculture, from improving soil health to enhancing crop yields and combating climate change. As biologically nitrogen-fixing crops, legumes naturally enrich the soil and reduce dependence on chemical fertilizers. They also enhance soil structure, promote microbial life, suppress insect pests and weeds, improve water use efficiency (Kokkini et al.; Akchaya et al.; Rajpoot et al., 2016), improve crop nutritional quality and production sustainability (Nuemsi et al., 2018). These “service crops” align with the economic, social, and environmental goals of sustainable agriculture. Despite its potential, the adoption of legume intercropping remains limited by the lack of suitable adaptation strategies across various climates and socio-economic contexts (Akchaya et al.). Practical agronomic recommendations, such as optimal spacing, sowing methods, and management based on local conditions, are still emerging as research advances.

This Research Topic aimed to address these needs by compiling high-quality contributions provided by individual studies and reviews on the subject of legume intercropping and its role in sustainable agricultural practices. These works focus on: (i) Nutrient cycling and nitrogen fixation, human-centered ecosystem services, (ii) Soil quality and physico-chemical properties, (iii) Crop productivity and resilience, (iv) Microbial and pest interactions, and (v) Resource use efficiency and climate adaptation.

2 This Research Topic

This collection brings together nine insightful contributions that explore the ecological and agronomic roles of legume intercropping across diverse farming systems, from rice-fallows in India to maize-peanut fields and high-altitude grasslands.

Greening rice-fallow systems: Kumar et al. reviewed the potential of integrating pulses (e.g., chickpea, lentil) and oilseeds (mustard, safflower) into post-rainy fallow lands in eastern India. They emphasize that deploying short-duration, low-water-demand crops on the 11–12 million hectares of rice-fallow lands can significantly boost land-use efficiency, enhance system productivity, and support smallholder livelihoods with clear policy implications for sustainable intensification. Legume Intercropping and Ecosystem Services: Kokkini et al. presented a compelling mini-review on how legumes improve ecosystem services. The authors highlighted that intercropping legumes contributes to improved soil structure, enhanced microbial biodiversity, superior water retention, natural pest suppression, pollination, and biodiversity support, along with various human-centered services such as disease prevention, reduced risk of malnutrition, and food security, showcasing the deep ecological benefits these crops support.

Akchaya et al. systematically evaluated the role of legume-based intercropping in enhancing soil fertility, resource use efficiency (land, water, and nutrients), and climate resilience. Their study reported nitrogen fixation rates ranging from 50 to 300 kg N ha⁻¹ year⁻¹, alongside improvements in nutrient and water efficiency and overall yield advantages. These benefits were attributed to ecological mechanisms such as bio-littering, bio-plowing, bio-irrigation, and bio-pumping, which contribute to better nutrient cycling, soil conservation, and agroecosystem stability. However, the authors also noted challenges related to the complexity of managing multiple crops simultaneously.

Soybean rhizosphere microbiome: Han et al. explored how different soybean genotypes shaped the assembly of rhizosphere microbes and their subsequent influence on yield traits. They reported that the M579 genotype exhibited the highest bacterial alpha diversity. Their findings underscore the importance of cultivar selection in maximizing beneficial microbiome interactions correlating with yield. Maize-Peanut Strip Width Optimization: Sun et al. analyzed strip spacing in maize-peanut systems, demonstrating that four rows of peanut and four rows of maize (row spacing of 50 cm) maintained the highest water use efficiency significantly, influencing the edge effects of rainfall-redistribution, improving crop and land productivity. Summer legume residual effects: Sunil Kumar et al. investigated the residual impacts of summer legumes on kharif rice. They found that such rotations

enhance nutrient availability and efficiency for the following rice crop, underscoring the value of thoughtful cropping sequence design. Rice Fallow Sowing Strategies: Jaya Singh et al. examined seed rates and timing in machine-harvested rice fallows, finding that a 20% increase in seed rate resulted in higher grain yield and straw yield among the blackgram treatments, showing tailored sowing approaches improve crop establishment and yield potential in these challenging environments.

High-altitude legume-grass nitrogen fixation: Luo et al. demonstrated that mixtures of legumes and grasses enhance nodulation and nitrogen transfer, root system configuration bolstering system productivity under low-temperature stress. Soil legacy effects on maize: Jalloh et al. revealed that previous edible legume intercropping can reduce *Spodoptera frugiperda* damage in subsequent maize crops, highlighting how soil history influences pest dynamics and crop resilience.

3 Concluding remarks/future directions

The studies compiled in this Research Topic underscore the diverse and essential ecosystem services offered by legumes when integrated into intercropping systems. From enhancing nutrient cycling and biological nitrogen fixation to improving soil structure, microbial activity, and crop resilience, legumes consistently demonstrate their potential as cornerstone crops in sustainable agriculture. The success of legume intercropping depends on many factors like local climate, soil conditions, crop combinations, and how farmers manage their fields. To make it truly effective, region-specific practices, farmer involvement, and practical recommendations are essential. Future efforts should focus on long-term studies, develop suitable agronomic packages, and explore how legumes interact with soil life, especially under changing climates. Understanding the economic trade-offs and offering market support will also help farmers adopt these systems more widely.

In conclusion, legumes offer a practical and ecologically grounded solution to many of the pressing challenges in agriculture. Their role in building resilient, efficient, and sustainable agroecosystems continues to grow, and this Research Topic contributes meaningfully to the scientific and practical understanding of their multifaceted value.

Author contributions

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

References

Nuemi, K. P. P., Tonfack, L. B., Mbogne, T. J., Mir, B. A., Mbanga, B. M. R., Ntsomboh, N. G., et al. (2018). Cultivation systems using vegetation cover improves the sustainable production and nutritional quality of New Rice for Africa in the tropics. *Rice Sci.* 25, 286–292. doi: 10.1016/j.rsci.2018.08.003

Pinto, P., Long, M. E. F., and Piñeiro, G. (2017). Including cover crops during fallow periods for increasing ecosystem services: is it possible in croplands of

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Southern South America? *Agric. Ecosyst. Environ.* 248, 48–57. doi: 10.1016/j.agee.2017.07.028

Rajpoot, S. K., Rana, D. S., and Choudhary, A. K. (2016). Influence of diverse crop management practices on weed suppression, crop and water productivity and nutrient dynamics in Bt-cotton (*Gossypium hirsutum*) based intercropping systems in a semi-arid Indo-Gangetic plains region. *Indian J. Agric. Sci.* 86, 1637–1641. doi: 10.56093/ijas.v86i12.65688



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Soil legacies in maize-edible legume intercropping alter maize growth and reduce *Spodoptera frugiperda* larval feeding

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Plant-soil feedback can influence aboveground interactions between plants and herbivores by affecting plant chemistry. Such interactions can be utilized in pest management. However, cropping systems such as maize-legume intercropping (MLI) can influence these interactions which is not well understood. In this study, we explored effects of MLI systems on soil physico-chemical properties, maize growth, larval feeding and development of fall armyworm (*Spodoptera frugiperda*). We used sterile soil and soil conditioned by different MLI and maize-monoculture cropping systems to explore these interactions. Soil samples that included soil conditioned by different MLI and maize-monoculture cropping systems were collected from smallholder farmer fields in eastern Kenya, where different MLI and maize-monoculture cropping systems were being practiced. These soil samples were compared with sterile soils for physico-chemical properties using black oxidation and Walkley methods. Three-weeks-old maize plants grown in the different soil treatments in the greenhouse were used for larval feeding and development assays. Neonate *S. frugiperda* larvae were allowed to feed on maize leaf discs for 24 hours and another set of plants were inoculated with the neonates for 15 days and the larval survival and development monitored. Soil obtained from different maize-edible legume intercropping systems had a higher pH, electrical conductivity, nitrogen, organic carbon, potassium, phosphorus, calcium, magnesium, exchangeable acidity, copper, clay and silt compared to maize-monoculture and sterile soil. Maize plants grown in MLI soil had better growth parameters compared to those in maize-monoculture and sterile soils. A high correlation was found between pH and plant biomass, while no significant correlation with other physico-chemical properties was noted. There were significant differences in larval feeding by *S. frugiperda* neonates when exposed to constitutive and induced maize leaf discs with more leaf tissue fed on maize grown in maize-monoculture and sterile soil. When allowed to feed for 15 days, *S. frugiperda* larval weight and length were significantly lower on maize plants grown in soils conditioned by MLI than those grown in soil conditioned by maize-monoculture and sterile soils. Findings from

this study show how conditioning soil by MLI systems improve soil health, maize growth and reduces *S. spodoptera* larval feeding and development.

KEYWORDS

crop mixtures, fall armyworm, soil health, seed germination, plant growth

1 Introduction

Global population will reach about nine billion by 2050, requiring a significant increase in crop production and yields to meet the high food demand amid ecological pressures (Van Dijk et al., 2021). However, crop production is limited by factors including poor soil fertility, diseases and pests which are exacerbated by changing climate (Midega et al., 2018; Chiriboga et al., 2021; Davidson-Lowe et al., 2021; Mutyambai et al., 2022). One pest that has become a global threat to the production of staple food is the fall armyworm, *Spodoptera frugiperda* J.E Smith (FAW) (Lepidoptera: Noctuidae). Fall armyworm is native to South America, whose invasion on the African continent was first reported in Nigeria in early 2016. But by January 2018, it had spread through most of sub-Saharan Africa (SSA) (Stokstad, 2017; FAO, 2018; Koffi et al., 2020). Fall armyworm is a polyphagous pest, known to attack over 350 plant species in the Americas (Montezano et al., 2018), with maize being the most preferred host for feeding and offspring development. The larval feeding on young maize leaves, whorls, tassels, and ears, leads to substantial damage even resulting in plant death in severe infestation levels. Plants weakened because of the defoliation and damage of cobs by the larvae are more susceptible to diseases and environmental stresses (Hailu et al., 2018; Mutyambai et al., 2022). The invasion of FAW in Africa and its subsequent spread around the world has become a significant source of concern due to its feeding on various staple and economically important crops, especially maize, sorghum, and millets, causing significant yield losses, in the absence of proper control measures (Chiriboga et al., 2021; Makgoba et al., 2021; Overton et al., 2021; Yan et al., 2022; Peter et al., 2023). The multivoltine nature of FAW coupled with rapid reproduction capacity and high dispersal ability has contributed to the successful invasion and establishment of FAW in SSA and beyond (Stokstad, 2017; De Groote et al., 2020). Surveys in Kenya showed that 82% of maize smallholder farmers had been affected by FAW, causing yield losses of up to 30%, reducing maize productivity by up to 1 million tonnes (De Groote et al., 2020; Mutyambai et al., 2022). In Ethiopia, Abro et al. (2021) estimated up to 36% yield loss of maize valued at US\$ 200 million between 2017 and 2019. In spite of management efforts by farmers in Ethiopia, FAW caused up to 11.5% yield loss (Kassie et al., 2020). This reveals that there is an urgent need for effective control of FAW for food security and enhancing livelihoods of maize growers.

Several management practices have been implemented in SSA to tackle the menace of FAW. These include cultural practices,

biological control using natural enemies and chemical control using insecticides (Hailu et al., 2018; Midega et al., 2018; Makgoba et al., 2021). When FAW invaded Africa, chemical control was the main strategy deployed by many African governments (Tambo et al., 2020; Chiriboga et al., 2021). Moreover, this approach was adopted by most smallholder maize farmers, who frequently applied insecticides. However, overuse of these synthetic insecticides is not a sustainable option as these pose adverse effects on human and environmental health including loss of pollinators, and pests' natural enemies (Midega et al., 2018; Kumela et al., 2019; De Groote et al., 2020). Potential sustainable management strategies of FAW include agroecological-based approaches such as intercropping, conservation and augmentation of natural enemies as well as utilization of botanicals and beneficial microbes (Hailu et al., 2018; Midega et al., 2018; Kansime et al., 2019; Makgoba et al., 2021). Habitat diversification through cropping systems such as push-pull technology and maize-legume intercropping (MLI) systems have been shown to reduce FAW infestation and increase maize yield where they are practiced compared to maize-monocultures (MMC) and other farmer practices (Hailu et al., 2018; Midega et al., 2018; Mutyambai et al., 2022; Librán-Embid et al., 2023). However, the impact of these cropping systems on the belowground soil properties and their subsequent effect on plant-soil feedbacks in relation to invasive pest herbivores like FAW is not well known. Hence, there is needed to understand these cropping systems interactions with belowground soil and its properties and plant-soil feedbacks mediated by the soil changes resulting from this cropping diversification to inform development of more effective and sustainable strategies for managing this pest in SSA.

Cultivation systems, such as MLI systems and crop rotation, have been shown to impact soil and regulate plant-soil interaction (Drinkwater et al., 2021; Wang et al., 2021). Recently, our understanding of how cropping systems impact crop output, plant growth, chemistry, and insect resistance has increased. For example, cover crop, push-pull cropping system and crop rotation strategies have significantly increased crop health and yield, soil health and offer a potential management option for the herbivore pests (Mutyambai et al., 2019; Ndayisaba et al., 2020; Davidson-Lowe et al., 2021; Jalli et al., 2021). In addition, diverse cropping strategies, such as cover-crop and cereal-legume intercropping systems exhibited significant expression of defense genes and emission of herbivore-induced volatiles and secondary metabolites, enabling plants to resist herbivore pests (Kaplan et al., 2018; Mutyambai et al., 2019; Davidson-Lowe et al., 2021). Some of the intercropped plants, like push-pull and maize-bean,

release chemicals that attract insect herbivores away from the target or repel them from the area (Khan et al., 2012; Gordy et al., 2015; Peter et al., 2023). Moreover, companion crops improve soil health, increase organic content, mitigates erosion, inhibit the movement of larvae, prevent the laying of eggs, and provide a suitable habitat for natural enemies (Harrison and Bardgett, 2010; Khan et al., 2012; Sokame et al., 2020; Peter et al., 2023). Intercropping through simultaneous cultivation of different species masks volatile cues used by herbivores to locate hosts (Karban, 2011; Midega et al., 2018). According to Kaplan et al. (2018), plant species grown in a given soil have differential effects on subsequent plants that grow in the same soil. On the other hand, monoculture has been associated with detrimental impacts on plant soil feedback (PSF). This leads to negative consequences on plant development and pest resistance (Delgado and Gómez, 2016; Van der Putten et al., 2016), which is apparent in MMC systems (Ewel et al., 1991).

Plant-mediated effects affect soil composition through influence on nutrient accessibility, microbial communities, and organic composition, which are crucial for their growth and health. Different plant communities cause shifts in soil microbiota, affecting the performance of successive plants either positively or negatively (Agegnehu et al., 2016; Delgado & Gómez, 2016; Wang et al., 2021). This phenomenon, known as PSF, has been utilized as a cropping practice since the origin of agriculture (Harrison and Bardgett et al., 2010; Van der Putten et al., 2016; Sharma, 2022) to enhance agroecosystem services. However, only recently have ecologists become interested in PSF as a critical driver of plant dynamics and ecological processes (Mutiyambai et al., 2019; Pervaiz et al., 2020; Wang et al., 2021). The intrinsic soil characteristics determine the entire agricultural output and the soil's ability to support plant growth, which determines production potential (Agegnehu et al., 2016; Sharma, 2022). The soil's physico-chemical, and biological characteristics make up these attributes, which give such systems their dynamism. The fertility of the soil is significantly influenced by soil physico-chemical characteristics, including soil organic matter, maximum water-holding capacity, electrical conductivity, bulk density, and pH (Van der Putten et al., 2016; Ndayisaba et al., 2020; Ndayisaba et al., 2022; Sharma, 2022). The soil is the main reservoir of nutrients and carbon, influencing soil health and fertility (Li et al., 2020; Wang et al., 2021). These outcomes improve our understanding of how various cropping systems impact ecosystem functioning, allowing us to create more effective and sustainable agricultural systems. Because of this, elucidating how different cropping systems alter soil-conditioning properties and reduce plant damage on maize plant becomes imperative. Studies that examine the underlying phenomenon in plant-soil interaction and its consequences have been largely ignored, despite the recent focus on the influence of PSF on soil physico-chemical characteristics and plant performance (Loreau et al., 2001; Pervaiz et al., 2020; Drinkwater et al., 2021).

This study aimed at investigating the effect of conditioning soil with different MLI systems on: (1) soil physico-chemical properties; (2) maize seed germination, plant growth and biomass; and (3) FAW larval feeding and development as a measure of direct resistance. We hypothesized that soil conditioned by different MLI systems exhibited better physico-chemical characteristics,

mediates fast seed germination and enhance maize growth, and biomass compared to maize plants grown on MMC and S conditioned soil. We further hypothesized that FAW neonates fed less on plants grown in soil conditioned by different MLI systems compared to those grown in MMC conditioned and sterile soil.

2 Materials and methods

2.1 Study site and soil sample collection

Soil samples were collected from three counties in Kenya namely, Tharaka Nithi (N 00° 01' 58.5" E 37° 47' 23.1"; N 00° 18' 51.9" E 37° 46' 41.6"; 700 - 1113 meters above sea level (masl)), Embu (S 00° 30' 07.4" E 37° 27' 44.6"; S 00° 42' 17.6" E 37° 29' 32.7"; 1093 - 1541 masl), and Meru (N 00° 02' 26.1" E 37° 45' 55.5"; N 00° 01' 48.6" E 37° 45' 54.5"; 1110 - 1140 masl). These counties were selected based on the availability of different MLI and MMC cropping systems. Within each county, farms were chosen based on similarities in agronomical parameters, farm management, and minimum tillage to control weeds without applying synthetic fertilizers or pesticides. Rhizospheric soil samples were collected from different MLI and MMC cropping systems (Table 1) in farms that were already established. The major crops planted in these three counties include maize, millet, sorghum, black bean, common bean, pigeon pea, green gram, and cowpea, characterized by MLI systems. The climate in the area is sub-humid tropical with a bimodal rainfall distribution consisting of a long rain season

TABLE 1 Rhizospheric soil samples collected from different cropping systems in smallholder farm fields.

Cropping systems	Soil types	Acronym
Maize-edible legume intercropping (MLI)	maize (<i>Zea mays</i> L.) black bean (<i>Phaseolus vulgaris</i> L.) conditioned soil.	MBB
	maize pigeon pea (<i>Cajanus cajan</i> (L.) Millsp.) conditioned soil.	MPP
	maize common bean (<i>Phaseolus vulgaris</i> L.) conditioned soil.	MCB
	maize green gram (<i>Vigna radiata</i> (L.) Wilczek) conditioned soil.	MGG
Maize-monoculture (MMC)	maize-monoculture conditioned soil.	MMC
Bulk soil (BS)	soil collected from different cropping systems in the smallholder farm fields and used in experiments without any alteration.	BS (MBB, MPP, MCB, MGG and MMC)
Sterile/control soil (S)	soil was harvested from one point at the <i>icip</i> e experimental plots in Nairobi, Kenya as a control, which was sterilized for 24 h (through autoclaving) following a 24 h resting period.	S
Inoculated bulk soil	95% of S soil inoculated with 5% of MPP, MGG, MBB, MMC and MCB conditioned soil.	5% IBS

(March–August) and a short season (October–December). The soils in the study area are mainly Acrisols and Nitisols. Four smallholder farms representing MLI and MMC cropping systems provided samples for each of the cropping systems in Table 1. The soil sampling was done randomly between maize and legume rows for intercropped and maize rows for MMC cropping system during the vegetative growth (4–5 weeks old) stage of the plants. Twelve samples were collected per smallholder farm ($\approx 5\text{--}20$ cm depth) using a soil auger after cleaning surface organic contents around the rows of the plants. The soils from each farm (12 points sample) were then mixed to form a composite and packaged in separate Khaki bags (Paper bags Ltd., Nairobi, Kenya) before transporting to the International Centre of Insect Physiology and Ecology (*icipe*) for analysis and experiments.

2.2 Soil physico-chemical properties

Soil samples collected from various cropping systems as bulk soil (BS) and sterile soil (S) as described above (Table 1) were analyzed for micronutrients at Société Générale de Surveillance (SGS) Kenya Ltd Multi-laboratory, Nairobi, before the onset of the experiments in the greenhouse. Soil micronutrients including nitrogen (N), phosphorus (P), sodium (Na), organic carbon (OC), calcium (Ca), potassium (K), and other soil parameters such as potential of hydrogen (pH), electrical conductivity (EC) were measured following the methodology developed by Okalebo et al. (2002) and Sparks et al. (1996). Soil texture (silt, clay, and sand) and trace elements such as zinc (Zn), boron (B), copper (Cu), iron (Fe), and manganese (Mg) were analyzed through the Bouyoucos hydrometer method as described by Beretta et al. (2014).

2.3 Plants

Maize seeds (SC Duma 43), a variety commonly cultivated by small-scale farmers in Western and Eastern Kenya, were obtained from Simlaw Seeds, Nairobi, Kenya. The seeds were surface sterilized with 70% ethanol for 30 seconds and rinsed with distilled water before planting in a sterilized five-liter plastic container pot (previously sterilized in 70% ethanol) in a greenhouse ($25 \pm 2^\circ\text{C}$ during the day, $19 \pm 2^\circ\text{C}$ at night, and L12:D12 photoperiod) at *icipe*. Two seeds were planted in each conditioned soil type (MLI, MMC and S soils) collected from the farms within 48 h after sample collection. To prevent soil cross-contamination, precautions such as wearing gloves while handling soil from different fields, during measurements, and when dealing with the plant and FAW neonates were taken.

2.4 Insects

Using the protocol described by Onyango and Ochieng'-Odero (1994), FAW larvae were reared at the Animal Rearing and Containment Unit (ARCU), *icipe* Duduville campus on a maize-based artificial diet and leaves in 1000 mL plastic jar, with their lids

infused with steel wire for airflow. Optimal conditions for larvae rearing were $27 \pm 2^\circ\text{C}$, $75 \pm 5\%$ relative humidity (RH), and L12:D12 photoperiod until they pupated (Mutua et al., 2022). To develop into adults (moths), pupae were kept in cages measuring $40 \times 20 \times 20$ cm with wet cotton wool to provide moisture, while matured moths were then transferred to oviposition cages of $80 \times 50 \times 70$ cm. The matured moths were provided with maize plants for mating and as an oviposition substrate. They were also continuously provided with a 10% honey solution. To induce egg production, they were exposed to maize leaves and damp cotton cloth, acting as a water source. The eggs were collected and placed in plastic containers to regenerate the colony. One-day-old unfed FAW neonates were used for the experiments. The neonates were collected using a fine-camel brush. Second-generation insects were utilized in all tests. To avoid genetic degradation, laboratory-reared insects were infused with field-collected insects every two months to maintain their phenological characteristics.

2.5 Germination of maize seeds

Bulk soils (BS) collected from the various cropping systems (Table 1) were used to investigate the impact of soil conditioning on seed germination time and rate. In addition, the S soil was inoculated with 5% of the BS soils collected from different cropping systems above to form another type 5% IBS which was also used for the experiment. The BS and 5% IBS soils (Table 1) were distributed in plastic container pots (5 L) that were pre-sterilized with 70% ethanol. Two maize seeds were sown in each pot and kept in a greenhouse ($27 \pm 2^\circ\text{C}$, $75 \pm 5\%$ relative humidity (RH), and L12:D12). The experiment was replicated four times for each treatment with four experimental units in each replicate. In total, 384 seeds planted for the experiment. The planted seeds were watered daily with sterilized distilled water (0.2 L), and the germination was observed and recorded on daily bases. The time taken for the seed to germinate was expressed as germination time, while the germination rate in each treatment was calculated as the proportion of germinated seed from the total seeds that were planted. Three days post germination, the weakest seedling in each pot was thinned out and only one seedling per pot was kept for the subsequent experiments. At the end, each treatment (each cropping system in each soil conditioned type) had 16 plants for the subsequent experiments.

2.6 Plant growth parameters

Maize plant growth parameters including the number of leaves, stem diameter, plant height, and chlorophyll content for each maize grown in each soil type were measured weekly for three weeks' duration (W1, W2 and W3) (Chiriboga et al., 2021). Plant height was measured using a meter tap from the soil lines to the uppermost leaf's arch. The chlorophyll content of the leaves was measured using a chlorophyll meter (SPAD-502) (Konica Minolta Sensing, Inc., Japan). Vernier callipers (Toolstream Ltd. BA22 BHZ, United Kingdom) were used to measure the diameter of the plant stem.

After 21 days of growth, four plants from each soil type were cut at the baseline. Thereafter, the soil was removed from the shoots and roots by washing them with excess water and then dried with a paper towel. Maize plant biomass was determined by weighing fresh and dry root and shoot using a weighing balance (Kern & Sohn GmgH, D-72336 Balingen, Germany).

2.7 Larval feeding assay

A no-choice feeding assay was conducted in the laboratory to determine FAW leaf feeding on maize plants grown on BS and 5% IBS soils (Table 1). For each soil type, four maize plants that are three weeks old were selected. This is the age when maize is highly preferred and susceptible to FAW (De Lange et al., 2020). For each plant, leaf discs of 15 mm diameter were removed from the second youngest fully expanded maize leaf and used for the constitutive feeding experiment. The leaf disc was placed in a 30 mL transparent plastic cup (TPC) that was midway filled with technical agar #3 (TA3), to prevent leaf discs from desiccating. Ten unfed FAW neonates were placed on the leaf disc within the media TPC, sealed with parafilm to prevent the neonates from escaping (Mutiyambai et al., 2019), and a slit was made with a sharp scalpel at the cup lid for air circulation. The neonates were allowed to feed for 24 h, and thereafter the leaf discs were photographed to assess the area consumed by the neonates using ImageJ software (National Institutes of Health, Bethesda, USA) (Schneider et al., 2012). A similar experiment was conducted after initial exposure of maize plant for 24 h (induced assay) with 10 FAW neonates in a greenhouse.

2.8 Growth and development of *Spodoptera frugiperda* larvae

This experiment was conducted to investigate the effects of maize plants grown on BS and 5% IBS soils (Table 1) on the fitness performance of FAW neonates under semi-field conditions in a greenhouse. Ten neonates were placed on a three-week-old undamaged maize whorl plant using a fine camel-hair brush, and allowed to feed for 15 days. The plants were placed on metal stands elevated above the ground and covered with sticky glue to prevent predators like ants from climbing up the stands. A 0.2 L of sterilized distilled water was used to water the 5 L pot daily at the base of each maize plant. After 15 days, larval survival rates, length, weight, and instar stage of development were recorded from each replicate per cropping system (Mutua et al., 2022). The experiment was replicated four times for each soil type.

2.9 Data analyses

All data were subjected to a normality test using Shapiro-Wilk test. Soil physico-chemical properties, plant growth, larval feeding and development data obtained from each soil type (Table 1) were

analyzed using one-way ANOVA. Tukey's post hoc test was used to carry out a pairwise comparison for mean separation at $\alpha = 0.05$. The germination time data were analyzed using a generalized linear model (GLM) with Poisson distribution since they were not normally distributed. A two-sample (unpaired) Student's t-test was used to compare constitutive and induced larval feeding for each soil type. Pearson correlation analysis was used to determine the relationship between soil physico-chemical properties and plant growth parameters. The principal component analysis (PCA) was conducted to determine the relationship between soil physico-chemical parameters and the different cropping systems. All analyses were carried out using R (v4.1.2.) statistical software packages (R Core Team, 2018).

3 Results

3.1 Soil physico-chemical properties

Bulk soils (BS) obtained from different cropping systems (MBB, MGG, MPP, MCB, MMC) and control (S) soils significantly varied in their physico-chemical characteristics ($F_{5,30} = 44.27$, $P = 0.001$; $F_{5,30} = 2.610$, $P = 0.01$; $F_{5,30} = 1.128$, $P = 0.05$; $F_{5,30} = 2.708$, $P = 0.01$; $F_{5,30} = 6.132$, $P = 0.001$; $F_{5,30} = 2.218$, $P = 0.01$; $F_{5,30} = 4.574$, $P = 0.001$; $F_{5,30} = 2.232$, $P = 0.02$; $F_{5,30} = 2.653$, $P = 0.01$; $F_{5,30} = 17.200$, $P = 0.001$; $F_{5,30} = 13.600$, $P = 0.001$; $F_{5,30} = 2.685$, $P = 0.01$; and $F_{5,30} = 3.635$, $P = 0.01$; for pH, EC, K, Ca, Mg, EA, Fe, Cu, N, OC, clay and silt; Table 2). There were significant differences across soil physico-chemical parameters in different cropping systems, except for Na, Mn, Zn, S and sand. We observed that the lowest pH was recorded on MMC and S soils. Overall, BS soils obtained from different MLI systems had a higher pH, EC, K, Ca, Mg and Cu soil parameters compared to MMC and S soil (Table 2).

There is a strong correlation between soil conditioned by MLI and MMC cropping systems (principal component biplot (PCA)). A strong positive correlation was observed between soil conditioned by MBB and MPP on parameters such as S, Na, EC, K, pH, Ca and Mg (Figure 1). MGG and MCB cropping system correlated negatively with N, OC, sand and silt. These results indicate that MLI systems have a significant influence on soil properties, making them favorable for farm mechanization. In contrast, the MMC cropping system has no impact on these properties. It's worth noting that PCA1 and PCA2, which collectively account for 58.2% of the total variance, played a vital role in elucidating the interactions between the selected soil properties (Figure 1).

3.2 Germination rate and time of maize seeds

3.2.1 Germination rate

SC Duma 43 maize seeds planted in different cropping systems conditioned BS (MMP, MPP, MCB, MGG, MMC and S) significantly affected seed germination rate (ANOVA: $F_{5,18} = 6.99$, $P < 0.001$). The germination rate was significantly higher in MPP

TABLE 2 Physico-chemical characteristics of soil conditioned by different maize-legume intercropping, maize-monoculture cropping systems and the sterilized soil control.

Soil parameters	Maize-edible legume intercropping systems				MMC	S	F value (5,30)	P - value
	MBB	MPP	MCB	MGG				
pH	6.15 ± 0.17 ^c	7.45 ± 0.25 ^d	5.95 ± 0.17 ^c	6.53 ± 0.21 ^c	5.19 ± 0.11 ^b	4.15 ± 0.00 ^a	44.27	<0.001
EC	0.11 ± 0.02 ^{ab}	0.37 ± 0.16 ^b	0.07 ± 0.01 ^a	0.30 ± 0.15 ^b	0.06 ± 0.01 ^a	NA	2.610	>0.01
P	24.48 ± 10.64 ^a	44.45 ± 13.19 ^b	14.15 ± 4.09 ^a	42.91 ± 34.28 ^b	14.43 ± 2.16 ^a	3.26 ± 0.00 ^a	1.128	>0.05
K	436.38 ± 81.74 ^{ab}	569.64 ± 151.80 ^b	264.46 ± 43.01 ^{ab}	427.73 ± 113.52 ^{ab}	244.62 ± 52.82 ^{ab}	186.88 ± 0.00 ^a	2.708	>0.01
Na	44.63 ± 6.25 ^a	114.51 ± 24.45 ^a	43.72 ± 7.66 ^a	58.53 ± 18.16 ^a	51.41 ± 6.59 ^a	33.44 ± 0.00 ^a	4.741	>0.06
Ca	1791.10 ± 411.46 ^{bc}	2876.61 ± 540.07 ^c	1340.79 ± 283.24 ^{ab}	1410.05 ± 167.41 ^{ab}	889.18 ± 173.00 ^{ab}	678.32 ± 0.00 ^a	6.132	<0.001
Mg	302.11 ± 65.33 ^a	371.41 ± 63.32 ^a	252.14 ± 65.24 ^a	380.92 ± 123.51 ^a	167.57 ± 33.85 ^a	131.86 ± 0.00 ^a	2.218	>0.01
EA	0.43 ± 0.10 ^a	NA	0.37 ± 0.17 ^a	NA	0.25 ± 0.12 ^a	NA	4.574	<0.001
Fe	127.76 ± 25.35 ^a	69.63 ± 9.84 ^a	89.48 ± 6.79 ^a	112.13 ± 22.57 ^a	102.47 ± 12.37 ^a	70.58 ± 0.00 ^b	2.232	>0.02
Mn	233.12 ± 51.83 ^a	169.02 ± 24.55 ^a	221.37 ± 63.86 ^a	193.40 ± 40.61 ^a	244.83 ± 41.14 ^a	175.11 ± 0.00 ^a	0.556	>0.71
Cu	4.34 ± 1.16 ^a	1.95 ± 0.73 ^a	2.99 ± 1.11 ^a	5.86 ± 1.71 ^a	1.73 ± 0.77 ^a	1.59 ± 0.00 ^a	2.653	>0.01
Zn	7.09 ± 1.78 ^a	3.57 ± 0.42 ^a	7.74 ± 2.85 ^a	5.64 ± 1.62 ^a	6.31 ± 2.31 ^a	3.00 ± 0.00 ^a	1.122	>0.19
S	12.99 ± 2.35 ^a	36.12 ± 13.02 ^a	14.24 ± 1.65 ^a	21.61 ± 11.48 ^a	19.26 ± 3.54 ^a	17.90 ± 0.00 ^a	1.300	>0.17
N	0.29 ± 0.024 ^c	0.16 ± 0.02 ^b	0.16 ± 0.02 ^b	0.24 ± 0.03 ^{bc}	0.19 ± 0.02 ^b	0.03 ± 0.00 ^a	17.200	<0.001
OC	3.02 ± 0.35 ^c	1.56 ± 0.15 ^b	1.64 ± 0.15 ^b	2.41 ± 0.34 ^{bc}	2.06 ± 0.27 ^{bc}	0.39 ± 0.00 ^a	13.600	<0.001
Clay	28.74 ± 3.58 ^{ab}	21.67 ± 1.24 ^a	34.16 ± 5.76 ^{ab}	34.55 ± 2.52 ^{ab}	37.90 ± 4.79 ^b	34.95 ± 0.00 ^{ab}	2.685	>0.01
Silt	40.82 ± 3.08 ^b	21.25 ± 3.69 ^{ab}	24.16 ± 5.86 ^{ab}	30.81 ± 5.08 ^{ab}	25.83 ± 6.73 ^{ab}	14.990 ± 0.00 ^a	3.635	>0.01
Sand	30.44 ± 2.85 ^a	57.08 ± 4.49 ^a	41.69 ± 11.04 ^a	34.64 ± 4.27 ^a	36.27 ± 8.93 ^a	50.06 ± 0.00 ^a	5.27	>0.06

MBB, maize black bean; MPP, maize pigeon pea; MCB, maize common bean; MGG, maize green gram intercropping; MMC, maize-monocultures; S, sterilized soil; NA, negligible; pH, potential of hydrogen; EC, electrical conductivity; P, phosphorus; K, potassium; Na, sodium; Ca, calcium; Mg, magnesium; EA, exchangeable acidity; Mn, manganese; Cu, copper; S, sulphur; N, nitrogen; OC, organic carbon; Fe, iron; and Zn, zinc. Different letter indicates significant difference between the different cropping systems soil conditioned types (Mean ± SE) ($P < 0.05$) according to Tukeys honest significance test (HSD). Significant effects are indicated in bold at $P < 0.05$.

and MGG soils followed by MBB and MMC soils (Figure 2A). Similar trends were observed for S soil inoculated with 5% IBS where the germination rate was significantly higher in MPP and MGG soils (ANOVA: $F_{5,18} = 4.89$, $P < 0.001$) (Figure 2B).

3.2.2 Germination time

The time taken for SC Duma 43 maize seeds to germinate significantly varied across BS. The germination time was significantly lower in MBB and MPP soils which was on average 4 days after planting (GLM: $\chi^2 = 8.98$, $df = 135$, $P = 0.01$) (Figure 3A). However, seeds planted in MMC and S soil took on average 6 days to germinate (Figure 3A). On the other hand, there was no significant difference in germination time for the seeds planted in 5% IBS (MPP, MGG, MBB, MMC, MCB) (GLM: $\chi^2 = 12.31$, $df = 143$, $P = 0.589$) (Figure 3B).

3.3 Maize plant growth parameters

3.3.1 Plant height

There were significant differences in plant height for maize grown in BS and 5% IBS soils during the first week (W1), second week (W2) and third (W3) weeks after germination (ANOVA: $F_{5,18} = 33.77$, $P < 0.001$), (ANOVA: $F_{5,18} = 21.37$, $P < 0.001$) and (ANOVA: $F_{5,18} = 33.77$, $P < 0.001$), respectively (Figure 4). Among BS soils, maize planted in MCB soil were significantly higher in W1 and W2 after germination, compared to other soils (S, MMC, MBB, and MGG). However, during W3, the height of maize plants grown in MPP soil was significantly higher at ≈ 35 cm, followed by MCB and MBB soils ($P < 0.001$). Plant height in S, MMC and MGG soils were relatively similar and shorter across W3 duration. We observed similar trends in 5% IBS soils. In W1, the plant height

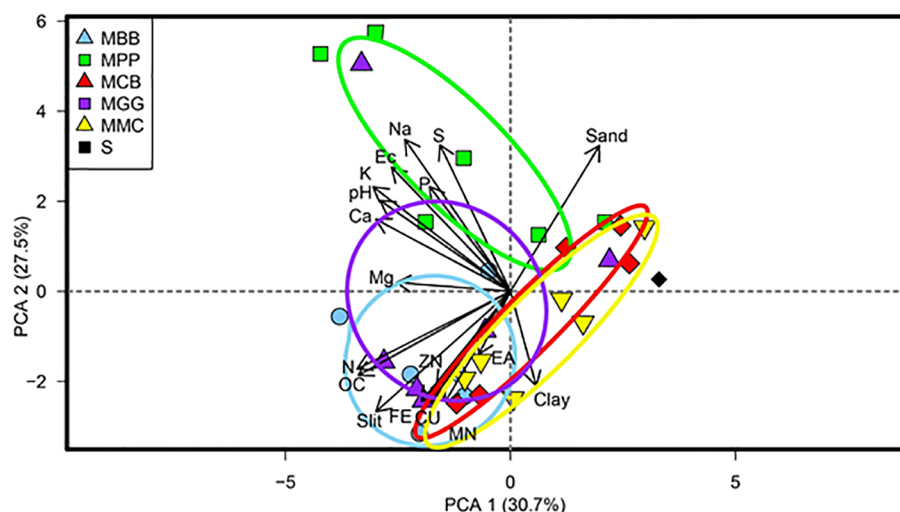


FIGURE 1

Principal component biplot, for the relationship between soil physico-chemical properties of different cropping systems soil conditioned. Principal components 1 = PCA1 and principal components 2 = PCA2. MBB, maize black bean; MPP, maize pigeon pea; MCB, maize common bean; MGG, maize green gram intercropping; MMC, maize-monocultures; S, sterilized soil; pH, potential of hydrogen; EC, electrical conductivity; P, phosphorus; K, potassium; Na, sodium; Ca, calcium; Mg, magnesium; EA, exchangeable acidity; Mn, manganese; Cu, copper; S, sulphur; N, nitrogen; OC, organic carbon; Fe, iron; and Zn, zinc.

was significantly higher in MCB followed by MPP soil, while it was lowest in MGG and S soil ($P < 0.001$). During W2, the plants were significantly taller in MPP followed by MCB and then MBB soils. Although plants in MGG soil were short during the first two weeks, they reached ≈ 30 cm in W3, accounting for the tallest level across the 5% IBS soils. Indeed, the plants in S soil were shorter across the three weeks regardless of soil type (BS and 5% IBS) or cropping system (Figure 4).

3.3.2 Plant diameter

There were significant differences in maize plant diameter between maize plants grown in BS and 5% IBS soils during W1, W2 and W3 after germination (ANOVA: $F_{5,18} = 33.77$, $P < 0.001$), (ANOVA: $F_{5,18} = 21.37$, $P < 0.001$) and (ANOVA: $F_{5,18} = 33.77$, $P < 0.001$), respectively (Figure 5). In BS, maize plant diameter was significantly wider ($P < 0.001$) for plants grown in MPP compared to MGG, S, and MMC soils during W1. In W2, the diameter of

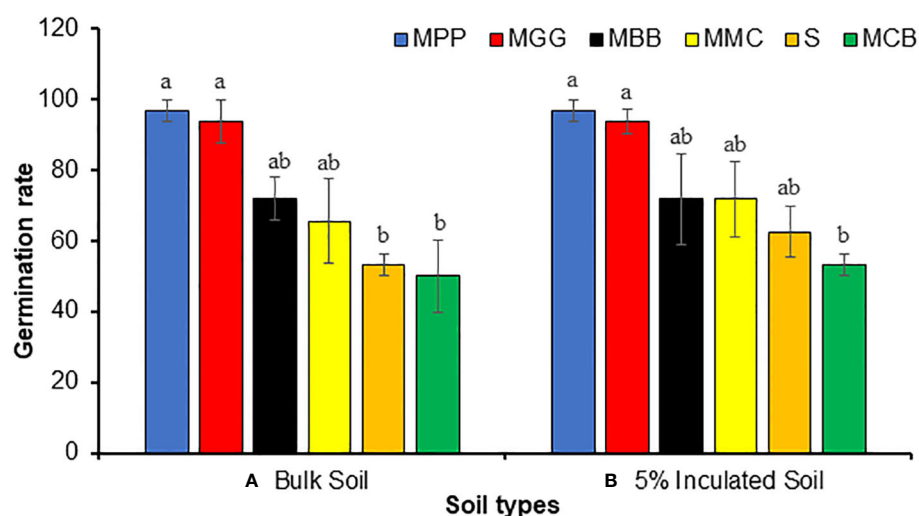


FIGURE 2

Mean (\pm SE) germination rate of SC Duma 43 maize seeds planted in soil conditioned by different cropping systems. (A) Bulk soils (BS) collected from smallholder farms with different cropping systems; MBB, maize black bean; MPP, maize pigeon pea; MCB, maize common bean; MGG, maize green gram intercropping; MMC, maize-monocultures; S, sterilized soil; (B) sterile soil inoculated with 5% soil conditioned by different BS cropping systems (5% IBS). Different letters above the bars indicate a significant difference ($P < 0.05$) between the means. $N = 384$ plants.

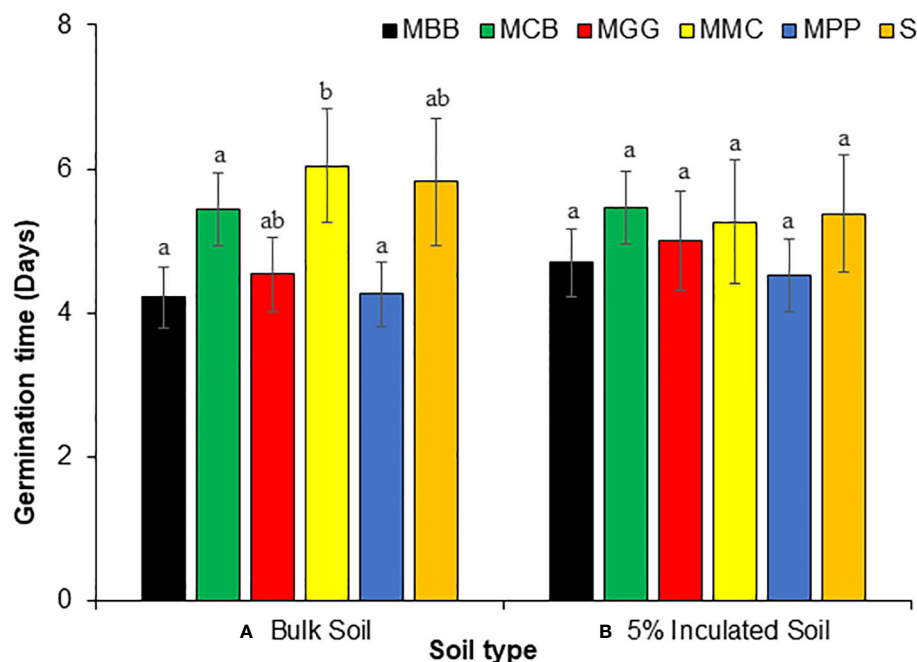


FIGURE 3

Germination time (in days) (Mean \pm SE) taken by SC Duma 43 maize seeds grown in soils conditioned by different cropping systems. (A) Bulk soils (BS) collected from smallholder farms with different cropping systems; MBB, maize black bean; MPP, maize pigeon pea; MCB, maize common bean; MGG, maize green gram intercropping; MMC, maize-monocultures; S, sterilized soil; (B), sterile soil inoculated with 5% soil conditioned by different BS cropping systems (5% IBS). Different letters above the bars indicate a significant difference ($P < 0.05$) between the means. $N = 384$ plants.

maize plants grown in MPP soil was statistically different from those grown in MMC, MBB and S ($P < 0.001$) soils. In W3, the diameter of maize plants grown in MBB soil was significantly wider compared to the diameters of plants grown in MMC, MGG and S soils ($P < 0.001$). We observed similar trends when the experiment was set in 5% IBS soil. The diameter of maize plants grown in 5% inoculated soil by MCB soil was significantly higher than plants grown in S soil ($P < 0.001$), but MCB was not significantly different from maize plant diameters grown in S soil inoculated with 5% of MGG, MBB, and MPP soils during W1 after germination ($P < 0.05$). During W2 and W3, there were no significant differences between maize plant diameters grown in all 5% IBS soils ($P < 0.05$, Figure 5).

3.3.3 Number of maize leaves

There were significant differences in the number of maize leaves of plants grown in BS and 5% IBS soils during W1, W2 and W3 after germination (ANOVA: $F_{5,18} = 33.77$, $P < 0.001$), (ANOVA: $F_{5,18} = 21.37$, $P < 0.001$) and (ANOVA: $F_{5,18} = 33.77$, $P < 0.001$), respectively (Figure 6). During W1 of BS soils, the number of leaves per plant was significantly higher for plants grown in MCB and MBB soils compared to the other soil types ($P < 0.001$). A similar trend was observed among the BS soils in W2 after germination where the number of leaves was significantly higher in MPP, MBB and MCB soil types. During W3, the number of leaves of maize plants grown in MPP soils was significantly different from MGG, MMC, MCB and S soils ($P < 0.001$). We observed similar trends with experiment with soils inoculated with 5% IBS, where the number of leaves was significantly higher in sterile soil inoculated

with 5% different soil types (MCB, MBB, and MPP) in W1, W2 and W3 respectively after germination ($P < 0.001$). However, the number of leaves was lowest in plants grown in S soil inoculated with 5% of MMC, MGG and S soils, regardless of the weeks after germination (Figure 6).

3.3.4 Leaf chlorophyll content

The leaf chlorophyll content of maize plants grown in BS and 5% IBS soils were significantly different in W1, W2 and W3 after germination (ANOVA: $F_{5,18} = 27.05$, $P < 0.001$), (ANOVA: $F_{5,18} = 19.64$, $P < 0.001$) and (ANOVA: $F_{5,18} = 47.55$, $P < 0.001$), respectively (Figure 7). Among soil conditioned by BS, the chlorophyll content throughout the experimental period was higher on the leaves of maize plants grown in MBB, MPP and MCB soil types ($P < 0.001$). However, chlorophyll content on the leaves from MGG, MMC and S soil types, were the lowest, during all the weeks after germination. Similar trend was observed for a plant grown in 5% IBS soils, where chlorophyll content was higher in sterile 5% soil (MBB, MPP, MCB and MGG soils) during the three weeks of the experiment. Indeed, chlorophyll content was lowest in MMC and S soil regardless of soil type (BS and 5% IBS) or duration of the plant after germination (W1, W2, and W3) (Figure 7).

3.3.5 Plant biomass

Shoot fresh (SFW) and dry weight (SDW) of maize plants grown in BS and sterilized soils were significantly different (ANOVA: $F_{5,18} = 33.77$, $P < 0.001$) and (ANOVA: $F_{5,18} = 21.37$, $P < 0.001$), respectively (Table 3). Plants grown in MPP and MCB

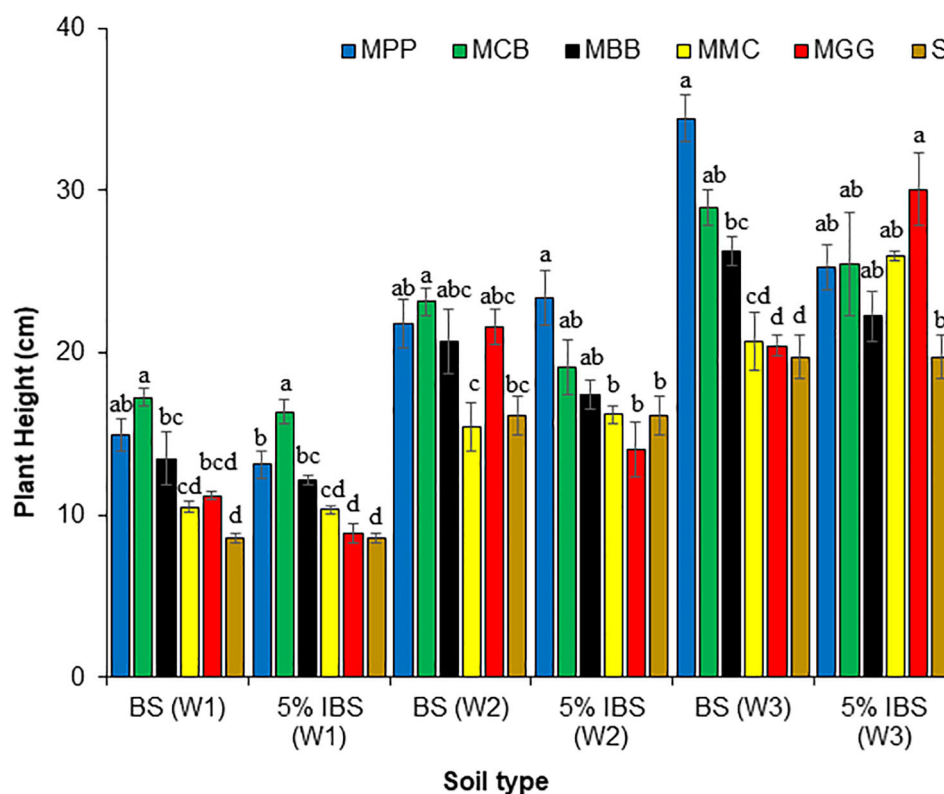


FIGURE 4

Maize plant height (cm) (Mean \pm SE) in first (W1), second (W2), and third (W3) weeks for plants grown in soils conditioned by different cropping systems. Bulk soils (BS) collected from smallholder farms with different cropping systems with MBB, maize black bean; MPP, maize pigeon pea; MCB, maize common bean; MGG, maize green gram intercropping; MMC, maize-monocultures; S, sterilized soil; (5% IBS), sterile soil inoculated with 5% soil conditioned by different cropping systems. Different letters above the bars in each week (W1, W2, W3) for each soil's conditioned cropping system type (BS and 5% IBS) indicate a significant difference ($P < 0.05$) between the treatments. $N = 384$ plants.

soils recorded the highest SFW and SDW when compared to MBB, MGG, MMC and S soils. Similarly, the highest root fresh (RFW) and dry weight (RDW) was recorded for plants grown in MPP and MCB soils, compared to other soil types (ANOVA: $F_{5,18} = 12.92$, $P < 0.001$) and (ANOVA: $F_{5,18} = 28.64$, $P < 0.001$). We observed similar trends when the above experiment was conducted in 5% IBS (MBB, MPP, MCB, MGG and MMC soils, Table 3).

3.3.6 Correlation between maize plant biomass and soil physico-chemical parameters

We found a negative correlation between pH in BS and plant biomass (SFW, RFD, SDW and RDW). This correlation was strong with a significant correlation coefficient (r) ranging between -0.65 and -0.77 for SFW, SDW and RDW ($P < 0.05$, Table 4). The SFW, SDW, RFW and RDW were significantly and positively correlated with EA in BS soils, with r ranging between 0.62 and 0.69. However, the correlation between plant biomass and P, K, Mg, N, OC, Fe and Zn in BS was weak and not significant. For maize grown in 5% IBS soils, a similar trend as above was observed where soil pH negatively correlated with plant biomass (Table 4). In addition, Na and Ca in 5% IBS soil had a moderate negative correlation with plant biomass, but the correlation was not significant (Table 4).

3.3.7 Correlation between maize plant growth and soil physico-chemical parameters

The pH in BS soils had a strong negative correlation with leaf number (NL), leaf chlorophyll content (CC), plant diameter (PD) and plant height (PH) ($P < 0.05$) (Table 5). However, other parameters of BS had a weak correlation with plant growth parameters except, EA which had a moderate positive and negative significant correlation with NL. Similar correlation trends were observed when maize plants grown in 5% IBS (Table 5). However, all correlation coefficients between plant growth parameters and 5% IBS soil parameters were not significant (Table 5).

3.4 Spodoptera frugiperda larval feeding

A comparison of leaf discs consumed area between different soil types (MMC, S, MBB, MPP, MCB and MGG) is illustrated in Figure 8. A significant difference was detected in leaf consumed area of constitutive and induced leaf disc plants grown in BS soils ($F_{5,18} = 19.58$, $P < 0.001$); ($F_{5,18} = 2.38$, $P < 0.001$, respectively) (Figure 8). For plants grown in BS soils, there was increased consumption in leaf disc of plant grown in MMC and S soil in

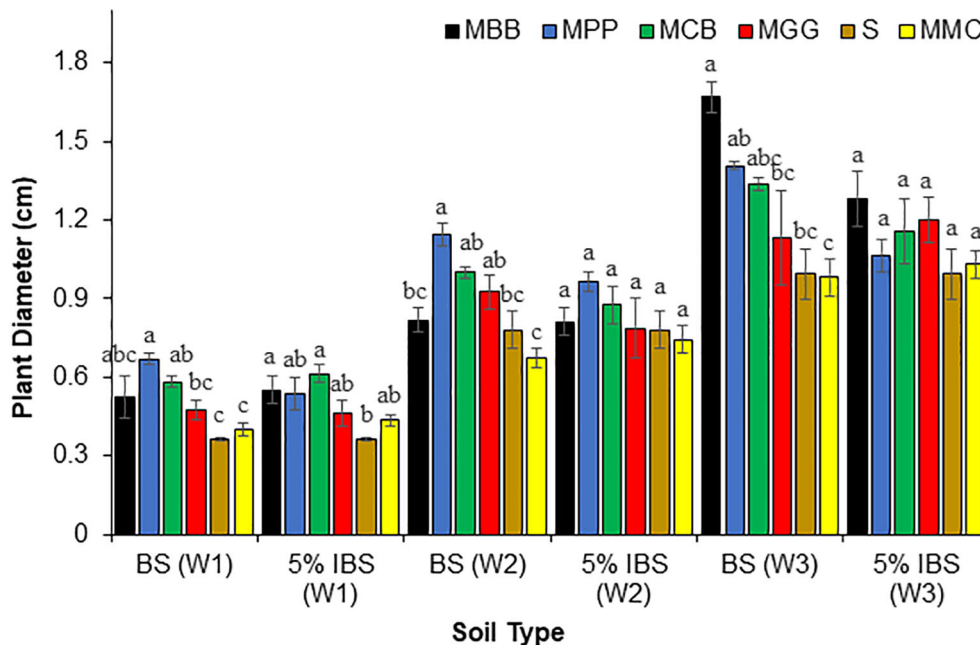


FIGURE 5

Diameter (cm) (Mean \pm SE) of maize plants in the first (W1), second (W2), and third (W3) weeks for plants grown in soil conditioned by different cropping systems. Bulk soil (BS) collected from smallholder farms with different cropping systems; MBB, maize black bean; MPP, maize pigeon pea; MCB, maize common bean; MGG, maize green gram intercropping; MMC, maize-monocultures; S, sterilized soil; S soil inoculated with 5% soil conditioned by different cropping systems (5% IBS). Different letters above the bars in each week (W1, W2, W3) for each soil conditioned type (BS and 5% IBS) indicates a significant difference ($P < 0.05$) between the treatment. N = 384 plants.

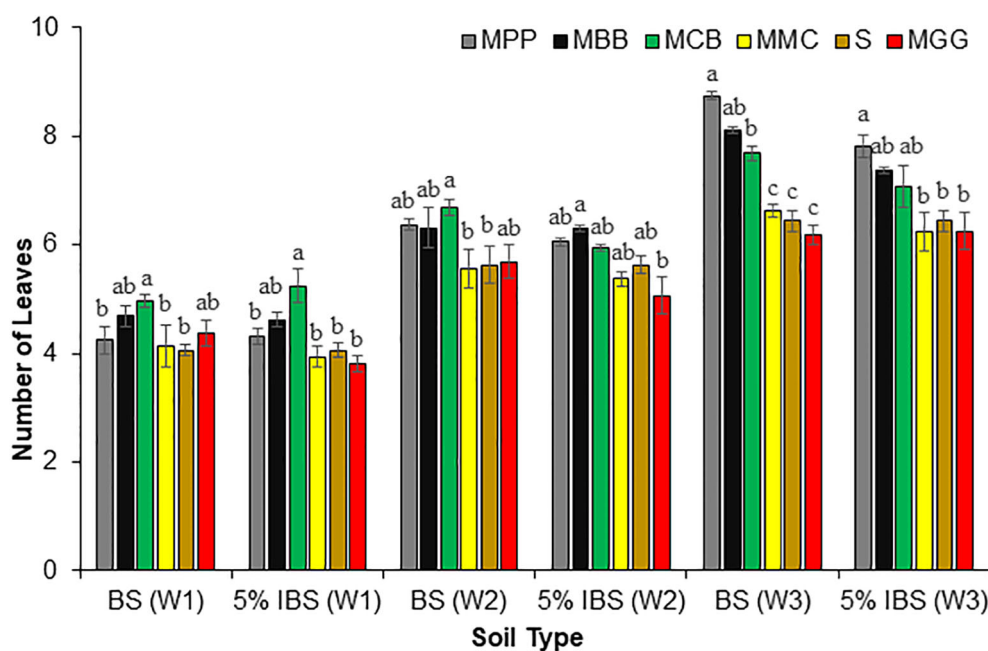


FIGURE 6

Number of maize plant leaves (Mean \pm SE) in first (W1), second (W2), and third (W3) weeks for plants grown in soil conditioned by different cropping systems. Bulk soil (BS) collected from smallholder farms with different cropping systems; MBB, maize black bean; MPP, maize pigeon pea; MCB, maize common bean; MGG, maize green gram intercropping; MMC, maize-monocultures; S, sterilized soil; S soil inoculated with 5% soil conditioned by different cropping systems (5% IBS). Different letters above the bars in each week (W1, W2, W3) for each soil conditioned type (BS and 5% IBS) indicate a significant difference ($P < 0.05$) between the treatments. N = 384 plants.

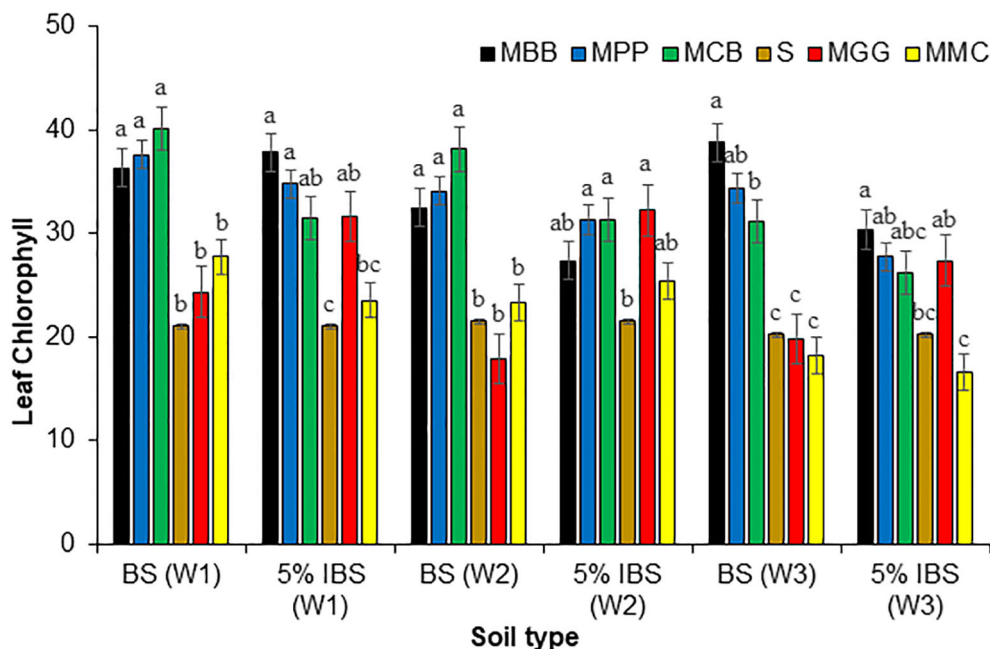


FIGURE 7

Leaf chlorophyll (Mean \pm SE) content of maize plant in first (W1), second (W2), and third (W3) weeks for plants grown in soil conditioned by different cropping systems. Bulk soils (BS) collected from smallholder farms with different cropping systems; MBB, maize black bean; MPP, maize pigeon pea; MCB, maize common bean; MGG, maize green gram intercropping; MMC, maize-monocultures; S, sterilized soil; S soil inoculated with 5% soil conditioned by different cropping systems (5% IBS). Different letters above the bars in each week (W1, W2, W3) for each soil conditioned type (BS and 5% IBS) indicate a significant difference ($P < 0.05$) between the treatments. $N = 384$ plants.

both constitutive and induced assay. Similar results were obtained when the experiment was conducted with a plant grown in 5% IBS. Consumption by FAW neonates was higher in leaf discs of plants grown in 5% IBS conditioned by MMC soil type (Figure 8).

Comparison between constitutive and induced feeding assay for each different cropping system in each soil type is presented in Figure 9. Overall, the disc consumed area by FAW neonates was significantly higher in constitutive feeding assay, compared to induced feeding assay irrespective of soils types (both BS and 5% IBS soils).

3.5 *Spodoptera frugiperda* larval growth and development

There were significant differences in FAW larval weight (FLW) when neonates were exposed for 15 days in the greenhouse on maize plants grown in BS soil types ($F_{5,18} = 14.58$, $P < 0.001$) (Table 6). Fall armyworm larval weight of MCB, MPP and MBB soil was less compared to those grown in MMC, S and MGG soils ($P < 0.001$). FAW larval lengths (FLL) were also significantly different across BS soils ($F_{5,18} = 16.12$, $P < 0.001$). The smallest FAW larvae length (FLL) was observed in MBB and MCB soils. Moreover, there were significant differences in FAW larval instar (FLI) across BS soils ($F_{5,18} = 27.36$, $P < 0.001$). The survival rates of FAW larvae number (FLN) on maize plants grown in BS soil types were significantly higher in S, MGG and MMC cropping systems

($F_{5,18} = 33.53$, $P < 0.001$) (Table 6). Similar results as above were obtained when the experiment was conducted in 5% IBS (Table 6).

4 Discussion

We showed here that maize-legume intercropping system's soil legacies positively impact seed germination, maize plant growth, soil physico-chemical properties, health, and FAW resistance by reducing larval feeding on maize plants constitutively and when feeding is induced. Thus, our findings bring to fore an additional pest-regulating effect of MLI systems on the widespread maize pest FAW which is novel to SSA. Notably, in this case, plant-soil feedback effects on maize-plant performance not only reduce FAW feeding but also mediate the enhancement of soil fertility, thus improving maize plant growth. Through this different larval feeding, MLI systems affect insect pest pressure. The findings here suggest a significant mechanism that involves feedback of maize-legume intercropping system-mediated pest resistance that is facilitated by soil conditioning.

There is a body of literature which indicates that prior vegetation contributes significantly to soil properties and communities, with a cascading effect on successive crops (Kaplan et al., 2018). The physico-chemical properties of soil can enhance plant growth by providing significant micronutrients (Agegnehu et al., 2016; Van der Putten et al., 2016; Pervaiz et al., 2020). We observed that the increased levels of certain soil micronutrients (pH,

TABLE 3 Maize plant biomass after three weeks of germination for plants grown in soil conditioned by different maize-edible legume intercropping, maize-monoculture cropping systems and sterilized soil.

Cropping systems	Soil types	Maize plant biomass (g)			
		Shoot fresh weight	Shoot dry weight	Root fresh weight	Root dry weight
MBB	BS	22.96 ± 1.02 ^{bc}	3.63 ± 0.16 ^b	16.45 ± 2.43 ^b	2.11 ± 0.31 ^{bc}
	5% IBS	17.56 ± 2.55 ^{bc}	2.50 ± 0.27 ^{ab}	8.71 ± 2.94 ^{bc}	0.74 ± 0.21 ^b
MPP	BS	42.99 ± 2.22 ^a	7.30 ± 0.92 ^a	27.56 ± 1.78 ^a	4.10 ± 0.41 ^a
	5% IBS	25.51 ± 1.49 ^{ab}	4.03 ± 0.38 ^a	24.88 ± 1.56 ^a	2.61 ± 0.18 ^a
MCB	BS	40.71 ± 2.75 ^a	7.24 ± 0.65 ^a	21.08 ± 1.08 ^{ab}	3.58 ± 0.11 ^a
	5% IBS	28.29 ± 0.65 ^a	3.80 ± 0.54 ^a	17.57 ± 2.68 ^{ab}	2.86 ± 0.39 ^a
MGG	BS	28.83 ± 2.91 ^b	4.34 ± 0.77 ^b	18.31 ± 2.51 ^b	2.30 ± 0.23 ^b
	5% IBS	24.11 ± 1.38 ^{ab}	3.14 ± 0.33 ^a	23.09 ± 1.66 ^a	2.20 ± 0.19 ^a
MMC	BS	13.43 ± 1.49 ^{cd}	1.90 ± 0.23 ^{bc}	13.35 ± 1.55 ^{bc}	1.11 ± 0.23 ^{cd}
	5% IBS	8.70 ± 1.34 ^d	1.30 ± 0.17 ^{bc}	4.33 ± 1.09 ^c	0.33 ± 0.05 ^b
S	BS	8.93 ± 3.21 ^d	0.84 ± 0.28 ^c	6.82 ± 1.99 ^c	0.52 ± 0.14 ^d
	5% IBS	8.93.21 ^{cd}	0.84 ± 0.28 ^c	6.82 ± 1.99 ^c	0.52 ± 0.14 ^b
F-value	BS	33.77	21.37	12.92	28.64
	5% IBS	18.88	14.28	17.7	27.55
Df	BS/5% IBS	5,18	5,18	5,18	5,18
P-value	BS	<0.001	<0.001	<0.001	<0.001
	5% IBS	<0.001	<0.001	<0.001	<0.001

MBB, maize black bean; MPP, maize pigeon pea; MCB, maize common bean; MGG, maize green gram intercropping; MMC, maize-monocultures; S, sterilized soil. Different letters across the columns indicate a significant difference ($P < 0.05$) according to Tukeys honest significance test (HSD). Significant effects are indicated in bold at $P < 0.05$.

TABLE 4 Correlation between maize plant biomass (plant grown in bulk conditioned soil) (in gram) and soil physico-chemical properties.

Soil parameters	Soil types	Plant growth biomass (g)			
		Shoot fresh weight	Shoot dry weight	Root fresh weight	Root dry weight
pH	BS	-0.71*	-0.72**	-0.65	-0.77**
	5% IBS	-0.63	-0.72**	-0.67*	-0.65
EC	BS	-0.41	-0.43	-0.23	-0.34
	5% IBS	-0.34	-0.34	-0.38	-0.27
P	BS	-0.26	-0.33	-0.31	-0.33
	5% IBS	-0.28	-0.44	-0.32	-0.25
K	BS	-0.24	-0.29	-0.19	-0.20
	5% IBS	-0.25	-0.23	-0.18	-0.19
Na	BS	-0.49	-0.54	-0.38	-0.51
	5% IBS	-0.54	-0.58	-0.58	-0.60
Ca	BS	-0.51	-0.46	-0.43	-0.49
	5% IBS	-0.59	-0.56	-0.52	-0.52
Mg	BS	-0.18	-0.23	-0.03	-0.18
	5% IBS	-0.17	-0.08	-0.09	-0.22

(Continued)

TABLE 4 Continued

Soil parameters	Soil types	Plant growth biomass (g)			
		Shoot fresh weight	Shoot dry weight	Root fresh weight	Root dry weight
EA	BS	0.62	0.66*	0.64*	0.69
	5% IBS	0.47	0.53	0.51	0.54
N	BS	0.10	-0.07	0.22	0.04
	5% IBS	0.09	0.24	0.26	0.11
OC	BS	0.13	NA	0.24	0.11
	5% IBS	0.12	0.31	0.33	0.16
Fe	BS	0.03	0.02	0.02	0.01
	5% IBS	-0.02	-0.79	0.18	0.05
Zn	BS	0.32	0.29	0.31	0.41
	5% IBS	0.32	0.50	0.47	0.52

Significance different: * <0.05 ; ** <0.01 ; *** <0.001 .

NA negligible, pH, potential of hydrogen; EC, electrical conductivity; P, phosphorus; K, potassium; Na, sodium; Ca, calcium; Mg, magnesium; EA, Exchangeable acidity; N, nitrogen; OC, organic carbon; Fe, iron; and Zn, zinc.

TABLE 5 Correlation between maize plant growth parameters in bulk soils conditioned and soil physico-chemical properties.

Soil parameters	Soil types	Plant growth parameters			
		Number of leaves	Plant diameter (cm)	Leaf chlorophyll content	Plant height (cm)
pH	BS	-0.69*	-0.63*	-0.69	-0.71*
	5% IBS	-0.63	-0.26	-0.61	-0.22
EC	BS	-0.19	-0.63	-0.20	-0.24
	5% IBS	-0.27	-0.11	-0.26	-0.19
P	BS	-0.37	-0.25	-0.29	-0.24
	5% IBS	-0.34	-0.37	-0.39	-0.28
K	BS	-0.16	-0.29	-0.19	-0.17
	5% IBS	-0.19	-0.23	-0.29	-0.11
Na	BS	-0.39	-0.17	-0.46	-0.48
	5% IBS	-0.44	-0.31	-0.55	-0.24
Ca	BS	-0.36	-0.48	-0.49	-0.37
	5% IBS	-0.35	-0.18	-0.48	-0.23
Mg	BS	-0.34	-0.37	-0.41	-0.45
	5% IBS	-0.29	0.08	-0.14	0.15
EA	BS	0.66*	-0.45	0.51	0.33**
	5% IBS	0.47	-0.09	0.22	-0.06
N	BS	0.04	0.33	-0.03	-0.05
	5% IBS	0.01	-0.06	-0.17	0.02
OC	BS	0.16	-0.05	0.11	0.12
	5% IBS	0.12	0.06	-0.04	0.03

(Continued)

TABLE 5 Continued

Soil parameters	Soil types	Plant growth parameters			
		Number of leaves	Plant diameter (cm)	Leaf chlorophyll content	Plant height (cm)
Fe	BS	-0.12	0.12	-0.06	0.2
	5% IBS	-0.15	-0.08	-0.15	-0.21
Zn	BS	0.37	0.26	0.19	0.09
	5% IBS	0.43	NA	0.13	0.18

Significance different: * <0.05 ; ** <0.01 ; *** <0.001 .

pH, potential of hydrogen; EC, electrical conductivity; P, phosphorus; K, potassium; Na, sodium; Ca, calcium; Mg, magnesium; EA, exchangeable acidity; N, nitrogen; OC, organic carbon; Fe, iron; and Zn, zinc.

N, OC, P and Zn) can significantly improve maize growth and biomass. Soil OC levels serve as a reliable indicator for soil, plant health and yield (Li et al., 2020; Ndayisaba et al., 2022). Our study found that soil conditioned by MLI systems had higher OC levels than soil conditioned by MMC and S systems. Furthermore, most rhizosphere samples from conditioned soil by MLI systems exhibited high levels of pH, N, K, and P, while soil conditioned by MMC and S systems had a pH below 5.5. Studies have shown that a pH below 5.5 can be detrimental to agroecosystems because it negatively affects plant growth and environment interactions (Wahome et al., 2023), indicating that the soil pH in MMC and S poses a significant threat to farming systems (Delgado and Gómez, 2016). This finding corresponds with the effect of multiple cropping systems on soil characteristics such as pH, OC, P, and N compared to monoculture (Chen et al., 2021; Chen et al., 2022). Other intercropping systems, like push-pull technology and various soil-preserving methods, have been proven to enhance soil function and fertility by increasing soil OC levels and enhancing the availability of N and P (Ndayisaba et al., 2020; Drinkwater et al., 2021; Ndayisaba et al., 2022). Our findings support the general

prediction that crop diversification can have a profound impact on many soil properties (Ndayisaba et al., 2020; Chen et al., 2021; Ndayisaba et al., 2022).

Eyheraguibel et al., 2008, reported that maize seeds germinate between four to ten days approximately. Hence, this germination period boosts maize plant growth and production (Wimalasekera, 2015). One of the best strategies to promote seed germination is to soak or imbibe the seeds in water for hours before planting (Ashraf & Foolad, 2005; Dezfuli et al., 2008; Ahmed et al., 2018). In our study we observed that the germination rate and time of SC Duma 43 maize seeds planted in soil conditioned by MLI systems germinated faster than those planted in soil conditioned by MMC and S soils.

Generally, there is a common consensus that intercropping systems are essential for maintaining optimum ecosystem functioning, thereby strengthening agricultural practices in environmental dynamics (Picasso et al., 2008; Harrison and Bardgett, 2010; Ndayisaba et al., 2022). However, disentangling the cropping system significantly affects biomass accumulation, and plant quality remains superficial. We expected that maize plants'

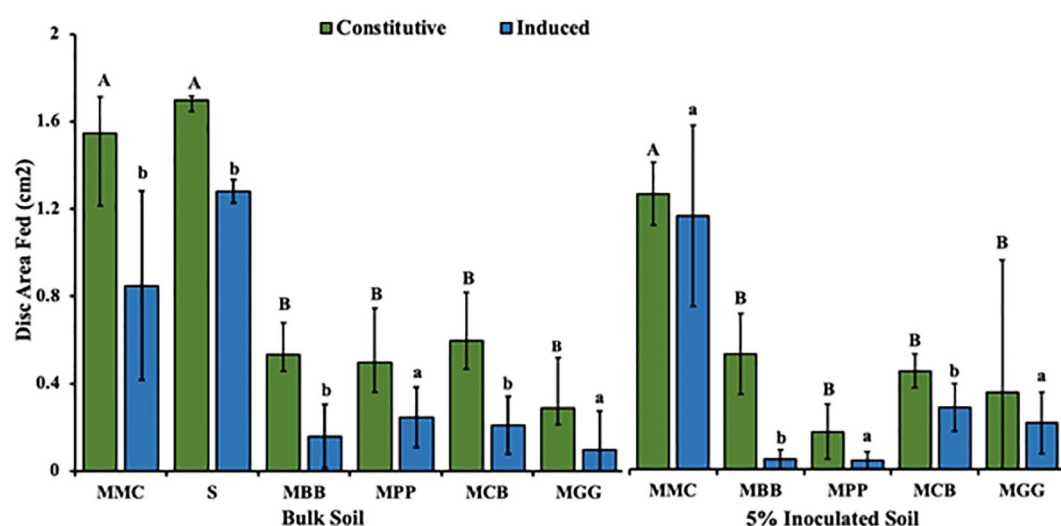


FIGURE 8

Mean (\pm SE) of maize leaf disc fed by *Spodoptera frugiperda* neonates. (BS) Bulk soil, soil conditioned by different cropping systems collected from smallholder farms; MBB, maize black bean; MPP, maize pigeon pea; MCB, maize common bean; MGG, maize green gram intercropping; MMC, maize-monocultures; S, sterilized soil; S soil inoculated with 5% soil conditioned by different cropping systems (5% IBS). Different capital letter above the error bars indicates significantly different across the different cropping systems soil conditioned types ($P < 0.05$).

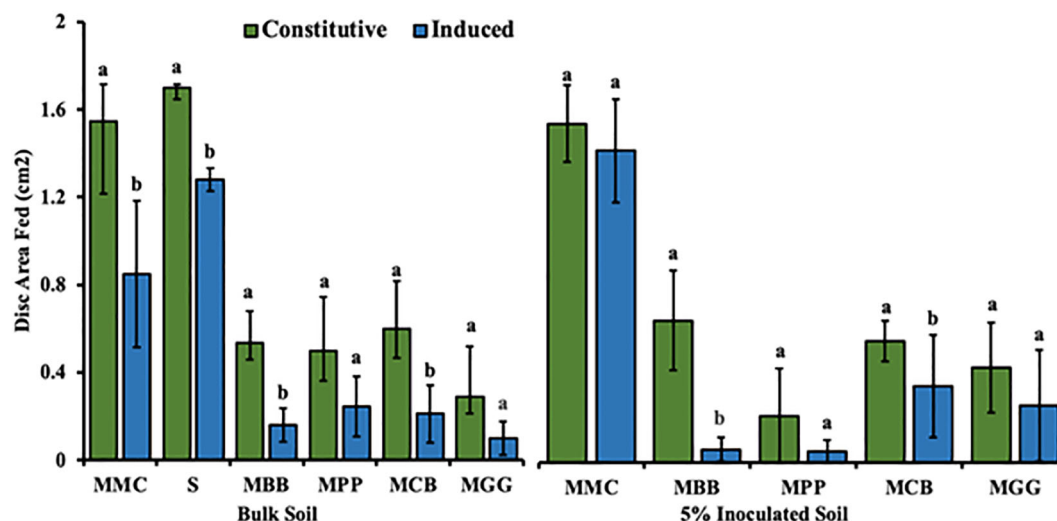


FIGURE 9

Comparison of leaf disc (Students T-test (Mean \pm SE)) fed by *Spodoptera frugiperda* neonates through constitutive against induced feeding. Bulk soil, soils conditioned by different cropping systems from smallholder farms; MBB, maize black bean; MPP, maize pigeon pea; MCB, maize common bean; MGG, maize green gram intercropping; MMC, maize-monocultures; S, sterilized soil; S soil inoculated with 5% soil conditioned by different cropping systems (5% IBS). Different capital letter above the error bars indicates significantly different across the different cropping systems soil conditioned types ($P < 0.05$).

TABLE 6 Effects of soil conditioned by different cropping systems on *Spodoptera frugiperda* larval growth and development on bulk soil.

Cropping systems	Soil types	Fall armyworm larvae weight (g)	Fall armyworm length (cm)	Fall armyworm larvae instar	Fall armyworm larvae number
MBB	BS	0.08 \pm 0.03 ^{bc}	1.26 \pm 0.12 ^{bc}	2.40 \pm 0.25 ^c	2.25 \pm 0.75 ^b
	5% IBS	0.08 \pm 0.0 ^c	1.47 \pm 0.19 ^{abc}	3.38 \pm 0.38 ^{bc}	32.53 \pm 4.91 ^c
MPP	BS	0.03 \pm 0.01 ^c	1.17 \pm 0.04 ^a	2.3 \pm 0.17 ^c	1.50 \pm 0.29 ^b
	5% IBS	0.04 \pm 0.01 ^{bc}	1.22 \pm 0.17 ^{bc}	2.68 \pm 0.19 ^c	43.49 \pm 3.69 ^{bc}
MCB	BS	0.04 \pm 0.01 ^c	1.27 \pm 0.15 ^{bc}	2.75 \pm 0.14 ^{bc}	2.25 \pm 0.25 ^b
	5% IBS	0.04 \pm 0.03 ^{bc}	1.18 \pm 0.13 ^c	2.59 \pm 0.16 ^c	42.12 \pm 1.67 ^{bc}
MGG	BS	0.12 \pm 0.01 ^{ab}	1.65 \pm 0.05 ^{ab}	3.15 \pm 0.15 ^b	6.00 \pm 0.41 ^a
	5% IBS	0.09 \pm 0.02 ^{ab}	1.88 \pm 0.22 ^{ab}	3.66 \pm 0.24 ^a	47.95 \pm 3.77 ^{ab}
S	BS	0.18 \pm 0.01 ^a	2.12 \pm 0.01 ^a	4.85 \pm 0.09 ^a	7.50 \pm 0.50 ^a
	5% IBS	0.16 \pm 0.01 ^a	2.05 \pm 0.018 ^a	4.26 \pm 0.09 ^{ab}	58.45 \pm 1.66 ^a
MMC	BS	0.17 \pm 0.001 ^a	2.02 \pm 0.04 ^a	4.40 \pm 0.14 ^a	6.25 \pm 0.25 ^a
	5% IBS	0.18 \pm 0.01 ^a	2.12 \pm 0.01 ^a	4.85 \pm 0.09 ^a	60.27 \pm 3.17 ^a
F-value	BS	14.58	16.12	27.36	33.53
	5% IBS	15.17	8.177	17.07	10.42
Df	BS/ 5% IBS	5,18	5,18	5,18	5,18
P-value	BS	<0.001	<0.001	<0.001	<0.001
	5% IBS	<<0.001	<0.001	<0.001	<0.001

MBB, maize black bean; MPP, maize pigeon pea; MCB, maize common bean; MGG, maize green gram; S, sterilized soil; MMC, maize-monoculture. Different letters across the columns indicate a significant difference ($P < 0.05$) according to Tukeys honest significance test (HSD). "Significant effects are indicated in bold at $P < 0.05$."

above-ground and below-ground biomasses were higher in soil conditioned by MLI systems compared to MMC and S measured in this current study. Different cropping systems positively impact soil fertility, increasing plant biomass accumulation and crop production (Wardle et al., 2003; Picasso et al., 2008). This study examined four plant parameters, including plant height, diameter, number of leaves, and leaf chlorophyll concentration, as growth parameters altered by soil conditioned by different cropping systems. These growth parameters in soil conditioned by MLI systems were higher compared to soil conditioned by MMC and S. These phenomena were partly linked with improved soil fertility of soil conditioned by different cropping systems allowing plants to grow faster and healthier compared to MMC and S conditioned soil. These findings concurred with recent studies where cropping systems, such as push-pull technology, mixed grassland, and forage, improved plant growth (Loreau et al., 2001; Sanderson et al., 2004; Harrison and Bardgett, 2010; Mutyambai et al., 2019). Therefore, farmers are encouraged to practice different intercropping systems to improve soil fertility, plant quality, and subsequent crop production. Interestingly, the enhanced growth of maize plants in soil conditioned by MLI systems is linked to a substantial rise in their expression of direct and indirect resistance by reducing larval feeding on maize plants.

Unravelling key mechanisms driving interactions between farming practices and anti-herbivory has remained challenging, as most studies focused on the effects of soil properties on plants' physical attributes (Harrison and Bardgett, 2010; Wang et al., 2021; Davidson-Lowe et al., 2021). Here, in addition to the impact of cropping systems on the physical properties of plants, we investigated how MLI systems play a role in deterring herbivory. Generally, plant growth and insect resistance are often negatively correlated (Stamp, 2003) with growth matching plant quality and metabolism, thus defense and growth trade-offs. Given that plants can protect themselves against herbivory through induce and constitutive defense mechanisms (Chuang et al., 2014; Acevedo et al., 2019), plants are unpalatable for herbivore feeding (Karban, 2011). Larval feeding assays in this study demonstrated significant differences in the consumed area by FAW neonates in soil conditioned by MLI systems compared to MMC and S systems. It showed that FAW consumed less leaf disc tissue from soil conditioned by MLI systems while consuming more in the MMC system and S soil plant. Feeding by FAW adversely affects subsequent herbivory (Mutua et al., 2022), thus the differences in larval feeding observed here could be attributed to the levels of defense in soil conditioned by MLI systems. However, defense genes and secondary metabolites in different cropping systems can be constitutively or induced by herbivory, and such mechanisms can provide a clear explanation of the observed phenomenon (Makgoba et al., 2021).

Infestation of FAW neonates on maize plants for 15 days revealed that their larval growth and development, instars, and survival differed significantly across the different soil conditions by MLI systems. In soil conditioned by MLI systems, the FAW larvae attained reduced growth indices in FAW larvae weight (FLW), FAW larvae length (FLN), FAW larvae instar; (FLI), and FAW larvae number (FLN) compared to MMC and S systems. Although the

underlying mechanisms of these observed behavioural responses were beyond the scope of this study, previous studies have shown changes in defense metabolite profiles and reduced larval feeding in maize plants grown in soil conditioned by maize-*Desmodium* intercropping (Mutyambai et al., 2019). Similar mechanisms could be behind the observed responses and are currently under investigation in a separate study. Reduction in survival and growth indices are indicators of poor insect performance and the negative effects of plant defense on insect herbivores (Karban, 2011; Gordy et al., 2015; Kaplan et al., 2018). Our findings demonstrated that the MLI systems negatively affected herbivory by affecting behavior and population dynamics throughout the colonization, establishment, and population development phases of infestation. It has been shown that changing cropping systems and diversifying agricultural practices can decrease the prevalence and harm caused by insect pests (Midega et al., 2018; De Groot et al., 2020; Guera et al., 2021; Mutyambai et al., 2022). This study has demonstrated that there is a reduction in FAW feeding in maize plants grown in soil conditioned by different MLI systems compared to soil conditioned by MMC and S, thereby reducing the damage and increasing maize plant biomass. We postulate that changes in the soil physico-chemical properties could have affected the morphological and chemistry of the maize plant resulting to the observed responses. Indeed, maize has been shown to exhibit changes in metabolism in favour of known defense metabolites like phenolics and benzoxazinoids when grown in soil conditioned by different cropping systems (Mutyambai et al., 2019). These findings, establish the resilience of MLI systems in its functionality against the invasive FAW pest. Therefore, it paves the way for integrating intercropping systems in IPM strategies to manage FAW infestation. As such, farmers need to avoid planting the same crops in successive years and adopt the use of intercropping systems and crop rotation, as shown in this study to reduce insect-pest build-up and improve soil health. Plant-soil feedback can govern both positive and negative feedback since they are intimately linked to agricultural systems. Utilizing the potential for plant resistance in the soil left over from previous farming practices might be crucial for long-term integrated insect pest control and production enhancement (Kaplan et al., 2018; Davidson-Lowe et al., 2021).

5 Conclusions

Our findings showed that maize-edible legume intercropping systems remarkably improved soil health by altering physico-chemical characteristics. Besides, we found significant differences in the impacts of various MLI systems on plant biomass. Maize-edible legume soil legacies enhanced maize's direct resistance to FAW damage. Soils from MLI systems significantly reduced FAW larval feeding and development on maize plants, therefore serving as controlling mechanisms. Though beyond the scope of the current study, underpinning mechanisms behind the observed responses in herbivore pest mainly plant changes in structure and chemistry should be the focus of the follow up study. These findings encourage the identification of optimal maize-legume combinations with overall positive interaction effects. Adopting such sustainable FAW control options through a farming system approach and

taking into account potential trade-offs requires an understanding of current smallholder agronomic management strategies and livelihood factors, as well as how these factors are likely to interact for optimal performance. There is need for future studies to examine the combined effects of intercropping, soil resources, secondary metabolites and genes, and soil microbes on fall armyworm feeding behaviour. Lastly, we need to encourage and train small-scale farmers to adopt these intercropping practices.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Ethics statement

The manuscript presents research on animals that do not require ethical approval for their study.

Author contributions

AJ: Data curation, Formal Analysis, Investigation, Methodology, Writing – original draft, Writing – review & editing. AY: Formal Analysis, Methodology, Writing – review & editing. FK: Data curation, Investigation, Methodology, Writing – review & editing. SS: Conceptualization, Investigation, Supervision, Writing – review & editing. DM: Conceptualization, Data curation, Formal Analysis, Investigation, Methodology, Writing – original draft, Writing – review & editing.

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Conflict of interest

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References

- Abro, Z., Kimathi, E., De Groote, H., Tefera, T., Sevgan, S., Niassy, S., et al. (2021). Socioeconomic and health impacts of fall armyworm in Ethiopia. *PLoS One* 16 (11), e0257736. doi: 10.1371/journal.pone.0257736
- Acevedo, F. E., Smith, P., Peiffer, M., Helms, A., Tooker, J., and Felton, G. W. (2019). Phytohormones in fall armyworm saliva modulate defense responses in plants. *J. Chem. Ecol.* 45, 598–609. doi: 10.1007/s10886-019-01079-z
- Agegneh, G., Nelson, P. N., and Bird, M. I. (2016). Crop yield, plant nutrient uptake and soil physico-chemical properties under organic soil amendments and nitrogen fertilization on Nitisols. *Soil Tillage Res.* 160, 1–13. doi: 10.1016/j.still.2016.02.003
- Ahmed, S., Raza, M. A., Zhou, T., Hussain, S., Khalid, M. H. B., Feng, L., et al. (2018). Responses of soybean dry matter production, phosphorus accumulation, and seed yield to sowing time under relay intercropping with maize. *Agronomy* 8 (12), 282. doi: 10.3390/agronomy8120282
- Ashraf, M., and Foolad, M. R. (2005). Pre-sowing seed treatment-A shotgun approach to improve germination, plant growth, and crop yield under saline and non-saline conditions. *Adv. Agron.* 88, 223–271. doi: 10.1016/S0065-2113(05)88006-X
- Beretta, A. N., Silberman, A. V., Paladino, L., Torres, D., Kassahun, D., Musselli, R., et al. (2014). Soil texture analyses using a hydrometer: modification of the Bouyoucos method. *Ciencia e investigación agraria: Rev. latinoamericana Cienc. la agricultura* 41 (2), 263–271. doi: 10.4067/S0718-16202014000200013
- Chen, J., Manevski, K., Lærke, P. E., and Jørgensen, U. (2022). Biomass yield, yield stability and soil carbon and nitrogen content under cropping systems destined for biorefineries. *Soil Tillage Res.* 221, 105397. doi: 10.1016/j.still.2022.105397
- Chen, S., Cade-Menun, B. J., Bainard, L. D., Luce, M. S., Hu, Y., and Chen, Q. (2021). The influence of long-term N and P fertilization on soil P forms and cycling in a wheat/fallow cropping system. *Geoderma* 404, 115274. doi: 10.1016/j.geoderma.2021.115274

- Chiriboga, M. X., Tamiru, A., Sobhy, I. S., Bruce, T. J., Midega, C. A., and Khan, Z. (2021). Evaluation of African maize cultivars for resistance to fall armyworm *Spodoptera frugiperda* (JE Smith) (Lepidoptera: Noctuidae) larvae. *Plants* 10 (2), 392. doi: 10.3390/plants10020392
- Chuang, W. P., Herde, M., Ray, S., Castano-Duque, L., Howe, G. A., and Luthe, D. S. (2014). Caterpillar attack triggers accumulation of the toxic maize protein RIP 2. *New Phytol.* 201 (3), 928–939. doi: 10.1111/nph.12581
- Davidson-Lowe, E., Ray, S., Murrell, E., Kaye, J., and Ali, J. G. (2021). Cover crop soil legacies alter phytochemistry and resistance to fall armyworm (Lepidoptera: Noctuidae) in maize. *Environ. Entomology* 50 (4), 958–967. doi: 10.1093/ee/nvab047
- De Groote, H., Kimenju, S. C., Munyua, B., Palmas, S., Kassie, M., and Bruce, A. (2020). Spread and impact of fall armyworm (*Spodoptera frugiperda* J.E. Smith) in maize production areas of Kenya. *Agriculture Ecosyst. Environ.* 292, 106804. doi: 10.1016/j.agee.2019.106804
- De Lange, E. S., Laplanche, D., Guo, H., Xu, W., Vlimant, M., Erb, M., et al. (2020). *Spodoptera frugiperda* caterpillars suppress herbivore-induced volatile emissions in maize. *J. Chem. Ecol.* 46, 344–360. doi: 10.1007/s10886-020-01153-x
- Delgado, A., and Gómez, J. A. (2016). “The soil physical, chemical and biological properties,” in *Principles of agronomy for sustainable agriculture*. Eds. F. Villalobos and E. Ferreres (Cham, Switzerland: Springer). doi: 10.1007/978-3-319-46116-8_2
- Dezfuli, P. M., Sharif-Zadeh, F., and Jan mohammadi, M. (2008). Influence of priming techniques on seed germination behavior of maize inbred lines (*Zea mays* L.). *ARN J. Agric. Biol. Sci.* 3 (3), 22–25.
- Drinkwater, L. E., Midega, C. A., Awuor, R., Nyagol, D., and Khan, Z. R. (2021). Perennial legume intercrops provide multiple belowground ecosystem services in smallholder farming systems. *Agriculture Ecosyst. Environ.* 320, 107566. doi: 10.1016/j.agee.2021.107566
- Ewel, J. J., Mazzarino, M. J., and Berish, C. W. (1991). Tropical soil fertility changes under monocultures and successional communities of different structure. *Ecol. Appl.* 1 (3), 289–302. doi: 10.2307/1941758
- Eyheraguibel, B., Silvestre, J., and Morard, P. (2008). Effects of humic substances derived from organic waste enrichment on the growth and mineral nutrition of maize. *Bioresource Technol.* 99 (10), 4206–4212. doi: 10.1016/j.biortech.2007.08.082
- FAO (2018) *Integrated management of the fall armyworm on maize: A guide for farmer field schools in africa*. Available at: <https://www.fao.org/documents/card/en/c/18741EN/>.
- Gordy, J. W., Leonard, B. R., Blouin, D., Davis, J. A., and Stout, M. J. (2015). Comparative effectiveness of potential elicitors of plant resistance against *Spodoptera frugiperda* (J. E. Smith) (Lepidoptera: Noctuidae) in four crop plants. *PLoS One* 10 (9), 1–14. doi: 10.1371/journal.pone.0136689
- Guera, O. G. M., Castrejón-Ayala, F., Robledo, N., Jiménez-Pérez, A., Sánchez-Rivera, G., Salazar-Marcial, L., et al. (2021). Effectiveness of push–pull systems to fall armyworm (*Spodoptera frugiperda*) management in maize crops in Morelos, Mexico. *Insects* 12 (4), 298. doi: 10.3390/insects12040298
- Hailu, G., Niassy, S., Zeyaur, K. R., Ochatum, N., and Subramanian, S. (2018). Maize–legume intercropping and push–pull for management of fall armyworm, stem borers, and striga in Uganda. *Agron. J.* 110 (6), 2513–2522. doi: 10.12134/agronj.2018.02.0110
- Harrison, K. A., and Bardgett, R. D. (2010). Influence of plant species and soil conditions on plant–soil feedback in mixed grassland communities. *J. Ecol.* 98 (2), 384–395. doi: 10.1111/j.1365-2745.2009.01614.x
- Jalli, M., Huusela, E., Jalli, H., Kauppi, K., Niemi, M., Himanen, S., et al. (2021). Effects of crop rotation on spring wheat yield and pest occurrence in different tillage systems: a multi-year experiment in Finnish growing conditions. *Front. Sustain. Food Syst.* 5. doi: 10.3389/fsufs.2021.647335
- Kansiime, M. K., Mugambi, L., Rwomushana, I., Nunda, W., Lamontagne-Godwin, J., Rware, H., et al. (2019). Farmer perception of fall armyworm (*Spodoptera frugiperda* J.E. Smith) and farm-level management practices in Zambia. *Pest Manage. Sci.* 75 (10), 2840–2850. doi: 10.1002/ps.5504
- Kaplan, I., Pineda, A., and Bezemer, M. (2018). Application and theory of plant–soil feedbacks on aboveground herbivores. In: T. Ohgushi, S. Wurst and S. N. Johnson, eds. *Aboveground-belowground community ecology*. Cham, Switzerland: Springer International, 319–343. doi: 10.1007/978-3-319-91614-9_14
- Karban, R. (2011). The ecology and evolution of induced resistance against herbivores. *Funct. Ecol.* 25 (2), 339–347. doi: 10.1111/j.1365-2435.2010.01789.x
- Kassie, M., Wossen, T., De Groote, H., Tefera, T., Sevgan, S., and Balew, S. (2020). Economic impacts of fall armyworm and its management strategies: evidence from southern Ethiopia. *Eur. Rev. Agric. Economics* 47 (4), 1473–1501. doi: 10.1093/erae/jbz048
- Khan, Z. R., Midega, C. A., Pittchar, J., Bruce, T. J., and Pickett, J. A. (2012). ‘Push–pull’ revisited: the process of successful deployment of a chemical ecology based pest management tool. *Biodiversity Insect pests: key Issues Sustain. Manage.*, 259–275. doi: 10.1002/9781118231838.ch16
- Koffi, D., Agboka, K., Adenka, D. K., Osa, M., Tounou, A. K., Anani Adjevi, M. K., et al. (2020). Maize infestation of fall armyworm (Lepidoptera: Noctuidae) within agro-ecological zones of togo and ghana in west africa 3 yr after its invasion. *Environ. Entomol.* 49 (3), 645–650. doi: 10.1093/ee/nvaa048
- Kumela, T., Simiyu, J., Sisay, B., Likhayo, P., Mendesil, E., Gohole, L., et al. (2019). Farmers’ knowledge, perceptions, and management practices of the new invasive pest, fall armyworm (*Spodoptera frugiperda*) in Ethiopia and Kenya. *Int. J. Pest Manag.* 65 (1), 1–9. doi: 10.1080/09670874.2017.1423129
- Li, J., Nie, M., Powell, J. R., Bissett, A., and Pendall, E. (2020). Soil physico-chemical properties are critical for predicting carbon storage and nutrient availability across Australia. *Environ. Res. Lett.* 15 (9), 094088. doi: 10.1088/1748-9326/ab9f7e
- Librán-Embida, F., Olagoke, A., and Martin, E. A. (2023). Combining milpa and push-pull technology for sustainable food production in smallholder agriculture. A review. *Agron. Sustain. Dev.* 43 (4), 45. doi: 10.1007/s13593-023-00896-7
- Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J. P., Hector, A., et al. (2001). Ecology: Biodiversity and ecosystem functioning: Current knowledge and future challenges. *Science* 294 (5543), 804–808. doi: 10.1126/science.1064088
- Makgoba, M. C., Tshikhudo, P. P., Nnzeru, L. R., and Makhado, R. A. (2021). Impact of fall armyworm (*Spodoptera frugiperda*) (J.E. Smith) on small-scale maize farmers and its control strategies in the Limpopo province, South Africa. *Jamba: J. Disaster Risk Stud.* 13 (1), 1016. doi: 10.4102/jamba.v13i1.1016
- Midega, C. A. O., Pittchar, J. O., Pickett, J. A., Hailu, G. W., and Khan, Z. R. (2018). A climate-adapted push–pull system effectively controls fall armyworm, *Spodoptera frugiperda* (J. E. Smith), in maize in East Africa. *Crop Prot.* 105, 10–15. doi: 10.1016/j.cropro.2017.11.003
- Montezano, D. G., Sosa-Gómez, D. R., Specht, A., Roque-Specht, V. F., Sousa-Silva, J. C., Paula-Moraes, S. D., et al. (2018). Host plants of *Spodoptera frugiperda* (Lepidoptera: Noctuidae) in the Americas. *Afr. entomology* 26 (2), 286–300. doi: 10.4001/003.026.0286
- Mutua, J. M., Mutiyambai, D. M., Asudi, G. O., Khamis, F., Niassy, S., Jalloh, A. A., et al. (2022). Competitive plant-mediated and intraguild predation interactions of the invasive *Spodoptera frugiperda* and resident stem borers *Busseola fusca* and *Chilo partellus* in maize cropping systems in Kenya. *Insects* 13 (9), 790. doi: 10.3390/insects13090790
- Mutyambai, D. M., Bass, E., Luttermoser, T., Poveda, K., Midega, C. A. O., Khan, Z. R., et al. (2019). More than “push” and “pull”? plant–soil feedbacks of maize companion cropping increase chemical plant defenses against herbivores. *Front. Ecol. Evol.* 7 (217). doi: 10.3389/fevo.2019.00217
- Mutyambai, D. M., Niassy, S., Calatayud, P.-A., and Subramanian, S. (2022). Agronomic factors influencing fall armyworm (*Spodoptera frugiperda*) infestation and damage and its co-occurrence with stem borers in maize cropping systems in Kenya. *Insects* 13 (3), 266. doi: 10.3390/insects13030266
- Ndayisaba, P. C., Kuyah, S., Midega, C. A. O., Mwangi, P. N., and Khan, Z. R. (2020). Intercropping *desmodium* and maize improves nitrogen and phosphorus availability and performance of maize in Kenya. *Field Crops Res.* 263, 108067. doi: 10.1016/j.fcr.2021.108067
- Ndayisaba, P. C., Kuyah, S., Midega, C. A. O., Mwangi, P. N., and Khan, Z. R. (2022). Push–pull technology improves carbon stocks in rainfed smallholder agriculture in Western Kenya. *Carbon Manage.* 13 (1), 127–141. doi: 10.1080/17583004.2022.2035823
- Okalebo, J. R., Gathua, K. W., and Woomer, P. L. (2002). Laboratory methods of soil and plant analysis: a working manual second edition. *Sacred Africa Nairobi* 21, 25–26.
- Onyango, F. O., and Ochieng’-Odero, J. P. R. (1994). Continuous rearing of the maize stem borer *Busseola fusca* on an artificial diet. *Entomologia Experimentalis Applicata* 73 (2), 139–144. doi: 10.1111/j.1570-7458.1994.tb01848.x
- Overton, K. M., Maino, J. L., Day, R., Umina, P. A., Bett, B., Carnovale, D., et al. (2021). Global crop impacts, yield losses and action thresholds for fall armyworm (*Spodoptera frugiperda*): A review. *Crop Prot.* 145, 105641. doi: 10.1016/j.cropro.2021.105641
- Pervaiz, Z. H., Iqbal, J., Zhang, Q., Chen, D., Wei, H., and Saleem, M. (2020). Continuous cropping alters multiple biotic and abiotic indicators of soil health. *Soil Syst.* 4 (4), 59. doi: 10.3390/soilsystems4040059
- Peter, E., Tamiru, A., Sevgan, S., Dubois, T., Kelemu, S., Kruger, K., et al. (2023). Companion crops alter olfactory responses of the fall armyworm (*Spodoptera frugiperda*) and its larval endoparasitoid (*Cotesia icipe*). *Chem. Biol. Technol. Agriculture*. 10, 61. doi: 10.1186/s40538-023-00415-6
- Picasso, V. D., Brummer, E. C., Liebman, M., Dixon, P. M., and Wilsey, B. J. (2008). Crop species diversity affects productivity and weed suppression in perennial polycultures under two management strategies. *Crop Sci.* 48 (1), 331–342. doi: 10.2135/cropsci2007.04.0225
- R Core Team (2018) *R: A Language and Environment for Statistical Computing*. Available at: <https://www.R-project.org/> (Accessed 4 January 2023).
- Sanderson, M. A., Skinner, R. H., Barker, D. J., Edwards, G. R., Tracy, B. F., and Wedin, D. A. (2004). Grazing land ecosystems. *Crop Sci.* 44 (4), 1132–1144. doi: 10.2135/cropsci2004.1132
- Schneider, C. A., Rasband, W. S., and Eliceiri, K. W. (2012). NIH image to imageJ: 25 years of image analysis. *Nat. Methods* 9 (7), 671–675. doi: 10.1038/nmeth.2089
- Sharma, S. B. (2022). Trend setting impacts of organic matter on soil physico-chemical properties in traditional vis-a-vis chemical-based amendment practices. *PLoS Sustainability Transformation* 1 (3), e0000007. doi: 10.1371/journal.pstr.0000007
- Sokame, B. M., Subramanian, S., Kilalo, D. C., Juma, G., and Calatayud, P. A. (2020). Larval dispersal of the invasive fall armyworm, *Spodoptera frugiperda*, the exotic

- stemborer *Chilo partellus*, and indigenous maize stemborers in Africa. *Entomologia Experimentalis Applicata* 168 (4), 322–331. doi: 10.1111/eea.12899
- Sparks, D. L., Page, A. L., Helmke, P. A., and Loeppert, R. H. (1996). *Methods of soil analysis, part 3, chemical methods*. (Madison, WI, USA: Soil Science Society of America Inc).
- Stamp, N. (2003). Out of the quagmire of plant defense hypotheses. *Q. Rev. Biol.* 78 (1), 23–55. doi: 10.1086/367580
- Stokstad, E. (2017). New crop pest takes Africa at lightning speed. *Science* 356 (6337), 473–474. doi: 10.1126/science.356.6337.473
- Tambo, J. A., Kansiime, M. K., Mugambi, I., Rwomushana, I., Kenis, M., Day, R. K., et al. (2020). Understanding smallholders' responses to fall armyworm (*Spodoptera frugiperda*) invasion: evidence from five African countries. *Sci. Total Environ.* 740, 140015. doi: 10.1016/j.scitotenv.2020.140015
- Van der Putten, W. H., Bradford, M. A., Pernilla Brinkman, E., van de Voorde, T. F., and Veen, G. F. (2016). Where, when and how plant–soil feedback matters in a changing world. *Funct. Ecol.* 30 (7), 1109–1121. doi: 10.1111/1365-2435.12657
- Van Dijk, M., Morley, T., Rau, M. L., and Saghai, Y. (2021). A meta-analysis of projected global food demand and population at risk of hunger for the period 2010–2050. *Nat. Food* 2 (7), 494–501. doi: 10.1038/s43016-021-00322-9
- Wahome, C. N., Maingi, J. M., Ombori, O., Njeru, E. M., Muthini, M., and Kimiti, J. M. (2023). Diversity and abundance of bacterial and fungal communities in rhizospheric soil from smallholder banana producing agroecosystems in Kenya. *Front. Horticulture* 2, 1061456. doi: 10.3389/fhort.2023.1061456
- Wang, G., Bei, S., Li, J., Bao, X., Zhang, J., Schultz, P. A., et al. (2021). Soil microbial legacy drives crop diversity advantage: Linking ecological plant–soil feedback with agricultural intercropping. *J. Appl. Ecol.* 58 (3), 496–506. doi: 10.1111/1365-2664.13802
- Wardle, D. A., Yeates, G. W., Williamson, W., and Bonner, K. I. (2003). The response of a three trophic level soil food web to the identity and diversity of plant species and functional groups. *Oikos* 102 (1), 45–56. doi: 10.1034/j.1600-0706.2003.12481.x
- Wimalasekera, R. (2015). Role of seed quality in improving crop yields. In *Crop production and global environmental issues*. Cham, Switzerland: Springer 2015, 153–168. doi: 10.1007/978-3-319-23162-4_6
- Yan, X. R., Wang, Z. Y., Feng, S. Q., Zhao, Z. H., and Li, Z. H. (2022). Impact of temperature change on the fall armyworm, *Spodoptera frugiperda* under global climate change. *Insects* 13 (11), 981. doi: 10.3390/insects13110981



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Legume–grass mixtures improve biological nitrogen fixation and nitrogen transfer by promoting nodulation and altering root conformation in different ecological regions of the Qinghai–Tibet Plateau

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Introduction: Biological nitrogen fixation (BNF) plays a crucial role in nitrogen utilization in agroecosystems. Functional characteristics of plants (grasses vs. legumes) affect BNF. However, little is still known about how ecological zones and cropping patterns affect legume nitrogen fixation. This study's objective was to assess the effects of different cropping systems on aboveground dry matter, interspecific relationships, nodulation characteristics, root conformation, soil physicochemistry, BNF, and nitrogen transfer in three ecological zones and determine the main factors affecting nitrogen derived from the atmosphere (%Ndfa) and nitrogen transferred (Ntransfer).

Methods: The ¹⁵N labeling method was applied. Oats (*Avena sativa* L.), forage peas (*Pisum sativum* L.), common vetch (*Vicia sativa* L.), and fava beans (*Vicia faba* L.) were grown in monocultures and mixtures (YS: oats and forage peas; YJ: oats and common vetch; YC: oats and fava beans) in three ecological regions (HZ: Huangshui Valley; GN: Sanjiangyuan District; MY: Qilian Mountains Basin) in a split-plot design.

Results: The results showed that mixing significantly promoted legume nodulation, optimized the configuration of the root system, increased aboveground dry matter, and enhanced nitrogen fixation in different ecological regions. The percentage of nitrogen derived from the atmosphere (%Ndfa) and percentage of nitrogen transferred (%Ntransfer) of legumes grown with different legume types and in different ecological zones were significantly different, but mixed cropping significantly increased the %Ndfa of the legumes. Factors affecting Ndfa included the cropping pattern, the ecological zone (R), the root nodule number, pH, ammonium-nitrogen, nitrate-nitrogen, microbial nitrogen mass (MBN), plant nitrogen content (N%), and aboveground dry biomass. Factors

affecting Ntransfer included R, temperature, altitude, root surface area, nitrogen-fixing enzyme activity, organic matter, total soil nitrogen, MBN, and N%.

Discussion: We concluded that mixed cropping is beneficial for BNF and that mixed cropping of legumes is a sustainable and effective forage management practice on the Tibetan Plateau.

KEYWORDS

cropping pattern, legume forage, symbiotic nitrogen fixation, rhizoma, root system, soil physicochemical, ecoregion

1 Introduction

Soil nitrogen is a key factor influencing crop growth in cropping systems (Mcgraw et al., 2008; Thilakarathna et al., 2012). Modern agriculture achieves high yields by using large amounts of inorganic nitrogen fertilizer and non-renewable resources, a practice that is now being questioned (Hatano et al., 2002). Studies have shown that such production practices negatively affect the nitrogen cycle and nitrogen balance (Moorhead et al., 2013), are costly in terms of public health and environmental safety (Tilman et al., 2002; Francis et al., 2016), and are a serious impediment to sustainable agricultural development (Song et al., 2020). Thus, agroecology emphasizes the design of cropping systems using ecosystem services and the sustainability of agricultural production systems (Clergue et al., 2005; Faucon et al., 2017; Olounlade et al., 2017). Biological nitrogen fixation (BNF) by legumes is an important way to replenish soil nitrogen (Yao et al., 2019). Mixed grass and legume forage cropping systems, which significantly optimize the cropping system by increasing plant diversity and improving soil health (Crème et al., 2015; Zhao et al., 2015), are a way to develop sustainable ecological agriculture (Luo et al., 2023).

Legume forage plays a crucial role in livestock development by providing a protein-rich source for grass-fed livestock and by improving soil quality by symbiotic nitrogen fixation with soil rhizobacteria (Rochon et al., 2010; Rispaill et al., 2015). Including legumes in mixed cropping systems increases crop yield (Tilman et al., 2002), improves forage quality (Tahir et al., 2023), increases resource utilization (Loreau et al., 2001) and soil quality (Wichern et al., 2007; Hinsinger et al., 2009), and maintains the nitrogen balance in the soil system (Ledgard and Steele, 1992), which reduce chemical inputs and environmental pollution (Hinsinger et al., 2009; Frankow-Lindberg and Dahlin, 2013). This is because prokaryotic microorganisms are catalyzed by nitrogen-fixing enzymes in mixed cropping systems of grasses and legumes, which reduces atmospheric nitrogen to plant-available nitrogen (ammonia), providing an additional source of nitrogen for the grasses (Fitter, 1994). At the same time, nitrogen is transferred from high-nitrogen-producing plants (Leguminosae) to low-nitrogen-producing plants (Gramineae) due to the reservoir

source relationship, and this mechanism of nitrogen transfer frees Gramineae from nitrogen limitations (Jalonen et al., 2009; Poffenbarger et al., 2015). In addition, due to interspecific competition among crops, competition for soil nitrogen from grass crops stimulates legumes to fix more nitrogen from the atmosphere for crop growth and development and also reduces the nitrogen deterrent effect of legumes (Mtambanengwe and Mapfumo, 1999; Peoples et al., 2015).

Plants use interspecific complementarity and interspecific competition to access soil resources and promote rhizomatous nitrogen fixation through positive plant–root–soil interactions (Duchene et al., 2017). Grass–bean mixed grasslands rely on the symbiotic relationship between rhizomes attached to legume root systems and soil nitrogen-fixing bacteria to fix nitrogen, which affects the soil carbon/nitrogen balance and improves nitrogen utilization and mineralization rates (Odu and Akerele, 1973; Sainju et al., 2003). In addition, mixes of grassland increase organic matter input and beneficial soil microorganisms to maintain the soil nutrient balance (Fornara and Tilman, 2008; Fornara et al., 2009; Deyn et al., 2011). However, promoting and suppressing nitrogen fixation efficiency depends on the pattern of competition for soil nitrogen between the root systems of grasses and legumes, which is a dynamic equilibrium (Haynes, 1980; Stern, 1993; Bouma et al., 2001). In addition, the efficiency of nitrogen transfer from legumes to grasses is related to root system secretions and the characteristics of the rhizomes. A high rate of BNF does not represent a high nitrogen transfer efficiency (Rui et al., 2022). BNF in legume crops is affected by biological factors (crop type and inter-root mycorrhizal flora) (Meng et al., 2015) and environmental factors (moisture, temperature, and soil nutrients) (Dollete et al., 2023). Therefore, it is necessary to analyze the nodulation characteristics, root phenotypic traits, soil physicochemical properties, and interspecific relationships of grasses planted in a mixed cropping system of grasses with different species of legumes in different ecological zones to assess BNF and nitrogen translocation capacity of leguminous pasture grasses and the productivity of grasses to improve livestock production.

The Tibetan Plateau, with an average elevation of 4,000 m above sea level (Li et al., 2022), is known as the “third pole”. The

unique geographical location and climatic conditions of the Tibetan Plateau create an alpine meadow ecosystem (Zhang et al., 2014). The alpine meadows of the Tibetan Plateau are the largest alpine grassland distribution area in the world, covering an area of approximately $2.27 \times 10^6 \text{ km}^2$ (Liu et al., 2023), which serves as an ecological barrier and an important source of forage (Hu et al., 2021). Livestock husbandry is the leading industry in this area (Wei et al., 2017). In recent years, human activities and climatic factors have led to grassland degradation, and bare vegetation has reduced the total amount of nitrogen fixation in natural grasslands and lowered the ecological service function (Harris, 2010; Ren et al., 2014; Xue et al., 2017). Therefore, optimizing cropping systems with ecologically sound forage is essential to restore the grasslands and develop animal husbandry practices (Dong et al., 2010). Introducing a mixed forage cropping system with legumes improves forage quality and replaces inorganic nitrogen fertilizer inputs (Tahir et al., 2022). Symbiotic nitrogen fixation accounts for 70% of the overall BNF in agroecosystems (Herridge et al., 2008), and leguminous crops provide $32\text{--}149 \text{ kg}\cdot\text{hm}^{-2}$ of nitrogen to growing crops through BNF, increasing the total amount of nitrogen in the nitrogen cycle of the agroecosystem (Mueller and Thorup-Kristensen, 2001). However, different cropping patterns and crop types have different effects on the rates of BNF and nitrogen transfer in leguminous crops. Climate is another key factor influencing BNF in leguminous crop fields (Liu et al., 2019). The altitude and climate of the different alpine ecological zones are different, and microclimates predominate. However, the forage production capacity, BNF, and nitrogen transfer rates of different species of leguminous forage mixed with oats in different ecological zones are unclear. Therefore, there is a need to study BNF and nitrogen transfer in legumes under various cropping patterns and in different ecological zones to increase forage production and to mitigate the negative impacts on the environment.

This study investigated the effects of different cropping patterns on aboveground dry matter, interspecific relationships, nodulation characteristics, root phenotypic traits, soil physicochemical properties, BNF, and nitrogen transfer in different alpine ecological zones. The results of this study will guide mixed forage cropping in the Qinghai region of China, which will reduce hazards to the environment and promote sustainable development of agroecosystems.

2 Materials and methods

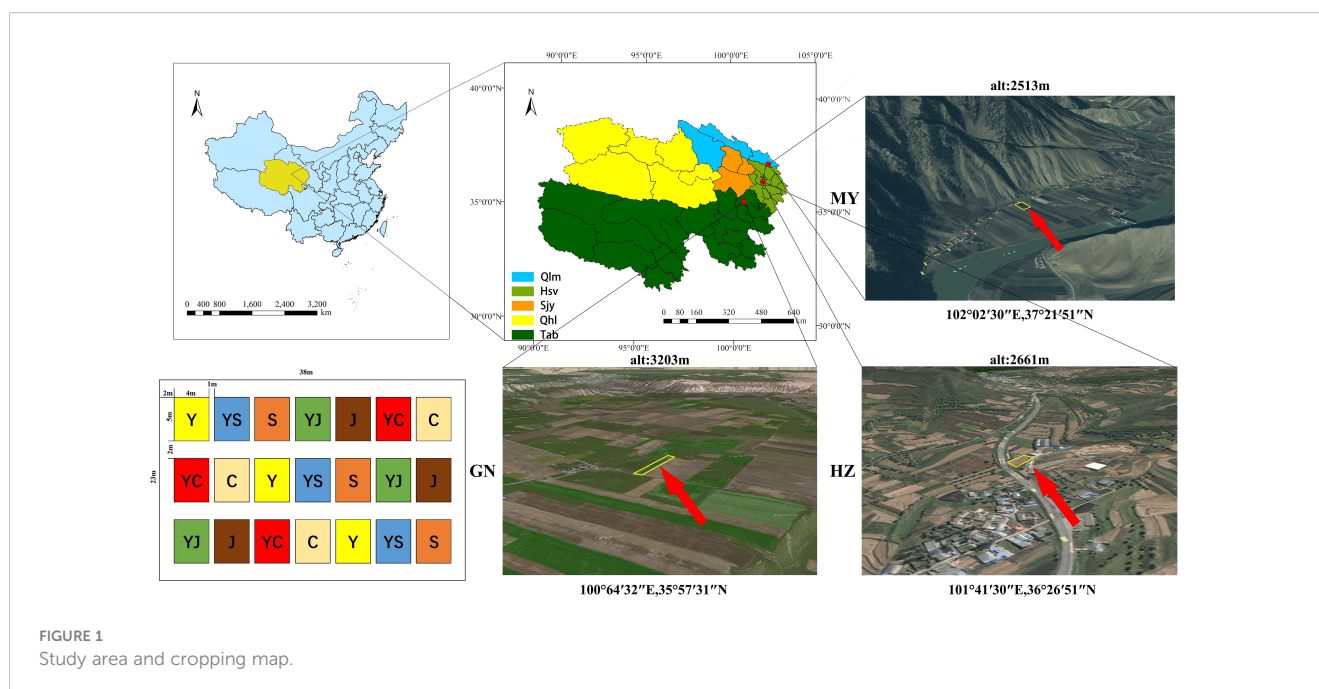
2.1 Study site

The experiment was conducted at a planting site in each of the three ecological zones in Qinghai Province, China (Figure 1):

1) HZ (Huangzhong County in Huangshui Valley): located in Garur Village, Garur Township, Tumen Pass Township. No irrigation was present, and it was a typical shallow mountain cultivation area. The area has a highland continental climate, with a short warm season and a long winter. The average annual temperature and precipitation are 5.3°C and 490 mm, respectively, and the soil type is calcium chestnut soil, with oats and legume forage as the previous crops in 2022.

2) GN (Guinan County, Sanjiangyuan District): located in Tashiu Village, Tashiu Township. No irrigation was present; it has a highland continental climate with long winters and short summers, and a cold and humid climate. The average annual temperature and precipitation are 3.2°C and 403 mm, respectively, and the soil type is clay loam, with oats and legume pasture as the previous crops in 2022.

3) MY (Menyuan County, Qilian Mountain Basin): located in Xianmi Township, Xianmi Township. No irrigation was present, and the plateau continental climate is typical of the cold, warm,



and humid climate of the plateau. It has a snowy and windy spring, a cool and rainy summer, a mild and short autumn, and a cold and long winter. The average annual temperature and precipitation are 4.2°C and 518 mm, respectively, and the soil type is black calcium soil, with oats and legume pasture as the previous crops in 2022. The soil physicochemical properties are shown in Table 1.

2.2 Experimental design

The trial employed a randomized block group design, comprised of seven treatments. Each treatment had three replication plots, for a total of 21 plots. The plot was the experimental unit with an area of 20 m² (5 m × 4 m). The seeds were provided by the Qinghai Academy of Animal Husbandry and Veterinary Science (Table 2).

The HZ, MY, and GN test sites were sown based on the local climate and sowing dates. A total of 75 kg·ha⁻¹ of urea (46% N) and 150 kg·ha⁻¹ of calcium superphosphate (12% P₂O₅) were applied as basal fertilizers before sowing. The sowing amounts are listed in Table 1 (Xiang, 2022). Field management practices were consistent with other crops. Weeds were controlled twice manually.

TABLE 1 Soil physicochemical properties before sowing in the study area.

Soil indicators	Ecological region basic information		
	HZ	GN	MY
SOM (g·kg ⁻¹)	34.4	34.47	50.1
TN(g·kg ⁻¹)	2.2	2.4	3.1
TP(g·kg ⁻¹)	2.5	1.7	2
TK (g·kg ⁻¹)	24.4	18.1	21.1
AN(mg·kg ⁻¹)	120	105	124
APs(mg·kg ⁻¹)	27.6	20.3	26.1
AK (mg·kg ⁻¹)	290	244	258

TABLE 2 Planting systems and sowing rates.

Treatments	Crop and species	Seeding quantity/g·m ⁻²
Y	Oat (Qinghai 444)	22.50
S	Forage peas (Qingjian No. 1)	11.16
J	Common vetch (Ximu No. 324)	12.00
C	Fava bean (Qingcan No. 22)	16.53
Y/S	Oat/Forage peas	13.50/4.45
Y/J	Oat/Common vetch	15.8/6.61
Y/C	Oat/Fava bean	13.50/6.61

To assess nitrogen fixation by the plants in the mixed sowing plots, the plants were ¹⁵N-marked 2 weeks before harvest using the following method. A 0.25-m² marking strip of uniform length was selected for each single and mixed sowing plot. A perforated plastic sheet was used to identify the marking holes in the area using pieces of wire 15 cm apart, for a total of 28 marking holes. Then, a syringe with a 3-cm needle was attached, and 2 ml of a 0.08 g/m double-labeled ¹⁵NH₄¹⁵NO₃ (99%, supplied by the Shanghai Institute of Isotope Chemistry) solution was aspirated into the labeled holes for ¹⁵N labeling. After completion, four thick wires of 50 cm length were used to fix the position of the ¹⁵N markers for later sampling.

2.3 Sampling and measurements

Sampling was conducted at the oat milky stage, when the quality of the oat forage was optimum. Due to the different climates and altitudes at the three sites, the growing and harvesting periods of the crops were different. The HZ, MY, and GN sites were harvested, and soil samples were collected on 21 August, 28 August, and 9 September 2023, respectively.

2.3.1 Sampling

Whole plot yield measurements were used. The plants were mowed to the ground and weighed fresh (for mixed crops, the two crops were weighed separately). A 1,000 g sample of fresh forage was collected from each plot and brought back to the laboratory in air-dried bags, air-dried at 105°C for 30 min, then air-dried at 65°C to constant weight. The samples were ground in a ball mill to determine ¹⁵N abundance and total nitrogen (TN) content. The soil was carefully excavated with a spade to a depth of 35 cm along the root system, and the large pieces of soil were shaken off. Five intact legume and oat root systems were selected from each plot, the number of root tumors were counted, and the fresh weight of the root tumors were weighed. The root tumors and root systems were also brought to the laboratory for determination of nitrogen-fixing enzyme activity and scan of root structure. Then, the roots were dried at 105°C for 30 min and baked in an oven at 80°C to constant weight to determine root biomass. Soil samples were collected from the 0–10-cm layer using the five-point method. A portion of fresh soil was used to determine microbial biomass nitrogen (MBN) content, while the rest of the soil samples were dried naturally and sieved to determine other soil indicators.

2.3.2 Measurements

Plant ¹⁵N abundance was determined by mass spectrometry (DELTAplus XP, Thermo Finnigan Electron Corp., Mannheim, Germany). Root tumor nitrogen fixing enzyme activity was determined by acetylene reduction method, and nitrogen fixing enzyme activity was expressed as acetylene concentration (U/g) (Khan et al., 1994). TN in the plants and soil was determined by the Kjeldahl method. Soil organic matter (SOM) was determined by redox titration with K₂Cr₂O₇. Soil ammonium nitrogen (ANN) was determined by the indophenol blue colorimetric method. Soil nitrate–nitrogen (NN) was assessed using the phenol disulfonic acid colorimetric method. Soil MBN was determined by the chloroform

fumigation leaching method (Joergensen, 1996). Soil pH was determined by potentiometry (water–soil ratio, 2.5:1). Roots were scanned using a dual-light source color scanner (Sinocrystal ScanMaker i800 plus, Hangzhou Wanshen Inspection Science and Technology Co.)

2.4 Data collection and analysis

The land equivalent ratio (LER) of a mixed cropping system was calculated using Equation 1:

$$\text{LER} = \frac{L_{YI-Y}}{L_Y} + \frac{Y_{YI-I}}{L_I} \quad (1)$$

where Y represents oats and I represent legume forage. I = S, forage pea; I = J, common vetch; and I = C, fava bean. L_{YI-Y} and L_{YI-I} represent the aboveground dry matter mass of mixed-crop oats and the legume forage, respectively, and L_Y and L_I represent the aboveground dry matter mass of monocrop oats and the monocrop legume forage, respectively. When $\text{LER} > 1$, the aboveground dry matter mass of the mixed crop was more advantageous than that of the monoculture and *vice versa*.

Relative abundance of ^{15}N ($\delta^{15}\text{N}$) was calculated using Equation 2 (Yoneyama et al., 1986):

$$\delta^{15}\text{N}(\%) = \frac{\text{Atom } ^{15}\text{N}(\text{sample}) - \text{Atom } ^{15}\text{N}(\text{standard})}{\text{Atom } ^{15}\text{N}(\text{standard})} \times 1000 \quad (2)$$

where $\delta^{15}\text{N}$ is the relative abundance of ^{15}N in the sample; atom ^{15}N (sample) is the atomic abundance of ^{15}N in the sample; and atom ^{15}N (standard) is the atmospheric abundance of ^{15}N (0.3663%), which is used as the standard isotope abundance of ^{15}N .

The $\%N_{\text{dfa}}$ of the legume forage and the proportion of N transferred from the legume forage to oats ($\%N_{\text{transfer}}$) were calculated using Equation 3 and Equation 4, respectively (Herridge et al., 1995; Neumann et al., 2009):

$$\%N_{\text{dfa}} = \left(1 - \frac{A\%E_{YI-I}}{A\%E_Y} \right) \% \quad (3)$$

$$\%N_{\text{transfer}} = \left(1 - \frac{A\%E_{YI-Y}}{A\%E_I} \right) \% \quad (4)$$

where $A\%E_Y$ and $A\%E_I$ are the $\delta^{15}\text{N}$ of the single-crop oat and legume forage, respectively. $A\%E_{YI-Y}$ and $A\%E_{YI-I}$ are the $\delta^{15}\text{N}$ of mixed-crop oat and legume forage, respectively.

2.5 Statistical analysis

Differences in aboveground biomass, nitrogen yield, rhizome traits, root morphology, soil physicochemical properties, BNF, and nitrogen transfer between cropping systems and the cropping areas were tested using two-way analysis of variance followed by Duncan's multiple comparison test using SPSS 20.0 software (SPSS Inc., Chicago, IL, USA). A p -value < 0.05 was considered significant. Graphs were plotted using Origin 2021 software (OriginLab, Northampton, MA, USA). Relationships between the soil's physical properties, rhizome

characteristics, climatic factors, and aboveground biomass and variables, such as BNF and nitrogen transfer, were determined by calculating Mantle's test and Pearson's correlation coefficients. Statistical analyses and mapping were performed using R 4.3.1 for Windows and the "ggplot2", "linkET", "dplyr", and "piecewiseSEM" software packages (The R Foundation for Statistical Computing, Vienna, Austria).

3 Results

3.1 Effect of the cropping pattern on aboveground dry biomass and nitrogen accumulation in the different ecological zones

The cropping pattern, ecological zone, and their interactions had extremely significant ($p < 0.01$) or significant ($p < 0.05$) effects on aboveground dry biomass (Table 3). In all ecological zones, total aboveground dry biomass was significantly higher in all three mixed cropping patterns than in the oat monoculture, and the differences among the three mixed cropping combinations were significant in the same ecological zone. In addition, total aboveground dry matter in the three ecological zones was in the order of MY ($770.79 \text{ g}\cdot\text{m}^{-2}$) $>$ HZ ($750.04 \text{ g}\cdot\text{m}^{-2}$) $>$ GN ($740.90 \text{ g}\cdot\text{m}^{-2}$), and tended to decrease with increasing altitude. The LER of mixed cropping was > 1 in all ecological zones, indicating that the total aboveground biomass of the mixed cropping system was more advantageous than that of oat monoculture. The cropping pattern with the highest aboveground total dry matter in each ecological zone was in the order of HZ (YS), GN (YC), and MY (YS), which were 16.37%, 17.07%, and 12.16% higher than that of oat monoculture, respectively.

The cropping pattern, ecological zone, and their interaction had significant ($p < 0.05$) effects on nitrogen content and nitrogen accumulation of the aboveground biomass (Figure 2). In all ecological zones, nitrogen content and nitrogen accumulation of oats grown in mixes were significantly higher than that of oats grown in monoculture, and the differences were significant among the ecological zones. In addition, no significant differences in nitrogen content or nitrogen accumulation of oats grown in the three mixes were detected in the same ecoregion (Figures 2A, B). In all ecological zones, nitrogen content and nitrogen accumulation of the mixed legume forages were significantly higher than their respective counterparts in monoculture (Figures 2C, D). N content and total N accumulation were greater for mixed cropping than oat monocropping (Figures 2E, F).

3.2 Effect of the ecological zone planting pattern on root tumor characteristics of legume forage grasses

The cropping pattern, ecological zone, and their interactions had significant ($p < 0.05$) effects on root tumor number, root tumor fresh weight, and nitrogen-fixing enzyme activity (Figure 3). In all ecological zones, the number of tumors of mixed legume forages was significantly greater than that of the corresponding monocultures, and the highest number of tumors was found in the YS cropping pattern, followed by

TABLE 3 Aboveground dry biomass and the land equivalent ratio (LER) of monoculture and mixed cropping in the three ecological zones.

Ecological region	Cropping system	Oats (g·m ⁻²)	Leguminosae (g·m ⁻²)	Total (g·m ⁻²)	LER
HZ	Y	746.75 ± 8.99Ba	–	746.75 ± 8.99Bc	–
	YS	693.61 ± 5.83Bb	175.17 ± 8.78Ac	868.78 ± 14.45Ba	1.19
	S	–	658.3 ± 16.18Aab	658.3 ± 16.18Ade	–
	YJ	710.27 ± 7.14Ab	114.72 ± 11.56Abd	824.99 ± 8.48Bb	1.13
	J	–	644.08 ± 32.59Ab	644.08 ± 32.59Ae	–
	YC	674.1 ± 15.2Bc	145.19 ± 8.65Bc	819.28 ± 23.17Bb	1.11
	C	–	688.12 ± 11.55Aa	688.12 ± 11.55Ad	–
GN	Y	724.55 ± 12.25Ba	–	724.55 ± 12.25Bc	–
	YS	677.47 ± 2.53Cb	155.47 ± 6.68Bc	832.94 ± 4.19Ca	1.18
	S	–	629.68 ± 4.74Bb	629.68 ± 4.74Be	–
	YJ	693.27 ± 5.81Bb	110.48 ± 2.55Bd	803.75 ± 7.52Cb	1.13
	J	–	618.83 ± 18.3Ab	618.83 ± 18.3Ae	–
	YC	685.36 ± 20.23ABb	162.9 ± 5.98Ac	848.26 ± 24.07Aa	1.18
	C	–	686.09 ± 12.61Aa	686.09 ± 12.61Ad	–
MY	Y	799.9 ± 12.25Aa	–	799.9 ± 12.25Ac	–
	YS	726.06 ± 6.56Ab	171.03 ± 4.33Ac	897.09 ± 6.2Aa	1.16
	S	–	675.3 ± 13.97Aa	675.3 ± 13.97Ad	–
	YJ	713.2 ± 7.79Abc	131.31 ± 9.63Ad	844.51 ± 3.2Ab	1.10
	J	–	630.91 ± 19.55Ab	630.91 ± 19.55Ae	–
	YC	707.41 ± 3.34Ac	153.82 ± 4.3Abc	861.23 ± 5.07Ab	1.11
	C	–	686.61 ± 14.96Aa	686.61 ± 14.96Ad	–
Ecological region (R)		**	*	**	–
Cropping system (P)		**	**	**	–
R * P		**	*	**	–

Lowercase letters indicate significant differences in the same ecological region for different planting patterns, while uppercase letters represent significant differences in the same planting patterns for different ecological regions ($p < 0.05$). The same as below. * and ** represent significant differences at the 0.05 and 0.01 levels, respectively.

YJ). The number of rhizomes on C monocultures was significantly lower than that of the other cropping patterns (Figure 3A). Significant differences in tumor weight and nitrogen-fixing enzyme activity were observed in all ecological zones among the three legumes, and all showed the pattern of broad bean > forage pea > arrow end pea. In addition, in the same ecoregion, the tumor weight and nitrogen-fixing enzyme activity of the legume forage grasses grown in monoculture were significantly lower than those of the corresponding mixes, except for the root tumor weights of the C and YC cropping patterns of GN (Figures 3B, C).

3.3 Effect of the ecological region planting pattern on forage root characteristics

Root dry weight and root volume were significantly higher in monoculture than those in the corresponding mixtures in all

ecological zones and were highest in fava beans, followed by oats. Moreover, root dry weight and root volume were significantly higher in MY than in HZ or GN (Figures 4A–D, M–P). In contrast, in all ecological zones, root length and root surface area were significantly higher in the mixed cropping than in the corresponding monoculture cropping pattern. Root length and surface area revealed an overall pattern of broad bean > oat > arrow end pea > pea. In addition, root length and root surface area among regions were in the order of MY > HZ > GN (except broad bean) (Figures 4E–I, G, K, L). Root diameter was significantly higher in monoculture oats than in the mixed cropping pattern, and the YC cropping pattern had the smallest root diameter in oats. The root diameter of oats between regions followed the same trend as root dry weight and root volume, both indicating that MY was significantly higher than HZ and GN (Figure 4Q). Additionally, the root diameters of all three legume mixtures were lower than those of the corresponding monocultures, suggesting that root

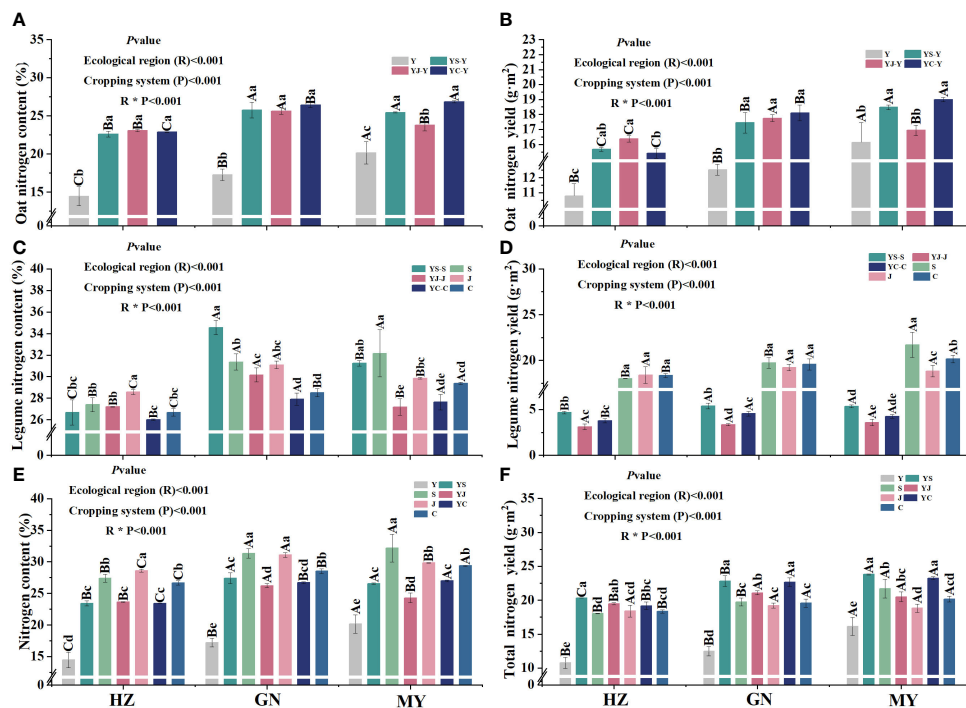


FIGURE 2

Nitrogen content and accumulation in aboveground dry matter of oats and legumes in the different ecological zones under different cropping patterns. (A) Nitrogen content of aboveground dry matter in oats. (B) Nitrogen accumulation of aboveground dry matter in oats. (C) Nitrogen content of aboveground dry matter in pulses. (D) Nitrogen accumulation of aboveground dry matter in pulses. (E) Nitrogen content of aboveground dry matter in cropping systems. (F) Nitrogen accumulation of aboveground dry matter in cropping systems.

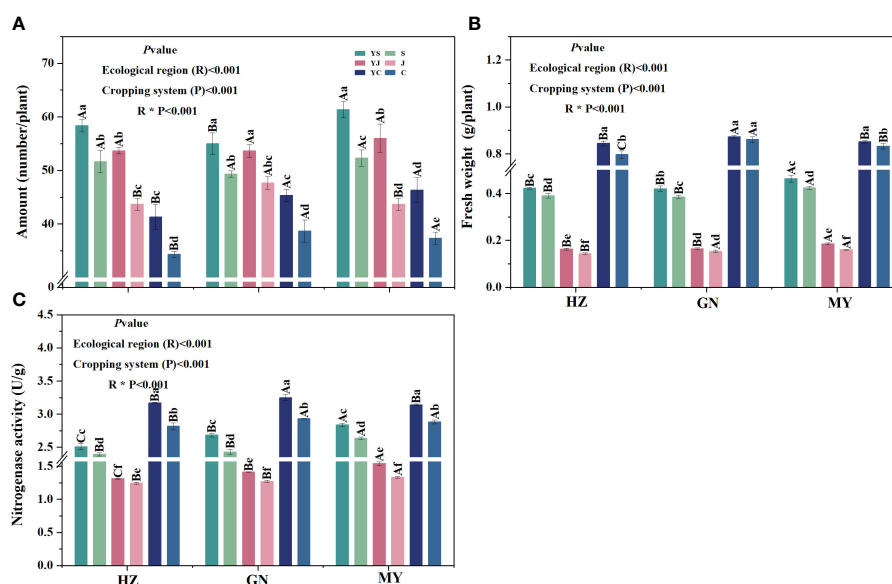


FIGURE 3

Characteristics of legume root tumors under different cropping patterns in different ecological zones. (A) Root tumor number. (B) Root tumor fresh weight. (C) Nitrogen-fixing enzyme activity.

growth of the legumes was inhibited in the mixed cropping system (Figures 4R–T). In addition, the root systems of crops in different ecological zones varied considerably, e.g., the root surface area of broad bean was largest in the GN region, whereas the root surface

area of arrow end pea and oat was largest in the MY region (Figures 4I, K, L).

The planting pattern, the ecological zone, and their interactions had significant or extremely significant ($p < 0.05$) effects on root dry

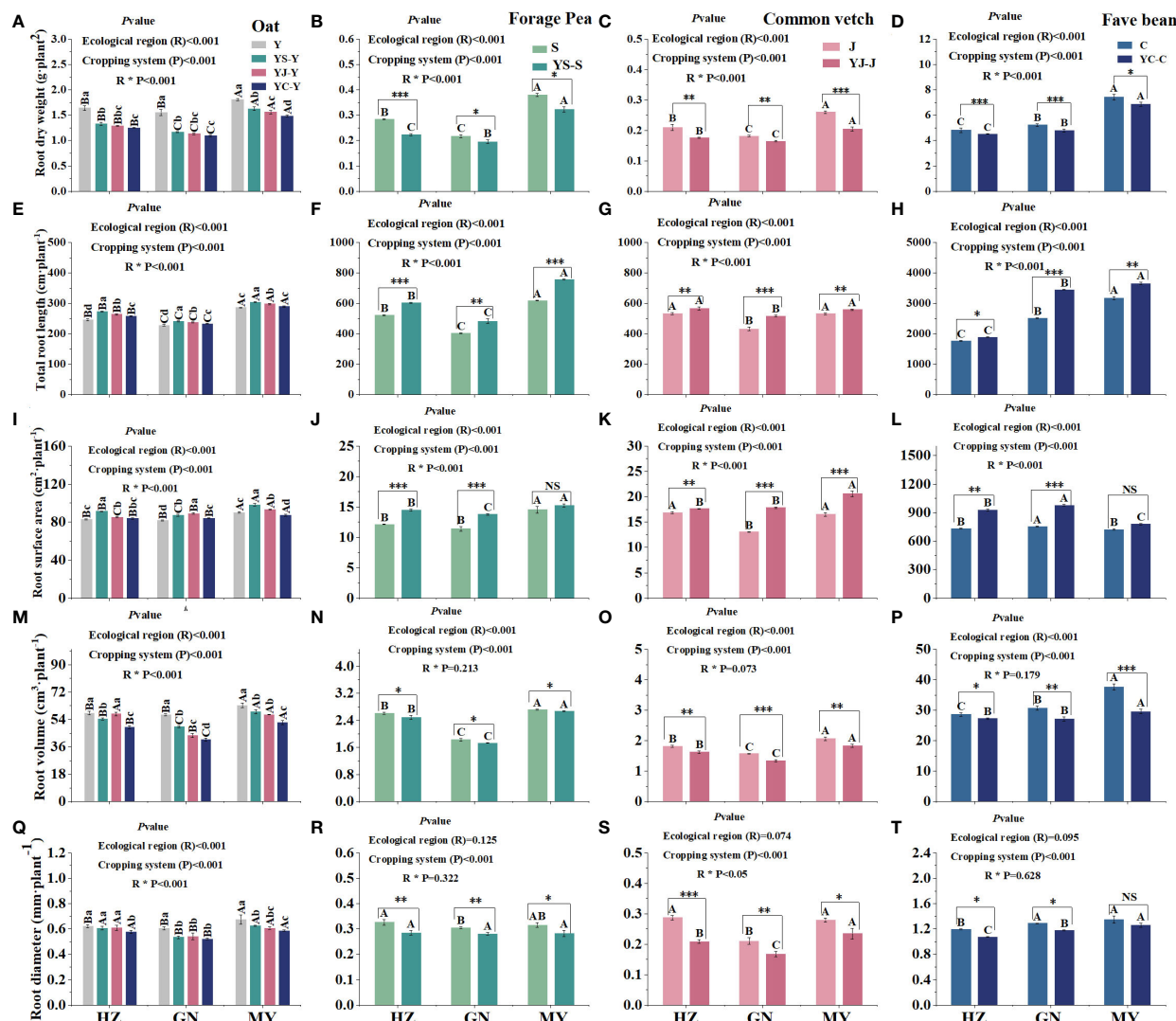


FIGURE 4

Root system characteristics of monoculture and mixed cropping of oat and legume forages in different ecological zones. (A–D) Root dry weight. (E–H) Total root length. (I–L) Root area. (M–P) Root volume. (Q–T) Root diameter. Lowercase letters indicate significant differences in the same ecological regions for different planting patterns, whereas uppercase letters represent significant differences in the same planting patterns for different ecological regions ($p < 0.05$). * denotes a significant difference between legume monoculture and mixture in the same ecoregion, * denotes $0.01 < p < 0.05$, ** denotes $p < 0.01$, and *** denotes $p < 0.001$.

weight, root length, root area, root volume, and root diameter for all crops, except for the ecological zones, which had no significant effect on the diameter of the three types of beans, or the volume of the three types of beans as a result of the interaction between the planting pattern and the ecological zone (Figure 4).

3.4 Effect of cropping pattern on soil physicochemical properties in different ecological zones

The planting pattern, ecological zone, and their interaction had extremely significant ($p < 0.01$) effects on pH, SOM, TN, NN, ANN, and MBN, except for the interaction between the planting pattern and the ecological zone, which did not have a significant effect on NN (Figure 5).

Mixed cropping tended to reduce soil pH compared to oat monoculture, but the difference was not significant (Figure 5A). Monocropping and mixed cropping of the three legumes increased SOM compared to oat monocropping in all ecological zones, with legume monocropping the highest, followed by mixing. SOM of the mixed crops was significantly higher than that of oat monoculture. In addition, the cropping patterns with the highest SOM in each ecological zone were HZ (YS), GN (YC), and HZ (YS) (Figure 5B). Soil TN content revealed that mixed cropping was significantly higher than oat monocropping and the corresponding bean monocropping in all ecological zones, but the differences among the three mixed cropping patterns were not significant. In addition, TN content increased the most in MY compared to pre-sowing (Figure 5C). Soil ANN and NN contents in all ecological zones were in the order of bean monoculture >

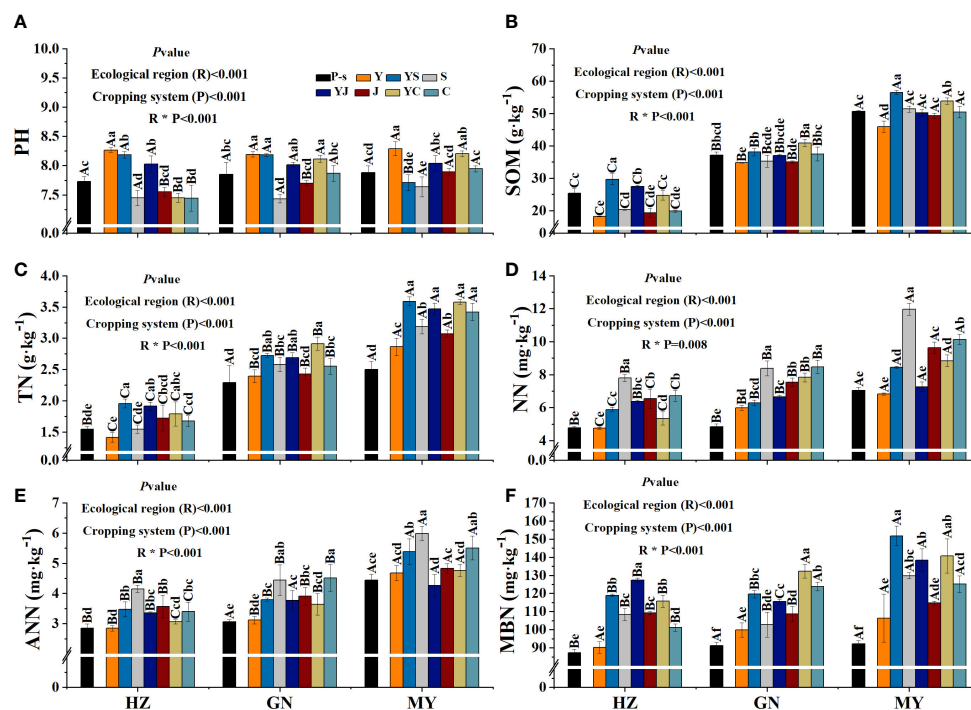


FIGURE 5

Soil physicochemical properties of the cropping patterns in different ecological regions. (A) Soil pH. (B) Soil organic matter. (C) Soil total nitrogen. (D) Soil amonium nitrogen. (E) Soil nitrate nitrogen. (F) Soil microbial nitrogen.

mixed > oat monoculture, and soil ANN and NN were significantly greater than the pre-sowing soils, except for oat monoculture (Figures 5D, E). Soil MNB content increased in all ecological zones and all cropping patterns compared to pre-sowing. Among them, oat monoculture was the lowest, and the mixed cropping pattern was the highest. The cropping patterns with the highest MBN in each ecological zone were HZ (YJ), GN (YC), and HZ (YS) (Figure 5F). MY had significantly higher SOM, TN, NN, ANN, and MBN contents than HZ or GN (Figure 5).

3.5 Effect of the cropping pattern on biological nitrogen fixation efficiency and the amount of nitrogen fixation by the legume forage in different ecological zones

The cropping pattern, ecological zone, and their interactions had extremely significant ($p < 0.01$) effects on the rate of BNF, the amount of BNF, and the contribution of nitrogen fixation of legume forages (Figure 6).

Nitrogen fixation efficiency of legumes was significantly higher in mixed cropping than in the corresponding monocropping in all ecological zones and was significantly different among the three legumes in the same area. Among them, the cropping patterns with the highest nitrogen fixation rates in all ecological zones were HZ (YS), GN (YC), and MY (YJ), respectively. In addition, the nitrogen fixation rate of common vetch was significantly different among the three ecological zones (Figure 6A). BNF and the contributions of BNF were higher in all ecological intervals for monocultures than the

corresponding mixtures and differed significantly among the three legumes in the same region. All three legumes in MY had higher biological nitrogen fixation rates than those in HZ and GN (except GN, fava bean). In addition, YS was the cropping pattern with the highest amount of BNF and contributions of BNF from mixed cropping in all regions. The amount of BNF and contribution of nitrogen fixation by fava bean were significantly higher in GN than in other regions (Figures 6B, C).

3.6 Effects of mixed sowing in the different ecological zones on the proportion of nitrogen transfer and the amount of nitrogen transferred by leguminous forage grasses

The cropping pattern, ecological zone, and their interactions had extremely significant ($p < 0.01$) effects on the N-transfer rate and the amount of N-transferred by legume forages (Figure 7). The nitrogen transfer rates of all three legume species were significantly different in the same region, and the order of the nitrogen transfer rates in the regions was HZ (YS > YC > YJ), MY (YC > YS > YJ), and GN (YC > YS > YJ), respectively. In addition, YS, YJ, and YC had the highest nitrogen fixation rates among the regions HZ, GN, and MY, respectively (Figure 7A). Significant differences in N transfer were detected among the three legume species in the same region, except for YC and YJ (HZ), and YS and YJ (MY), which were not significantly different. The order of the nitrogen transfer rate among regions was HZ (YS > YC > YJ), MY (YC > YS > YJ), and GN (YS > YJ > YC), respectively. Moreover, the

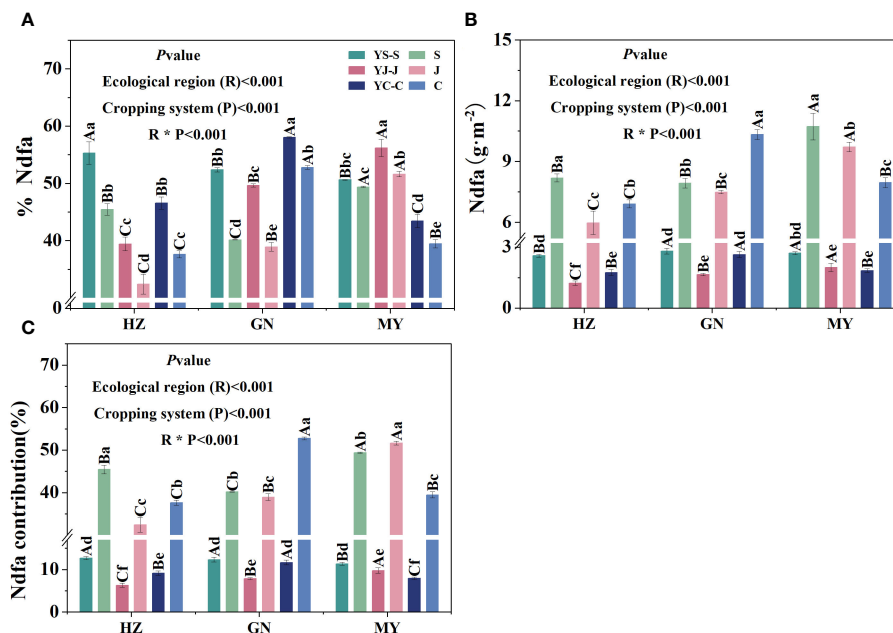


FIGURE 6

Biological nitrogen fixation characteristics of legume forage under the different cropping patterns in different ecological zones. (A) Biological nitrogen fixation rate. (B) Biological nitrogen fixation. (C) Biological nitrogen fixation contribution.

highest nitrogen fixation rates were found in the regions of YS, YJ, and YC: GN, MY, and GN, respectively (Figure 7B).

3.7 Factors affecting biological nitrogen fixation and nitrogen transfer

Pearson's correlation analysis showed that the ecological region (R) was significantly and positively correlated ($p < 0.05$) with N%, MBN, ANN, NN, TN, SOM, NN, pH, PPT, and T. The planting pattern (P) was significantly and positively correlated ($p < 0.05$) with NW, NRN,

RD, RV, RS, RL, and RW. Mantel's test showed that NRN, pH, NN, ANN, MBN, N%, and DM were significantly and positively correlated ($p < 0.05$) with BNF contribution (NC). P, R, NRN, pH, MBN, NN, ANN, N%, and DM were significantly and positively correlated ($p < 0.05$) with the amount of nitrogen fixation (Ndfa). P, R, T, NRN, NRN, pH, SOM, TN, NN, N%, and DM were significantly and positively correlated ($p < 0.05$) with BNF (%Ndfa). R, T, ALS, RS, GN, SOM, TN, MBN, and N% were significantly and positively correlated ($p < 0.05$) with nitrogen transfer (Ntransfer) (Figure 8).

R and NG had a significant direct positive effect on Ndfa, and P had a significant direct negative effect on Ndfa. The cropping pattern

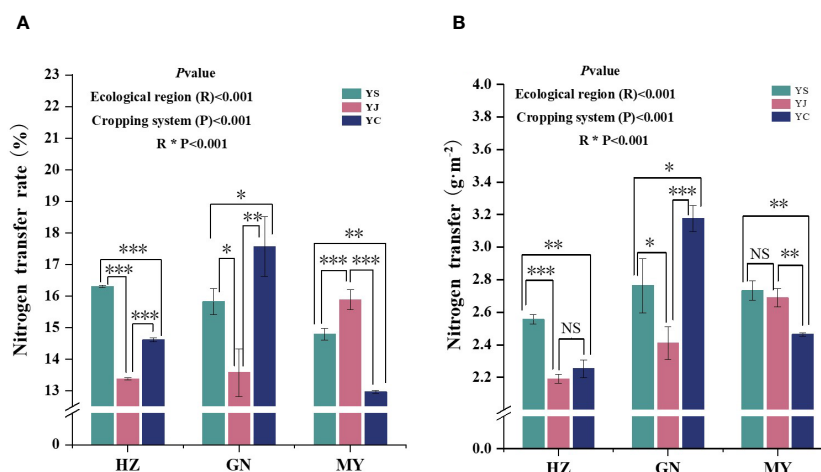


FIGURE 7

Nitrogen transfer from legume forage to oats under different cropping patterns in different ecological zones. (A) Nitrogen transfer rate. (B) Nitrogen transfer. * denotes $0.01 < p < 0.05$, ** denotes $p < 0.01$, *** denotes $p < 0.001$, and ns denotes $p > 0.05$.

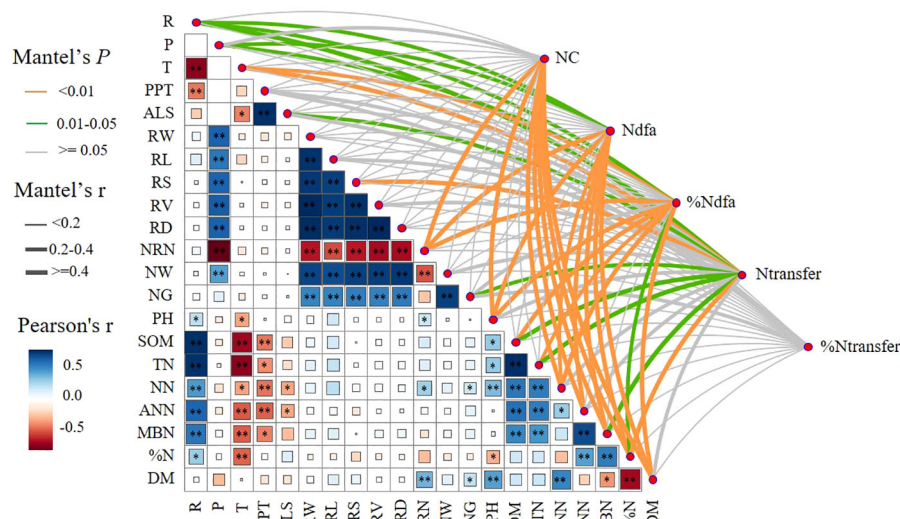


FIGURE 8

Correlation between biological nitrogen fixation, nitrogen transfer, and biological nitrogen fixation contribution with cropping system (P), ecological region (R), climatic factors, root tumor characteristics, soil physical properties, and aboveground dry biomass. T, temperature; ALS, altitude; RW, root dry weight; RL, root length; RS, root surface area; RV, heel volume; RD, root diameter; NRN, number of rhizomes; NW, fresh weight of rhizomes; NG, nitrogen-fixing enzyme activity; DM, aboveground dry biomass. The width of the Mantel edge corresponds to the Mantel r value, and the color of the edge indicates statistical significance. * denotes $0.01 < p < 0.05$, ** denotes $p < 0.01$.

indirectly affected Ndfa by increasing NG, and the ecological zone indirectly increased Ntransfer by significantly increasing NN. P had a significant direct negative effect on Ntransfer, and NW had a significant direct positive effect on Ntransfer. R increased NT by increasing N%, and P increased Ntransfer by increasing RS (Figure 9).

4 Discussion

The present study showed that the cropping pattern in different ecological zones increased crop aboveground dry matter and changed the root conformation. Mixed cropping improved soil

nutrients and had beneficial effects on the rhizomes, nitrogen fixation, and nitrogen transfer. Studying the changes in nodulation, nitrogen-fixing enzyme activities, root phenotypic traits, and soil physicochemical traits in legumes helped to understand the overall response of BNF and nitrogen transfer in legumes in different ecological zones. The ability of legumes to biologically fix nitrogen is a result of their symbiosis with rhizobacteria, which are present in the rhizomes of legumes, and different crop types and growing environments affect the formation and activity of nodules, which, in turn, affects the amount of nitrogen biologically fixed by the plant (Suter et al., 2015; Duchene et al., 2017). Nitrogen fixation in the aboveground portion of legumes in an intermixed cropping system yields

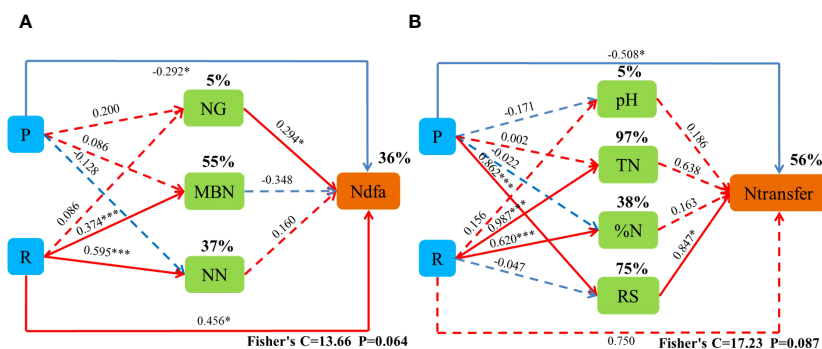


FIGURE 9

Piecewise structural equation modeling (SEM) describing the effects of the cropping system in different ecoregions on biological nitrogen fixation and nitrogen transfer in legume forage. Effect of cropping pattern (R) and ecological region (P), nitrogen-fixing enzyme activity (NG), microbial mass nitrogen (MBN), nitrate nitrogen (NN), pH (Ph), total nitrogen (TN), nitrogen content (%N), and root surface area (RS) on biological nitrogen fixation (Ndfa) and nitrogen transfer (Ntransfer). Solid lines indicate significant effects, and dashed lines indicate non-significant effects. * and *** indicate significant differences at 0.05 and 0.001 levels, respectively.

40–100 kg ha⁻², and legume nitrogen fixation in an intermixed cropping system is more than three times that in a monoculture (Jensen, 1996), whereas 7%–42% of the nitrogen in non-leguminous forage is transferred by legumes (Schipanski and Drinkwater, 2012; Thilakarathna et al., 2016). This is due to nitrogen fixation by leguminous crops, which alters the soil's carbon-to-nitrogen ratio, improves the soil's nitrogen balance, and accelerates the cycling of nutrients and enzymes required for normal plant growth and development, which has a positive effect on crop growth (Spiegel et al., 2007). Therefore, rational farming practices and cropping patterns not only add additional nitrogen to the soil and improve soil health but also effectively promote the agroecosystem cycle (Crème et al., 2015; Zhao et al., 2015).

Mixed cropping in all ecological regions had more aboveground dry matter than monocultures and LERs > 1, suggesting that interspecific complementarity is greater than interspecific competition in hybrid systems. Previous studies have reached the same conclusion (Willey, 1979) because plants use interspecific complementarity and interspecific competition to access soil resources and promote rhizomatous nitrogen fixation through positive plant–soil–microbe interactions (Duchene et al., 2017). Plant facilitation and competition coexist in intercropping/mixed cropping, and facilitation occurs when plant species positively interact to provide complementary services (Bedoussac and Justes, 2010; Amossé et al., 2013). The interspecific relationships of crops are related to root conformation and root depth, as root characteristics determine the depth of water and nutrient uptake (Peoples et al., 2004; Hauggaard-Nielsen et al., 2008). Plants use the plasticity of roots to avoid excessive root competition and to explore different regions of the soil, which in turn acts on the growth and development of the aboveground parts (Schroth, 1998; Hauggaard-Nielsen et al., 2001; Rich and Michelle, 2013). Our study confirmed that mixing oats with the three legumes promoted root growth, particularly increasing root length and surface area in the mixed cropping system, increasing nutrient uptake from the soil, and promoting aboveground growth. The amount of aboveground dry matter was significantly higher in all of the mixes than in monocropping and that the mixed cropping system was in an interspecific complementary situation. The aboveground N contents of oats planted under mixed cropping in the same ecoregion were all significantly higher than those of single-cropped oats, while the opposite was true for pulses, and there were differences in the N contents of oats among the three mixed cropping modes of pulses, YS, YJ, and YC. One was that N fixed by legume crops is taken up and utilized by grass crops, depleting the nitrogen in the soil and forcing legumes to increase their BNF rate to meet their own nitrogen needs, while utilization of nitrogen resources by oats is enhanced by interspecific intercropping (Wahbi et al., 2016; Ingraffia et al., 2019). Second, the N content of legumes is inherently higher than that of oats, and the difference in N between plants after mixed cropping establishes a reservoir–source relationship for oat–mungbean intercropping, resulting in the transfer of nitrogen from high- to low-N plants and an increase in the N content of the oats (Neumann et al., 2009; Rui et al., 2022).

The root tumor is the main site of BNF in leguminous plants (Gibson, 1977), and the strength of the nitrogen fixation capacity of

the root tumor is related to the number of root tumors, the weight of the root tumors, the activity of nitrogen-fixing enzymes, the habitat of the plant, and the characteristics and growth and reproduction of the plant (Vincent et al., 1980), such as farming practices, cropping pattern, and climatic conditions (Wheatley et al., 1995; Marcarelli and Wurtsbaugh, 2010; Ben-Chuan et al., 2022). In this study, the number of nodules, weight, and nitrogen-fixing enzyme activity of the legumes increased in the mixed cropping system, but the number of rhizomes varied considerably from crop to crop, with pea having the highest number of nodules and fava beans the largest rhizome weight, and the differences in rhizome characteristics among the different crop species were greater than those among the different cropping patterns. This finding suggests that plant nodulation is mainly determined by genetic characteristics (Hardarson and Atkins, 2003; Keneni et al., 2013), but cropping systems can also significantly increase the number and weight of rhizomes (Fujita et al., 1992; Bloem et al., 2009). In addition, the characteristics of crop rhizomes of the same cropping pattern varied considerably in different ecological zones; particularly, the number and weight of the legume nodules were significantly higher in MY than in HZ and GN, except for fava bean, which had the highest number and weight of nodules in GN. This may have occurred because of the fertile soil and suitable climate in MY, which was favorable for legume crop nodulation, and similar results were reported by related studies (Dollete et al., 2023). Beuselinck et al. (2005) confirmed that plants grown in fertile soils have dense and large rhizomes, whereas those grown in poor soils have fewer rhizomes. However, the fava bean tumor pattern is the opposite, with the lowest temperature and rainfall in the GN region inhibiting the growth and development of the crop, and the aboveground dry matter yield of the crop in the GN (highest altitude) region was lower than in all other regions. This may be due to the fact that broad beans are more adaptable to their environment and that low temperatures and dry conditions are more favorable for nodulation. This is contrary to the findings of Lumactud et al (Fernández-Luque et al., 2008; Belén et al., 2015). This may have occurred because of the different crop species studied; broad bean has a longer root system, greater volume and surface area, greater ability to draw water and nutrients, greater ability to cope with drought, and a lower effect on nodulation (Rowse and Goodman, 1981; Nyalemegbe and Kenneth, 1994). In addition, the mixed cropping increased nitrogen-fixing enzyme activity in the rhizomes of the leguminous crops, which was consistent across all three leguminous crops in all ecological zones. Root interactions in the mixed cropping system may be responsible for the increased oat root growth, root surface area, and spatial expansion of the oat root system (Hoad et al., 2001; Gao et al., 2010), which created a favorable microaerobic environment and promoted nitrogen-fixing enzyme activity (Serraj, 2003; González et al., 2015).

Nutrient composition of the soil and physicochemical factors, such as soil organic matter (SOM), soil TN, soil total phosphorus (TP), and electrical conductivity (EC) are soil factors that significantly affect the rhizomes of legumes. In turn, the tumor characteristics of the plant counteract soil quality (David and Khan, 2001; Massawel et al., 2016). Our study found that mixed cropping

significantly increased SOM, TN, nitrate–nitrogen, and ammonium–nitrogen compared to oat monoculture, but nitrate–nitrogen and ammonium–nitrogen contents were lower than those in monoculture legumes. This may have occurred because nutrients are released from the decomposition of withered material and root rot of leguminous crops, while the nitrogen fixation of legumes increases the number of beneficial microorganisms in the soil, accelerates nutrient mineralization (Wardle et al., 2006; Deyn et al., 2011; Zhao, 2014), and increases the organic matter content in the soil, providing a favorable environment for crop growth (Fontaine et al., 2003; Blagodatskaya and Kuzyakov, 2008; Bernard et al., 2009). Second, oat and legume root interactions were enhanced in the mixed cropping system and became closer as the reproductive period progressed, with root secretions inducing interactions between roots, soil microorganisms, and the surrounding soil particles (Burns, 1982; Dennis et al., 2010). Plant-secretion-enriched soil microorganisms play a key role in the decomposition of SOM and nutrient cycling by releasing and influencing various enzyme activities (Trasar-Cepeda et al., 2008; Kabiri et al., 2016; Zhou et al., 2016). Third, N released by legumes undergoes three pathways, including plant resorption–denitrification and loss–soil microbial fixation (Nasholm et al., 2009; Cameron et al., 2013). The main form of N in legume rhizome sediments is ammonium–N, which is converted to plant-available nitrogen by nitrification (Lesuffleur et al., 2007; Paynel et al., 2008), resulting in increased levels of nitrate and ammonium–N in mixed cropping systems.

The BNF rates of the three legumes varied significantly in the different ecological zones, and the BNF rates of the three legumes also varied significantly within the same ecological zone. The cultivation patterns with the highest BNF rates in each region were HZ (YS), GN (YC), and MY (YJ), respectively. This finding indicates that different crops have different adaptability to the environment and that climatic and soil factors affect nitrogen fixation in legume crops (Sprenst, 1999). A rational cropping pattern will increase the nitrogen fixation rate of the crop (Zang et al., 2015; Tsialtas et al., 2018). Smercina et al. (2019) showed that BNF is cumulatively sensitive to environmental changes that affect the growth and development of the aboveground parts and the belowground root systems of crops (Smercina et al., 2019; Chun et al., 2021). Intercropping improves N fixation (%Ndfa) in legumes because legumes take up less N from the soil in intercropping systems, which improves N fixation efficiency (Danso et al., 1987). This effect becomes more pronounced as grain density increases (Fan et al., 2018). This study showed that the YS cropping pattern had the highest BNF and BNF contribution in the three ecological zones, and in the mixed cropping system with oats, the forage pea was at a disadvantage in the utilization of soil nitrogen resources, stimulating its BNF and enabling oats to obtain more ground nitrogen (Ingraffia et al., 2019). The N transfer rate and N transfer of the three leguminous crops differed significantly in the same ecological zone and also among the ecological zones of the same cropping pattern. Of these, 11.38%–12.68%, 6.85%–9.77%, and 7.94%–11.65% of the nitrogen in oats from the mixed cropping systems of YS, YJ, and YC came from S, J, and C, respectively. This is due to differences in the characteristics of the different types of legume nodules and root systems (Rao and Ito, 1998), changes in

cropping patterns that can affect nitrogen fixation, and the different ecological conditions that affect root secretions. In addition, there are differences in soil nutrient cycling, the growth of aboveground parts of plants, and the uptake and translocation of nitrogen from the crop (Gupta et al., 2006; Collino et al., 2015). A high N fixation rate did not represent a high N transfer rate because N fixation is mainly associated with nodulation in legumes (Weaver, 1987), whereas N transfer is related to N uptake, the difference in N content between oats and legumes, and the closeness of root contact between the two (Stern, 1993; Shao et al., 2021).

Factors affecting nitrogen fixation and the nitrogen transfer rate in legumes are complex, with the cropping environment, cropping pattern, and crop type being the key factors (Rui et al., 2022). This study showed that the cropping pattern and ecological zone promoted BNF in legumes by increasing nitrogen-fixing enzyme activity and ammonium–nitrogen content. In addition, the ecological zone and cropping pattern improved the nitrogen transfer rate in the legumes by increasing rhizome weight and aboveground nitrogen content. In this study, we found that Legume–grass mixtures can improve the biological nitrogen fixation capacity of legume crops. By promoting rhizoma formation and optimizing root morphology, it promotes crop growth and development, increases soil nutrients and optimizes resource allocation. We also found that Legume–grass mixtures also affects root secretions, rhizobia, and nitrogen-fixing bacteria, thereby altering the inter-root microcosm. However, the molecular biological mechanisms by which nitrogen-fixing microorganisms affect legume–grass mixtures are not yet clear and can be further elucidated with the help of new technologies such as soil macrogenomics and macrotranscript genomics.

5 Conclusion

Legumes reduce atmospheric nitrogen to plant-available nitrogen (ammonia) catalyzed by nitrogen-fixing enzymes. Plants use interspecific complementarity and interspecific competition to access soil resources and promote the process of rhizomatous nitrogen fixation through plant–root–soil interactions. This finding provides further evidence that mixing legumes with oats is an effective sustainable forage management practice. We found significant differences in BNF rates of legumes grown with different types of legumes and in different ecological zones, but overall, mixed cropping significantly increased the BNF rates of legumes. In addition, high rates of BNF did not represent high rates of nitrogen transfer. Our study demonstrated the effects of the ecological zone and cropping pattern on BNF and nitrogen transfer in alpine mixed-seeded grassland. These results will help us to better understand nitrogen fixation and grass interactions in alpine grassland ecosystems.

Data availability statement

The original contributions presented in the study are included in the article/supplementary material. Further inquiries can be directed to the corresponding author.

Author contributions

FL: Data curation, Software, Writing – original draft, Writing – review & editing. WM: Investigation, Methodology, Writing – review & editing. WL: Funding acquisition, Methodology, Writing – review & editing.

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References

- Amossé, C., Jeuffroy, M.-H., Celette, F., and David, C. (2013). Relay-intercropped forage legumes help to control weeds in organic grain production. *Eur. J. Agron.* 49, 158–167. doi: 10.1016/j.eja.2013.04.002
- Bedoussac, L., and Justes, E. (2010). The efficiency of a durum wheat-winter pea intercrop to improve yield and wheat grain protein concentration depends on N availability during early growth. *Plant Soil* 330, 19–35. doi: 10.1007/s11104-009-0082-2
- Belén, M.-G., Daniel, S., William, C. J., Barbara, K., Dorcas, Q. M., Matome, M. E., et al. (2015). Redox markers for drought-induced nodule senescence, a process occurring after drought-induced senescence of the lowest leaves in soybean (*Glycine max*). *Ann. Bot.* 116, 497–510. doi: 10.1093/aob/mcv030
- Ben-Chuan, Z., Ying, Z., Ping, C., Xiao-Na, Z., Qing, D. U., Huan, Y., et al. (2022). Maize-legume intercropping promote N uptake through changing the root spatial distribution, legume nodulation capacity, and soil N availability. *J. Integr. Agric.* 21 (6), 1755–1771. doi: 10.1016/S2095-3119(21)63730-9
- Bernard, L., Maron, P. A., Mougel, C., Nowak, V., Lévêque, J., Marol, B., et al. (2009). Contamination of soil by copper affects the dynamics, diversity, and activity of soil bacterial communities involved in wheat decomposition and carbon storage. *Appl. Environ. Microbiol.* 75, 7565–7569. doi: 10.1128/AEM.00616-09
- Beuselinck, P. R., Brummer, E. C., Viands, D. K., Asay, K. H., and Brauer, D. K. (2005). Genotype and environment affect rhizome growth of birdsfoot trefoil. *Crop Sci.* 45, 1736–1740. doi: 10.2135/cropsci2004.0495
- Blagodatskaya, E., and Kuzyakov, Y. (2008). Mechanisms of real and apparent priming effects and their dependence on soil microbial biomass and community structure: critical review. *Biol. Fertility Soils* 45, 115–131. doi: 10.1007/s00374-008-0334-y
- Bloem, J. F., Trytsman, G., and Smith, H. J. (2009). Biological nitrogen fixation in resource-poor agriculture in South Africa. *Symbiosis* 48, 18–24. doi: 10.1007/BF03179981
- Bouma, T. J., Nielsen, K. L., Hal, J. V., and Koutstaal, B. (2001). Root system topology and diameter distribution of species from habitats differing in inundation frequency. *Funct. Ecol.* 15, 360–369. doi: 10.1046/j.1365-2435.2001.00523.x
- Burns, R. G. (1982). Enzyme activity in soil: Location and a possible role in microbial ecology. *Soil Biol. Biochem.* 14, 423–427. doi: 10.1016/0038-0717(82)90099-2
- Cameron, K. C., Di, H. J., and Moir, J. L. (2013). Nitrogen losses from the soil/plant system: a review. *Ann. Appl. Biol.* 162, 145–173. doi: 10.1111/aab.12014
- Chun, H. C., Lee, S., Choi, Y. D., Gong, D. H., and Jung, K. Y. (2021). Effects of drought stress on root morphology and spatial distribution of soybean and adzuki bean. *J. Integr. Agric.* 010, 020. doi: 10.1016/S2095-3119(20)63560-2
- Clergue, B., Amiaud, B., Pervanchon, F., Lasserre-Joulin, F., and Plantureux, S. (2005). Biodiversity: function and assessment in agricultural areas. A review. *Agronomie* 25, 6119–6125. doi: 10.1051/agro:2004049
- Collino, D. J., Salvagioti, F., Peticari, A., Piccinetti, C., Ovando, G., Urquiaga, S., et al. (2015). Biological nitrogen fixation in soybean in Argentina: relationships with crop, soil, and meteorological factors. *Plant Soil* 392, 239–252. doi: 10.1007/s11104-015-2459-8
- Crème, A., Rumpel, C., Gastal, F., de la Luz Mora Gil, M., and Chabbi, A. (2015). Effects of grasses and a legume grown in monoculture or mixture on soil organic matter and phosphorus forms. *Plant Soil* 402, 117–128. doi: 10.1007/s11104-015-2740-x
- Danso, S. K. A., Zapata, F., Hardarson, G., and Fried, M. (1987). Nitrogen fixation in fababeans as affected by plant population density in sole or intercropped systems with barley. *Soil Biol. Biochem.* 19, 411–415. doi: 10.1016/0038-0717(87)90031-9
- David, J., and Khan, K. S. (2001). Effect of nitrogen application on nodulation in inoculated chickpea (*Cicer arietinum* L.). *J. Biol. Sci.* 1, 87–89. doi: 10.3923/jbs.2001.87.89
- Dennis, P. G., Miller, A. J., and Hirsch, P. R. (2010). Are root exudates more important than other sources of rhizodeposits in structuring rhizosphere bacterial communities? *FEMS Microbiol. Ecol.* 72, 313–327. doi: 10.1111/j.1574-6941.2010.00860.x
- Deyn, G. B. D., Shiel, R. S., Ostle, N. J., McNamara, N. P., Oakley, S., Young, I., et al. (2011). Additional carbon sequestration benefits of grassland diversity restoration. *J. Appl. Ecol.* 48, 600–608. doi: 10.1111/j.1365-2664.2010.01925.x
- Dollete, D., Lumactud, R. A., Carlyle, C. N., Szczygłowski, K., Hill, B., and Thilakarathna, M. S. (2023). Effect of drought stress on symbiotic nitrogen fixation, soil nitrogen availability and soil microbial diversity in forage legumes. *Plant Soil*. doi: 10.1007/s11104-023-06348-1
- Dong, S. K., Li, J. P., Li, X. Y., Wen, L., Zhu, L., Li, Y. Y., et al. (2010). Application of design theory for restoring the black beach degraded rangeland at the headwater areas of the Qinghai-Tibetan Plateau. *Afr. J. Agric. Res.* 5, 3542–3552. doi: 10.5897/AJAR10.005
- Duchene, O., Vian, J.-F., and Celette, F. (2017). Intercropping with legume for agroecological cropping systems: Complementarity and facilitation processes and the importance of soil microorganisms. A review. *Agricul Ecosyst. Environ.* 240, 148–161. doi: 10.1016/j.agee.2017.02.019
- Fan, Z., Zhao, Y., Chai, Q., Zhao, C., Yu, A., Coulter, J. A., et al. (2018). Synchrony of nitrogen supply and crop demand are driven via high maize density in maize/pea strip intercropping. *Sci. Rep.* 9, 10954. doi: 10.1038/s41598-019-47554-1
- Faucon, M. P., Houben, and Lambers, (2017). Plant functional traits: soil and ecosystem services. *Trends Plant Sci.* 22, 385–394. doi: 10.1016/j.tplants.2017.01.005
- Fernández-Luque, F., Dendooven, L., Munive, A., Corlay-Chee, L., Serrano-Covarrubias, L. M., and Espinosa-Victoria, D. (2008). Micro-morphology of common bean (*Phaseolus vulgaris* L.) nodules undergoing senescence. *Acta Physiol Plantarum* 30, 545–552. doi: 10.1007/s11738-008-0153-7
- Fitter, A. H. (1994). Architecture and biomass allocation as components of the plastic response of root systems to soil heterogeneity. *Exploit. Environ. Heterog. Plants.* 11, 305–323. doi: 10.1016/B978-0-12-155070-7.50016-0
- Fontaine, S., Mariotti, A., and Abbadié, L. (2003). The priming effect of organic matter: a question of microbial competition? *Soil Biol. Biochem.* 35, 837–843. doi: 10.1016/S0038-0717(03)00123-8
- Fornara, D. A., and Tilman, D. (2008). Plant functional composition influences rates of soil carbon and nitrogen accumulation. *J. Ecol.* 96, 314–322. doi: 10.1111/j.1365-2745.2007.01345.x
- Fornara, D. A., Tilman, D., and Hobbie, S. E. (2009). Linkages between plant functional composition, fine root processes and potential soil N mineralization rates. *J. Ecol.* 97, 48–56. doi: 10.1111/j.1365-2745.2008.01453.x
- Francis, C. A., Jensen, E. S., Lieblein, G., and Breland, T. A. (2016). Agroecologist education for sustainable development of farming and food systems. *Agron. J.* 109, 23–32. doi: 10.2134/agronj2016.05.0267

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- Frankow-Lindberg, B. E., and Dahlin, A. S. (2013). N₂ fixation, N transfer, and yield in grassland communities including a deep-rooted legume or non-legume species. *Plant Soil*. 370, 567–581. doi: 10.1007/s11104-013-1650-z
- Fujita, K., Ofosu-Budu, K. G., and Ogata, S. (1992). Biological nitrogen fixation in mixed legume-cereal cropping systems. *Plant Soil*. 141, 155–175. doi: 10.1007/BF00011315
- Gao, Y., Duan, A., Qiu, X., Liu, Z., Sun, J., Zhang, J., et al. (2010). Distribution of roots and root length density in a maize/soybean strip intercropping system. *Agric. Water Manage.* 98, 199–212. doi: 10.1016/j.agwat.2010.08.021
- Gibson, A. H. (1977). The influence of the environment and managerial practices on the legume-Rhizobium symbiosis. *Treatise Dinitrogen Fixation*.
- González, E. M., Larrainzar, E., Marino, D., Wienkoop, S., and Arrese-Igor, C. (2015). *Physiological responses of N₂-fixing legumes to water limitation* (Springer International Publishing). 9, 5–33. doi: 10.1007/978-3-319-06212-9_2
- Gupta, V. V. S. R., Roper, M. M., and Roget, D. K. (2006). Potential for non-symbiotic N₂-fixation in different agroecological zones of southern Australia. *Soil Res.* 44, 343–354. doi: 10.1071/SR05122
- Hardarson, G., and Atkins, C. (2003). Optimising biological N₂ fixation by legumes in farming systems. *Plant Soil* 252, 41–54. doi: 10.1023/A:1024103818971
- Harris, R. B. (2010). Rangeland degradation on the Qinghai-Tibetan plateau: A review of the evidence of its magnitude and causes. *J. ARID Environ.* 74, 1–12. doi: 10.1016/j.jaridenv.2009.06.014
- Hatano, R., Shinano, T., Taigen, Z., Okubo, M., and Zuwei, L. (2002). Nitrogen budgets and environmental capacity in farm systems in a large-scale karst region, southern China. *Nutrient Cycling Agroecosystems* 63, 139–149. doi: 10.1023/A:1021159000784
- Hauggaard-Nielsen, H., Ambus, P., and Jensen, E. S. (2001). Temporal and spatial distribution of roots and competition for nitrogen in pea-barley intercrops – a field study employing 32P technique. *Plant Soil* 236, 63–74. doi: 10.1023/A:1011909414400
- Hauggaard-Nielsen, H., Jørgensen, B., Kinane, J., and Jensen, E. S. (2008). Grain legume-cereal intercropping: The practical application of diversity, competition and facilitation in arable and organic cropping systems. *Renewable Agric. Food Syst.* 23, 3–12. doi: 10.1017/S1742170507002025
- Haynes, R. J. (1980). Competitive aspects of the grass-legume association. *Adv. Agron.* 33, 227–261. doi: 10.1016/S0065-2113(08)60168-6
- Herridge, D. F., Marcellos, H., Felton, W. L., Turner, G. L., and Peoples, M. B. (1995). Chickpea increases soil-N fertility in cereal systems through nitrate sparing and N₂ fixation. *Soil Biol. Biochem.* 27, 545–551. doi: 10.1016/0038-0717(95)98630-7
- Herridge, D. F., Peoples, M. B., and Boddey, R. M. (2008). Global inputs of biological nitrogen fixation in agricultural systems. *Plant Soil* 311, 1–18. doi: 10.1007/s11104-008-9668-3
- Hinsinger, P., Bengough, A. G., Vetterlein, D., and Young, I. M. (2009). Rhizosphere: biophysics, biogeochemistry and ecological relevance. *Plant Soil* 321, 117–152. doi: 10.1007/s11104-008-9885-9
- Hoad, S. P., Russell, G., Lucas, M. E., and Bingham, I. J. (2001). The management of wheat, barley, and oat root systems. *Adv. Agron.* 74, 193–246. doi: 10.1016/S0065-2113(01)74034-5
- Hu, L., Zi, H., Luo, X., Lerdau, M., and Wang, C. (2021). Root dynamics along a restoration chronosequence of revegetated grasslands in degraded alpine meadows of the Qinghai-Tibetan Plateau, China. *Land Degradat. Dev.* 32, 1–34. doi: 10.1002/ldr.3954
- Ingraffia, R., Amato, G., Frenda, A. S., Giambalvo, D., and Aroca, R. (2019). Impacts of arbuscular mycorrhizal fungi on nutrient uptake, N₂ fixation, N transfer, and growth in a wheat/faba bean intercropping system. *PLoS One* 14, e0213672. doi: 10.1371/journal.pone.0213672
- Jalonen, R., Nygren, P., and Sierra, J. (2009). Root exudates of a legume tree as a nitrogen source for a tropical fodder grass. *Nutrient Cycling Agroecosystems* 85, 203–213. doi: 10.1007/s10705-009-9259-6
- Jensen, E. S. (1996). Grain yield, symbiotic N₂ fixation and interspecific competition for inorganic N in pea-barley intercrops. *Plant Soil* 182, 25–38. doi: 10.1007/BF00010992
- Joergensen, R. G. (1996). The fumigation-extraction method to estimate soil microbial biomass: calibration of the kEC value. *Soil Biol. Biochem.* 28, 25–31. doi: 10.1016/0038-0717(95)00102-6
- Kabiri, V., Raiesi, F., and Ghazavi, M. A. (2016). Tillage effects on soil microbial biomass, SOM mineralization and enzyme activity in a semi-arid Calcixerepts. *Agric. Ecosys. Environ.* 232, 73–84. doi: 10.1016/j.agee.2016.07.022
- Keneni, G., Assefa, F., Imtiaz, M., and Bekele, E. (2013). Genetic diversity for attributes of biological nitrogen fixation in Abyssinian field pea (*Pisum sativum* var. Abyssinicum) germplasm accessions. *Ethiop. J. Appl. Sci. Technol.* 4 (2), 1–21.
- Khan, M., Karim, Y., Yoshida, S., and Tomio, (1994). Nitrogen fixation in peanut determined by acetylene reduction method and ¹⁵N-isotope dilution technique. *Soil Sci. Plant Nutr.* 40, 283–291. doi: 10.1080/00380768.1994.10413302
- Ledgard, S. F., and Steele, K. W. (1992). Biological nitrogen fixation in mixed legume/grass pastures. *Plant Soil* 141, 137–153. doi: 10.1007/BF00011314
- Lesuffleur, F., Paynel, F., Bataillé, M.-P., Deunff, E. L., and Cliquet, J. B. (2007). Root amino acid exudation: measurement of high efflux rates of glycine and serine from six different plant species. *Plant Soil* 294, 235–246. doi: 10.1007/s11104-007-9249-x
- Li, C., Li, X., Shi, Y., Yang, Y., and Li, H. (2022). Effects of nitrogen addition on soil carbon-fixing microbial diversity on different slopes in a degraded alpine meadow. *Front. Plant Sci.* 13. doi: 10.3389/fpls.2022.921278
- Liu, L., Knight, J. D., Lemke, R. L., and Farrell, R. E. (2019). A side-by-side comparison of biological nitrogen fixation and yield of four legume crops. *Plant Soil* 442, 169–182. doi: 10.1007/s11104-019-04167-x
- Liu, Y., Zhao, X., Liu, W., Yang, X., Feng, B., Zhang, C., et al. (2023). Herbivore assemblages affect soil microbial communities by altering root biomass and available nutrients in an alpine meadow. *Front. Plant Sci.* 14. doi: 10.3389/fpls.2023.1117372
- Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J. P., Hector, A., et al. (2001). Ecology - Biodiversity and ecosystem functioning: Current knowledge and future challenges. *Science*. 294, 804–808. doi: 10.1126/science.1064088
- Luo, F., Liu, W., Mi, W., Ma, X., Liu, K., Ju, Z., et al. (2023). Legume-grass mixtures increase forage yield by improving soil quality in different ecological regions of the Qinghai-Tibet Plateau. *Front. Plant Sci.* 14. doi: 10.3389/fpls.2023.1280771
- Marcarelli, A. M., and Wurtsbaugh, W. A. (2010). Effects of upstream lakes and nutrient limitation on periphytic biomass and nitrogen fixation in oligotrophic, subalpine streams. *Freshw. Biol.* 52, 2211–2225. doi: 10.1111/j.1365-2427.2007.01851.x
- Massawel, P. I., Mtei, K. M., Munishi, L. K., and Ndakidem, P. A. (2016). Effect of Rhizobium and Intercropping Systems on Soil Nutrients and Biological Nitrogen Fixation as Influenced by Legumes (*Phaseolus vulgaris* and *Dolichos lablab*). *Int. J. Curr. Microbiol. Appl. Sci.* 5, 135–149. doi: 10.20546/ijcmas
- Mcgraw, R. L., Stamps, W. T., Houx, J. H., and Linit, M. J. (2008). Yield, maturation, and forage quality of alfalfa in a black walnut alley-cropping practice. *Agroforestry Syst.* 74, 155–161. doi: 10.1007/s10457-008-9162-1
- Meng, L., Zhang, A., Wang, F., Han, X., Wang, D., and Li, S. (2015). Arbuscular mycorrhizal fungi and rhizobium facilitate nitrogen uptake and transfer in soybean/maize intercropping system. *Front. Plant Sci.* 6, 339. doi: 10.3389/fpls.2015.00339
- Moorhead, D. L., Rinkes, Z. L., Sinsabaugh, R. L., and Weintraub, M. N. (2013). Dynamic relationships between microbial biomass, respiration, inorganic nutrients and enzyme activities: informing enzyme-based decomposition models. *Front. Microbiol.* 4, 223–. doi: 10.3389/fmicb.2013.00223
- Mtambanengwe and Mapfumo, P. (1999). Nitrogen cycling in non-N₂-fixing tree legumes: challenges for biological nitrogen fixation research in savanna ecosystems. *Symbiosis*. 27, 293–303.
- Mueller, T., and Thorup-Kristensen, K. (2001). N-fixation of selected green manure plants in an organic crop rotation. *Biol. Agric. Horticult.* 18, 345–363. doi: 10.1080/01448765.2001.9754897
- Nasholm, T., Kielland, K., and Ganeteg, U. (2009). Uptake of organic nitrogen by plants. *New Phytol.* 182, 31–48. doi: 10.1111/j.1469-8137.2008.02751.x
- Neumann, A., Werner, J., and Rauber, R. (2009). Evaluation of yield-density relationships and optimization of intercrop compositions of field-grown pea-oat intercrops using the replacement series and the response surface design. *Field Crops Res.* 114, 286–294. doi: 10.1016/j.fcr.2009.08.013
- Nyalemege, K., and Kenneth, K. (1994). *Growth, nodulation and nitrogen fixation of the faba bean (Vicia faba L.) under contrasting soil moisture conditions and under varied crop density and shading* (University of Reading).
- Odu, C. T. I., and Akerele, R. B. (1973). Effects of soil, grass and legume root extracts on heterotrophic bacteria, nitrogen mineralization and nitrification in soil. *Soil Biol. Biochem.* 5, 861–867. doi: 10.1016/0038-0717(73)90032-1
- Olounlade, A. O., Gucheng, L., Sodjinou, M., and Biao, G. (2017). Agroecological practices for sustainable agriculture in Benin. 12, 11–14. doi: 10.13140/RG.2.2.15209.75368
- Paynel, F., Lesuffleur, F., Bigot, J., Diquélou, S., and Cliquet, J. B. (2008). A study of 15N transfer between legumes and grasses. *Agron. Sustain. Dev.* 28, 281–290. doi: 10.1051/agro:2007061
- Peoples, M. B., Angus, J. F., Swan, A. D., Dear, B. S., Hauggaardiensen, H., Jensen, E. S., et al. (2004). Nitrogen dynamics in legume-based pasture systems. *Agric. Nit. Cycle*. 261.
- Peoples, M. B., Chalk, P. M., Unkovich, M. J., and Boddey, R. M. (2015). Can differences in 15N natural abundance be used to quantify the transfer of nitrogen from legumes to neighbouring non-legume plant species? *Soil Biol. Biochem.* 87, 97–109. doi: 10.1016/j.soilbio.2015.04.010
- Poffenbarger, H. J., Mirsky, S. B., Weil, R. R., Maul, J. E., Matthew, K., Spargo, J. T., et al. (2015). Biomass and nitrogen content of hairy vetch-cereal rye cover crop mixtures as influenced by species proportions. *Agron. J.* 107, 2069–2082. doi: 10.2134/agronj14.0462
- Rao, T. P., and Ito, O. (1998). Differences in root system morphology and root respiration in relation to nitrogen uptake among six crop species. *Japan Agric. Res. Q.* 32, 97–103.
- Ren, G. H., Wu, G. L., and Dong, Q. M. (2014). Above- and belowground response along degradation gradient in an alpine grassland of the qinghai-tibetan plateau. *Clean - Soil Air Water: A J. Sustainability Environ. Safety.* 42, 319–323. doi: 10.1002/clen.201200084
- Rich, S. M., and Michelle, W. (2013). Soil conditions and cereal root system architecture: review and considerations for linking Darwin and Weaver. *J. Exp. Bot.* 5, 1193–1208. doi: 10.1093/jxb/ert043
- Rispail, N., Fondevilla, S., Barilli, E., Castillejo Sánchez, M.Á., VillegasFernández, Á.M., AznarFernández, T., et al. (2015). Legumes in sustainable agriculture. *China-Spain Res Pol For.* 26–27.

- Rochon, J. J., Doyle, C. J., Greef, J. M., Hopkins, A., and Smith, C. J. (2010). Grazing legumes in Europe: a review of their status, management, benefits, research needs and future prospects. *Grass Forage Sci.* 59, 197–214. doi: 10.1111/j.1365-2494.2004.00423.x
- Rowse, H. R., and Goodman, D. (1981). Axial resistance to water movement in broad bean (*Vicia faba*) roots. *J. Exp. Bot.* 32, 591–598. doi: 10.1093/jxb/32.3.591
- Rui, L., Guo-Peng, Z., Dan-Na, C., Song-Juan, G., Mei, H., Jiu-Dong, Z., et al. (2022). Transfer characteristics of nitrogen fixed by leguminous green manure crops when intercropped with maize in northwestern China. *J. Integr. Agric.* 21, 1177–1187. doi: 10.1016/S2095-3119(21)63674-2
- Sainju, U. M., Terrill, T. H., Gelaye, S., and Singh, B. P. (2003). Soil aggregation and carbon and nitrogen pools under rhizoma peanut and perennial weeds. *Soil Sci. Soc. America J.* 67, 146–155. doi: 10.2136/sssaj2003.1460
- Schipanski, M. E., and Drinkwater, L. E. (2012). Nitrogen fixation in annual and perennial legume-grass mixtures across a fertility gradient. *Plant Soil.* 357, 147–159. doi: 10.1007/s11104-012-1137-3
- Schroth, G. (1998). A review of belowground interactions in agroforestry, focusing on mechanisms and management options. *Agroforestry Syst.* 43, 5–34. doi: 10.1023/A:1026443018920
- Serraj, R. (2003). Effects of drought stress on legume symbiotic nitrogen fixation: Physiological mechanisms. *Indian J. Exp. Biol.* 41, 1136–1141. doi: 10.1111/j.1151-2916.2001.tb00841.x
- Shao, Z. Q., Zheng, C. C., Postma, J. A., Lu, W. L., Gao, Q., Gao, Y. Z., et al. (2021). Nitrogen acquisition, fixation and transfer in maize/alfalfa intercrops are increased through root contact and morphological responses to interspecies competition ScienceDirect. *J. Integr. Agric.* 20, 2240–2254. doi: 10.1016/S2095-3119(20)63330-5
- Smercina, D. N., Evans, S. E., Friesen, M. L., and Tiemann, L. K. (2019). To fix or not to fix: controls on free-living nitrogen fixation in the rhizosphere. *Appl. Environ. Microbiol.* 85, e02546. doi: 10.1128/AEM.02546-18
- Song, X., Peng, C., Ciais, P., Li, Q., and Deng, L. (2020). Nitrogen addition increased CO₂ uptake more than non-CO₂ greenhouse gases emissions in a Moso bamboo forest. *Sci. Adv.* 6, eaaw5790. doi: 10.1126/sciadv.aaw5790
- Spiegel, H., Dersch, G., Hösch, J., and Baumgarten, A. (2007). Tillage effects on soil organic carbon and nutrient availability in a long-term field experiment in Austria. *Bodenkultur* 58, 47–58.
- Sprent, J. I. (1999). Nitrogen fixation and growth of non-crop legume species in diverse environments. *Perspect. Plant Ecol.* 2, 149–162. doi: 10.1078/1433-8319-00068
- Stern, W. J. (1993). Nitrogen fixation and transfer in intercrop systems. *Field Crops Res.* 34, 335–356. doi: 10.1016/0378-4290(93)90121-3
- Suter, M., Connolly, J., Finn, J. A., Loges, R., Kirwan, L., Sebastia, M. T., et al. (2015). Nitrogen yield advantage from grass-legume mixtures is robust over a wide range of legume proportions and environmental conditions. *Glob Chang Biol.* 21, 2424–2438. doi: 10.1111/gcb.12880
- Tahir, M., Li, C., Zeng, T., Xin, Y., Chen, C., Javed, H. H., et al. (2022). Mixture composition influenced the biomass yield and nutritional quality of legume–grass pastures. *Agronomy* 12, 1449. doi: 10.3390/agronomy12061449
- Tahir, M., Wei, X., Liu, H., Li, J., Zhou, J., Kang, B., et al. (2023). Mixed legume-grass seeding and nitrogen fertilizer input enhance forage yield and nutritional quality by improving the soil enzyme activities in Sichuan, China. *Front. Plant Sci.* 14. doi: 10.3389/fpls.2023.1176150
- Thilakarathna, M. S., McElroy, M. S., Chapagain, T., Papadopoulos, Y. A., and Raizada, M. N. (2016). Belowground nitrogen transfer from legumes to non-legumes under managed herbaceous cropping systems. A review. *Agron. Sustain. Dev.* 36, 58. doi: 10.1007/s13593-016-0396-4
- Thilakarathna, R. M. M. S., Papadopoulos, Y. A., Rodd, A. V., Gunawardena, A. N., Fillmore, S. A. E., and Prithiviraj, B. (2012). Characterizing nitrogen transfer from red clover populations to companion bluegrass under field conditions. *Can. J. Plant Sci.* 92, 1163–1173. doi: 10.4141/cjps2012-036
- Tilman, D., Cassman, K., Matson, P. A., Naylor, R., and Polasky, S. (2002). Agricultural sustainability and intensive production practices. *Nature.* 418, 671–677. doi: 10.1038/nature01014
- Trasar-Cepeda, C., Leirós, M. C., and Gil-Sotres, F. (2008). Hydrolytic enzyme activities in agricultural and forest soils. Some implications for their use as indicators of soil quality. *Soil Biol. Biochem.* 40, 2146–2155. doi: 10.1016/j.soilbio.2008.03.015
- Tsialtas, I. T., Dimitrios, B., Vlachostergios, D. N., Dordas, C., and Lithourgidis, A. (2018). Cultivar complementarity for symbiotic nitrogen fixation and water use efficiency in pea-oat intercrops and its effect on forage yield and quality. *Field Crops Res.* 226, 28–37. doi: 10.1016/j.fcr.2018.07.005
- Vincent, J. M., Newton, W. E., and Orme Johnson, W. H. (1980). Factors controlling the legume-Rhizobium symbiosis. *Nitrogen fixation.* 2, 103–129.
- Wahbi, S., Maghraoui, T., Hafidi, M., Sanguin, H., Oufdou, K., Prin, Y., et al. (2016). Enhanced transfer of biologically fixed N from faba bean to intercropped wheat through mycorrhizal symbiosis. *Appl. Soil Ecol.* 107, 91–98. doi: 10.1016/j.apsoil.2016.05.008
- Wardle, D. A., Yeates, G. W., Barker, G. M., and Bonner, K. I. (2006). The influence of plant litter diversity on decomposer abundance and diversity. *Soil Biol. Biochem.* 38, 1052–1062. doi: 10.1016/j.soilbio.2005.09.003
- Weaver, R. W. (1987). Interaction of root nodule size and oxygen pressure on the rate of nitrogen fixation by cowpea and peanut. *Plant Physiol. Suppl.; (United States)* 83, 4.
- Wei, Y., Wang, S., Fang, Y., and Nawaz, Z. (2017). Integrated assessment on the vulnerability of animal husbandry to snow disasters under climate change in the Qinghai-Tibetan Plateau. *Global Planetary Change* 157, 139–152. doi: 10.1016/j.gloplacha.2017.08.017
- Wheatley, D. M., Macleod, D. A., and Jessop, R. S. (1995). Influence of tillage treatments on N₂ fixation of soybean. *Soil Biol. Biochem.* 27, 0–574. doi: 10.1016/0038-0717(95)98633-Y
- Wichern, F., Mayer, J., Joergensen, R. G., and Müller, T. (2007). Release of C and N from roots of peas and oats and their availability to soil microorganisms. *Soil Biol. Biochem.* 39, 2829–2839. doi: 10.1016/j.soilbio.2007.06.006
- Willey, R. (1979). Intercropping its importance and research needs part 1. Competition and yield advantages vol-32. *Field Crop Abstracts* 32, 1–10. Available at: <http://krishikosh.egranth.ac.in/handle/1/2056350>.
- Xiang, Y. F. K. D. X. (2022). Effects of different mixtures and proportions of avena sativa and pea on forage yield and quality in alpine cold region. *Acta agrestia Sin.* 30, 487–494. doi: 10.11733/j.issn.1007-0435.2022.02.029
- Xue, X., You, Q., Peng, F., Dong, S., and Duan, H. (2017). Experimental warming aggravates degradation-induced topsoil drought in alpine meadows of the qinghai-tibetan plateau. *Land Degradat. Dev.* 28, 2343–2353. doi: 10.1002/ldr.2763
- Yao, X., Li, Y., Liao, L., Sun, G., and Ye, S. (2019). Enhancement of nutrient absorption and interspecific nitrogen transfer in a Eucalyptus urophylla × eucalyptus grandis and Dalbergia odorifera mixed plantation. *For. Ecol. Manage.* 449, 117465. doi: 10.1016/j.foreco.2019.117465
- Yoneyama, Y., Fujita, Y., Yoshida, M., Matsumoto, M., Kambayashi, Y., and Yazaki, (1986). Variation in natural abundance of N-15 among plant-parts and in N-15-N-14 fractionation during N-2 fixation in the legume-rhizobia symbiotic system. *Plant Cell Physiol.* 27, 791–799. doi: 10.1093/oxfordjournals.pcp.a077165
- Zang, H., Yang, X., Feng, X., Qian, X., and Zeng, Z. (2015). Rhizodeposition of Nitrogen and Carbon by Mungbean (*Vigna radiata* L.) and Its Contribution to Intercropped Oats (*Avena nuda* L.). *PLoS One* 10, e0121132. doi: 10.1371/journal.pone.0121132
- Zhang, W., Wu, X. K., Liu, G. X., Dong, Z. B., Zhang, G. S., Chen, T., et al. (2014). Tag-encoded pyrosequencing analysis of bacterial diversity within different alpine grassland ecosystems of the Qinghai-Tibet Plateau, China. *Environ. Earth Sci.* 72, 779–786. doi: 10.1007/s12665-013-3001-z
- Zhao, J. (2014). Legume-soil interactions: legume addition enhances the complexity of the soil food web. *Plant Soil* 385, 273–286. doi: 10.1007/s11104-014-2234-2
- Zhao, J., Zeng, Z., He, X., Chen, H., and Wang, K. (2015). Effects of monoculture and mixed culture of grass and legume forage species on soil microbial community structure under different levels of nitrogen fertilization. *Eur. J. Soil Biol.* 68, 61–68. doi: 10.1016/j.ejsobi.2015.03.008
- Zhou, D., Huang, X. F., Chaparro, J. M., Badri, D. V., and Guo, J. (2016). Root and bacterial secretions regulate the interaction between plants and PGPR leading to distinct plant growth promotion effects. *Plant Soil* 401, 259–272. doi: 10.1007/s11104-015-2743-7



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Impact of seed rate and time of sowing on rice fallow crops and their sustainable production system in machine-harvested rice fields

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A field experiment was conducted at the Department of Agronomy, Agricultural College and Research Institute, Tamil Nadu Agricultural University, Madurai to study the performance of rice fallow crops in machine-harvested rice fields. The primary objective of this study was to determine the optimal seed rate and the time of sowing rice fallow crops in machine-harvested rice fields. Rice fallow crop cultivation is the most significant low-cost production system in the delta region. However, the sustainability of the system is uncertain in the context of mechanical harvesting of rice using heavy machinery. The crops selected for the experimental trial were black gram (*Vigna mungo* (L.) Hepper.), sesame (*Sesamum indicum*), and proso millet (*Panicum miliaceum*). The field experiment was conducted using a strip plot design. Rice fallow crops were arranged in vertical plots, while various seed rates and sowing timings were arranged in horizontal plots. The results indicated that the sowing time and seed rate significantly influenced the growth and development of rice fallow crops in machine-harvested rice fields. On the day of rice harvest, a 20% increase in seed rate (36 kg ha⁻¹) resulted in greater grain and straw yield among the black gram treatments. The increased seed rate compensated for the damage caused by mechanical harvesting on the day of the harvest when a combine harvester was utilized, increasing the yield and sustainability of the rice fallow crops.

KEYWORDS

blackgram, machine harvest, rice, rice fallow, sowing

1 Introduction

Rice is the cornerstone of Indian agriculture, accounting for 46.2 m ha of cultivated area and producing 130.4 mt. A single rice crop, typically grown from August to January and using long-duration rice varieties (155–165 days) and medium-duration rice varieties during the *rabi* season, is harvested during the first fortnight of January and celebrated

as a harvest festival in South India and the rest of India. The “Rice Fallow Pulses” in the delta region are cultivated regularly after the rice crop in Tamil Nadu from January to March, encompassing a total area of 2.0 lakh ha and contributing significantly to pulse production in the state. Pulses, particularly black gram or green gram, are traditionally sown 7–10 days before the harvest of rice under zero tillage conditions by utilizing the residual soil moisture. The germinated pulse crop withstands disturbances during manual harvesting of rice and thrives under paddy stubble, which provides a favorable microenvironment. However, the yield of rice fallow crops during this period typically ranges from 300 to 500 kg ha⁻¹, which is significantly lower than the potential yield achievable under irrigation (Umamageswari et al., 2019).

The productivity of rice fallow crops is generally impeded by various factors, including biological and environmental stresses, inadequate crop management practices, and socioeconomic limitations. The most significant constraint for rice fallow crops is low soil moisture content after paddy harvest, along with a lack of irrigation facilities (Kumari and Rahaman, 2021). Among these factors, soil and water availability emerge as primary constraints contributing to low yields. With irrigation typically withheld 10–15 days before rice harvest, soil moisture rapidly diminishes as the crop cycle progresses. A notable period occurs in the second half of February, when an increase in the temperature exacerbates moisture stress, significantly impacting fallow crops during the flowering and pod development stages.

Early maturity, rapid growth, early ground cover, and deep roots have been recommended as desirable plant characteristics for water-limited rice fallow conditions (Bandyopadhyay et al., 2016; Hazra and Bohra, 2021). Ensuring an optimum plant population is essential for increasing yields in rice fallow pulse cultivation. Research suggests that diversifying rice fallows with short-duration pulses or oilseeds is a viable option for horizontal expansion, while also increasing productivity and profitability. This approach also facilitates the growth of soil organic carbon (SOC), nutrients, and microbial populations through nitrogen fixation, leaf shedding, and higher biomass accumulation (Gautam et al., 2021). In addition, pulses facilitate soil health restoration by fixing atmospheric nitrogen (N) and increasing crop biomass, which improves the soil organic carbon (SOC) status (Geethika et al., 2024).

Traditionally, seeds are distributed manually 7–10 days before the paddy harvest, when soil moisture is optimal. However, this method often results in challenges, such as uneven germination and plant distribution. Furthermore, the transition to machine harvesting of paddy has introduced an additional challenge, as machinery may inadvertently damage emerging pre-harvest sown crop plants through trampling during the paddy harvest. As mechanized harvesting becomes more prevalent, it not only alters soil physical conditions but also disturbs the soil moisture status in rice fallow cultivation. Consequently, rice fallow pulses are predominantly restricted to this region, and farmers are reluctant to cultivate rice fallow crops in machine-harvested rice fields. In response to these challenges, the present study was conducted to evaluate methods for mitigating mechanical damage and moisture stress as well as for enhancing crop establishment, ultimately aiming to increase the productivity of rice fallow crops.

2 Materials and methods

2.1 Experimental site

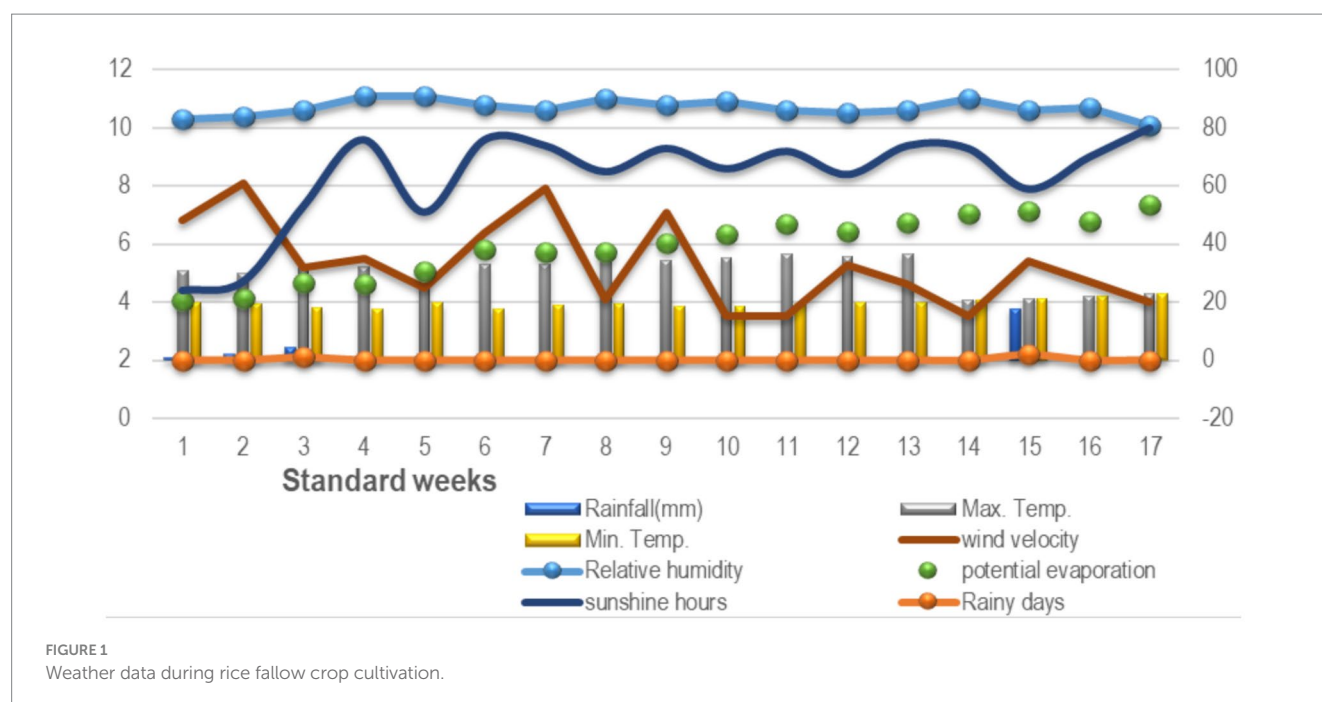
A field experiment was conducted during the rice fallow season of 2024 at the Agricultural College and Research Institute, Tamil Nadu Agricultural University, Madurai, Tamil Nadu. The study area has a subtropical climate characterized by distinct wet and dry seasons, with an average annual rainfall of 970 mm. The weather parameters of the experimental site are shown in Figure 1. The mean maximum temperature reaches up to 35.2°C, the minimum temperature drops to 18.9°C, and the pan evaporation rate is 5.2 mm, with relative humidity ranging between 45 and 82%.

2.2 Treatment design

A total of 18 combinations were evaluated, including three vertical strips and six horizontal strips. Rice fallow crops—V₁: black gram, V₂: sesame, and V₃: proso millet—were arranged in vertical strips. The time of sowing and seed rate for rice fallow crops were as follows: H₁ - recommended seed rate 7 days before harvest (RSR @7DBH), H₂ - recommended seed rate 1 day before harvest (RSR@1DBH), H₃ - recommended seed rate on the day of rice harvest (RSR on DRH), H₄-20% increased seed rate 7 days before harvest (20%ISR @7DBH), H₅-20% increased seed rate 1 day before harvest (20% ISR @ 1DBH), and H₆-20% increased seed rate on the day of rice harvest (20%ISR on DRH). The treatment combinations were replicated three times. The experimental soil texture was sandy loam with a pH value of 7.6, organic carbon content of 0.47%, medium-available nitrogen (212 kg ha⁻¹), available phosphorus (14 kg ha⁻¹), and medium-available potassium (189 kg ha⁻¹). Black gram ADT 6, sesame VRI 5, and proso millet ATL 1 were utilized as test varieties. The seeds were broadcast uniformly throughout the field manually as per the treatment protocol. Data on crop growth and yield attributes were recorded, with seed yield measured in kg plot⁻¹ and converted to kg ha⁻¹. Soil profile moisture depletion was assessed using the gravimetric method, with soil cores extracted at 0–5, 5–10, and 10–15 cm depths on the day of sowing, 30 days after sowing (DAS), and at harvest.

2.3 Experimental design

The experiment used a strip plot design with three replications and a plot size of 5 × 5 m for each combination of the rice fallow crops. To facilitate efficient drainage for each plot, 0.5-m wide irrigation channels were established between each strip. All agronomic practices, including plant protection and fertilizer management, were implemented according to the established agronomic protocols (Chandrasekaran et al., 2010). As the seeds were sown with a standing crop of rice, treatments were applied to the respective plots during the last stage of field preparation, according to the schedule. Statistical analysis was conducted following the method proposed by Gomez and Gomez (1984).



2.4 Biometric observations

The morphophysiological traits and growth attributes of rice fallow crops were examined. The survival rate of the crops after the standing rice crop was harvested with a combine harvester was also determined. Five plant samples were randomly selected from each plot at different phenological stages, specifically 20 and 60 days after sowing (DAS), to assess the impact of various seed rates and sowing times on the growth and yield of rice fallow crops. During sample collection, precautions were taken to prevent root damage. The shoot and root lengths of the selected plants from each plot were measured using a measuring scale. Moreover, 20 days after sowing, the plant density per unit area was determined.

2.5 Moisture content estimation

Soil moisture availability was measured using oven drying methods on the day of sowing, as well as at 20 and 60 days after sowing (DAS).

2.6 Estimation of soil nutrients

Soil samples were collected from each plot before land preparation and after harvest during the cropping season. Soil samples were obtained at a depth of 15 cm, shade-dried, and subsequently transported to the laboratory for further analysis. The quantities of available nitrogen (N), phosphorus (P), and potassium (K) were determined using the modified macro Kjeldahl method (Model KELPLUS Elite EXVA) (Gangopadhyay et al., 2022), the Olsen method (Olsen, 1954), and the flame photometer method (Black et al., 1965), respectively.

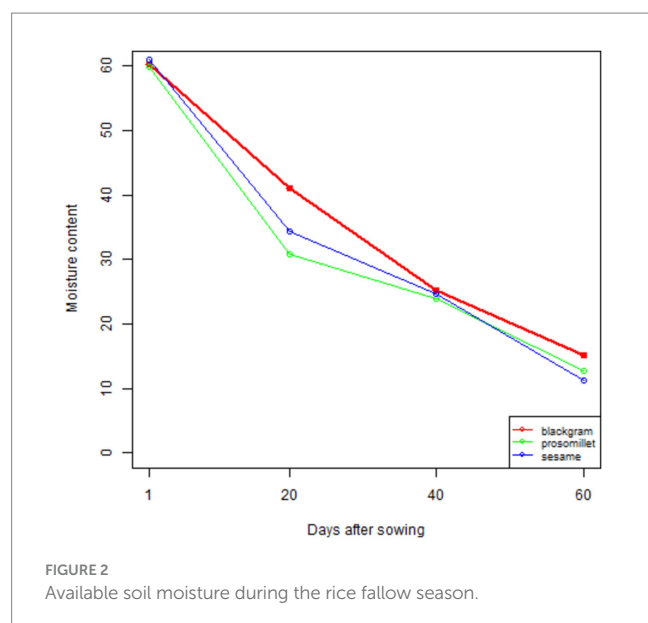
2.7 Statistical analysis

Two-way ANOVA was used to determine the significant differences in crop growth characteristics, yield attributes, and yields among the various treatment combinations. All statistical analyses were performed using R statistical software.

3 Results and discussion

3.1 Soil available moisture

Rice fallow crops are cultivated with residual moisture beneath the soil and supplemented with dew during the cropping season. During the rice fallow season, irrigation facilities are typically unavailable, and rainfall is scarce. Therefore, crop growth and development depend on the effective utilization of carryover residual soil moisture (Kar and Kumar, 2009). The results of moisture content estimation revealed that the moisture content of the soil was approximately 60.3% at the time of sowing and gradually decreased to 36.7 and 16.5% at 20 and 60 DAS (days after sowing), as shown in Figure 2. Severe stress inhibits both legume dry matter accumulation and proportional dependence on symbiotic N fixation as a source of N (Gull et al., 2020). Moisture depletion of up to 53.6% was recorded because it did not affect the growth of black gram, which matures at 60 DAS and is resistant to moisture stress. Midseason drought and heat stress can lead to early maturity and a reduction in grain yield by 50% in the tropics. This is more pronounced in the absence of rainfall during the fall or winter (Ali, 2015). The trend in the soil moisture content revealed that the soil retained a high moisture content due to ground cover by black gram, whereas the decrease in the moisture content in sesame and proso millet was predominantly due to less ground cover, mainly from narrow and erect leaves. Therefore, black gram is considered an ideal plant type for growing under rice fallow conditions.



3.2 Growth attributes

Data on the growth attributes of black gram, sesame, and proso millet indicated that plant population was higher in rice fallow black gram than in sesame and proso millet (Figure 3). The black gram with a 20% increase in the seed rate sown on the day of paddy harvest with the combine harvester had the maximum plant population m^{-2} (29.3 plants), which was comparable to the recommended sowing rate of black gram on the day of paddy harvest with the combine harvester and the sowing of black gram with a 20% increase in the seed rate a day before rice harvest. The ideal plant population for black gram is 32 plants m^{-2} , and the tested treatment, which included a 20% increase in seed rate on the day of harvest, produced results similar to those recommended. In the case of sesame, the plant population increased with a 20% increase in seed rate on the day of paddy harvest using a combine harvester. Unlike manual harvesting, machine harvesting of paddy causes damage to establishing pulse plants due to the trampling effect of wheels during field traversal (Subrahmaniyan et al., 2023). Crop establishment was poor, with proso millet (V3) being sown on the day of paddy harvest. The plant population per unit area was greater when the broadcasting method was used, as opposed to using seed drills in rice fallow for black gram (Amuthaselvi et al., 2019). Regardless of the type of crop, sowing on the day of rice harvest was found to be superior in terms of greater plant population. Therefore, in future, it may be feasible to carryout the sowing of rice fallow crops at the time of harvest.

A taller plant was obtained by sowing a 20% increase in the recommended rate of black gram seeds on the day of rice harvest at 20 DAS (13.7 cm) and 60 DAS (34.7 cm). Similarly, a taller sesame plant was obtained by sowing a 20% increase in the seed rate on the day of rice harvest at 20 DAS (23.4 cm) and 60 DAS (82.3 cm). Shorter plants were observed when the recommended seed rate of sesame was sown 7 days before rice harvest at 20 DAS (20.5 cm) and 60 DAS (79.4 cm). Taller proso millet plants were obtained by sowing a 20% increase in seed rate on the day of rice harvest at 20 DAS (1.83 cm) and 60 DAS (17.8 cm). The shorter plant observed in the proso millet was sown at the recommended seed rate of sesame 7 days before the rice harvest at 20 DAS (16.0 cm) and

60 DAS (34.5 cm) (Table 1). The moisture conditions provided by rice residue enhanced the growth of black gram during the early stages. The leaf area index was greater with a 20% increase in seed rate on the day of paddy harvesting with the combine harvester for all three rice fallow crops: black gram (1.42), sesame (1.83), and proso millet (1.98). This was followed by sowing the rice fallow crops with a 20% increase in seed rate a day before rice harvest in black gram (1.39), sesame (1.77), and proso millet (1.78). The leaf area index was found to be lower when the recommended seed rate was sown 7 days before the rice harvest in the rice fallow crops. The growth characteristics of the rice fallow crops indicated that sowing black gram with a 20% increase in seed rate on the day of the harvest was the ideal combination for effective ground cover and improved growth of the rice fallow crops.

3.3 Yield attributes

The experimental results of the rice fallow crops in machine-harvested rice fields revealed that sowing black gram on the day of paddy harvest produced more pods $plant^{-1}$ (13.7), followed by sowing a day before the harvest (10.2), which was similar to the normal seed rate on the day of the harvest. In the case of sesame, a greater number of capsules $plant^{-1}$ was recorded when broadcast-seeded on the day of paddy harvest using a combine harvester (25.4 $plant^{-1}$). For the proso millet, the maximum number of panicles was 5.0 $plant^{-1}$, as observed during the paddy harvest using a combine harvester. The number of pods $plant^{-1}$ varies significantly among different crop establishment methods, as lower populations per unit area may not favor per-plant yield parameters. Hence, the results indicate that plant density is an important characteristic for determining yield attributes under fallow conditions. This is due to the poor root establishment in plants that were sown before harvest and subjected to mechanical damage. No significant variation among the different treatments was observed for the number of seeds in pod $^{-1}$, the number of seeds in capsule $^{-1}$, or the number of seeds in panicle $^{-1}$. As crops are grown on residual moisture under rainfed conditions, terminal drought severely affects crop productivity (Ali et al., 2014).

Among the rice fallow crops, black gram had the highest grain and haulm yields, with a mean grain yield of 493 $kg\ ha^{-1}$ and a mean haulm yield of 826 $kg\ ha^{-1}$. Sesame produced a mean grain yield of 243 $kg\ ha^{-1}$ and a mean haulm yield of 392 $kg\ ha^{-1}$. Proso millet produced a mean grain yield of 172 $kg\ ha^{-1}$ and a mean straw yield of 434 $kg\ ha^{-1}$. The grain and straw yields were greater when black gram was broadcast on the day of the paddy harvest using a combine harvester. The higher yield of black gram was due to the effective mechanical dibbling of seeds by the combine harvester on the day of the harvest, which resulted in less seed damage and better utilization of residual moisture for crop growth and development (Table 2). Poor yield was observed in proso millet seeds because they were subjected to terminal drought and poor root establishment due to increased bulk density caused by the trampling effect of the combine harvester.

3.4 Soil nutrient status

Appropriate inclusion of summer legume crops in cereal rotation systems is an important aspect of N and C management in fragile soils (Prasad and Nagarajan, 2004). Post-harvest soil analysis (Figure 4) revealed that the soil samples from the rice fallow black gram contained

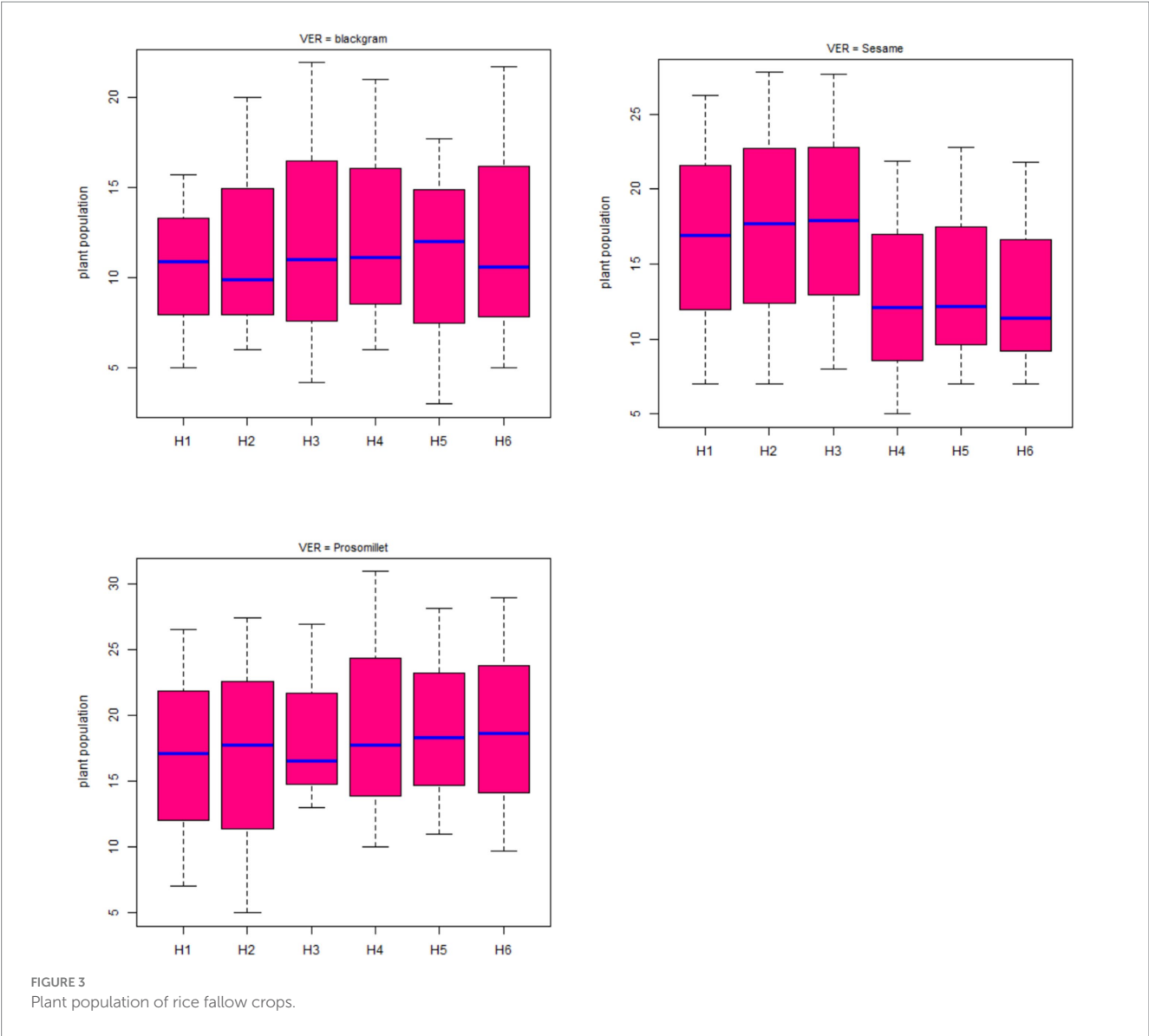
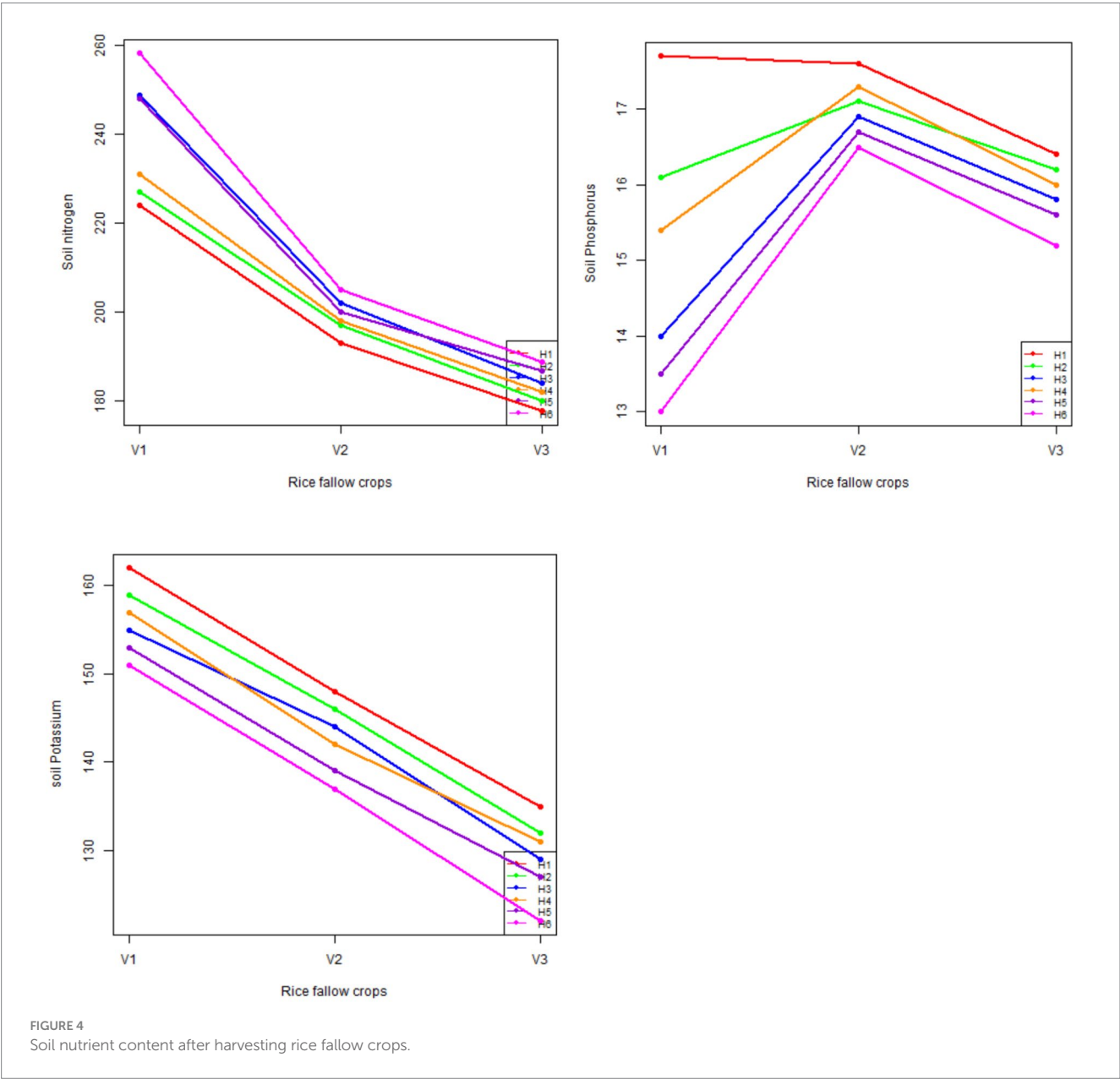


TABLE 1 Effect of seed rate and the time of sowing on the growth attributes of the rice fallow crops.

Crops	Black gram				Sesame				Proso millet			
	Plant height (cm)		LAI	Root length (cm)	Plant height (cm)		LAI	Root length (cm)	Plant height (cm)		LAI	Root length (cm)
Days of observation	20DAS	60 DAS	20DAS	20DAS	20DAS	60 DAS	20DAS	20DAS	20DAS	60 DAS	20DAS	20DAS
H ₁ -RSR @7DBH	11.4	30.3	1.29	15.0	20.5	79.4	1.17	16.1	16.0	34.5	1.21	11.9
H ₂ -RSR @1DBH	12.0	32.2	1.36	16.0	21.4	80.4	1.47	17.8	16.5	36.2	1.82	13.0
H ₃ -RSR on DRH	13.2	33.6	1.37	16.7	22.0	81.5	1.59	18.7	16.7	37.8	1.80	13.6
H ₄ -20% ISR @7DBH	11.7	32.4	1.34	15.9	20.9	80.5	1.23	17.6	16.1	36.9	1.64	12.0
H ₅ -20% ISR @1DBH	12.6	33.4	1.39	16.5	22.9	81.8	1.77	19.0	17.2	37.2	1.78	14.0
H ₆ -20% ISR on DRH	13.7	34.7	1.42	17.0	23.4	82.3	1.83	19.9	17.8	39.8	1.98	14.4
Mean	12.4	32.8	1.36	16.2	21.9	81.0	1.51	18.2	16.7	37.1	1.71	13.2
S.Ed	0.57	0.11	0.004	0.05	0.07	0.08	0.01	0.09	0.04	0.13	0.01	0.06
CD (<i>p</i> = 0.05)	1.14	0.25	0.006	0.10	0.14	0.21	0.03	0.19	0.09	0.26	0.039	0.11

TABLE 2 Effect of seed rate and the time of sowing on the grain yield (kg ha⁻¹) and straw yield (kg ha⁻¹) of rice fallow crops.

Crops/seed rates and days of sowing	Black gram			Sesame			Proso millet		
	Pods plant ⁻¹	Grain yield (kg ha ⁻¹)	Straw yield (kg ha ⁻¹)	Capsules plant ⁻¹	Grain yield (kg ha ⁻¹)	Straw yield (kg ha ⁻¹)	Panicles plant ⁻¹	Grain yield (kg ha ⁻¹)	Straw yield (kg ha ⁻¹)
H ₁ -RSR @7DBH	5.2	368	804	15.0	195	340	1.0	129	406
H ₂ -RSR @1DBH	8.0	440	810	18.0	234	390	2.3	144	430
H ₃ -RSR on DRH	10.0	507	840	20.0	248	407	3.0	177	447
H ₄ -20% ISR @7DBH	6.0	470	811	16.0	241	392	2.1	164	425
H ₅ -20% ISR @1DBH	10.0	577	842	22.3	256	405	3.4	189	445
H ₆ -20% ISR on DRH	13.0	592	851	25.0	280	418	5.2	227	454
Mean	8.6	493	826	19.3	243	392	2.83	172	434
S.Ed	0.18	5.6	1.17	0.25	2.12	1.95	0.11	2.45	1.70
CD (<i>p</i> = 0.05)	0.37	11.2	2.35	0.5	4.25	3.9	0.21	4.90	2.34



the highest quantity of nitrogen (239 kg ha^{-1}), followed by sesame (199 kg ha^{-1}) and proso millet (183 kg ha^{-1}). Similar results were observed when cereal–cereal sequences were used for longer periods with low system productivity and often with poor crop management practices, resulting in a loss of soil fertility due to the emergence of multiple nutrient deficiencies (Dwivedi et al., 2017). A greater amount of available nitrogen in the soil was found in the soil samples from the rice fallow black gram plot because pulses can fix atmospheric nitrogen by nodulating bacteria. The soil samples from rice fallow, sesame, and proso millet did not have the same conditions. The inclusion of pulses in rice fallows can reduce the overall nitrogen (N) requirement for rice while increasing rice yield, residual N content, and total income from the land (Hariharan et al., 2022). Therefore, the experimental results revealed that rice fallow cultivation is an ideal practice in delta regions, where high yields and high incomes may be achieved under farming conditions.

Advancements in agriculture, such as mechanical harvesting of paddy, adversely affect rice fallow crops, and farmers are psychologically hesitant to cultivate rice fallow crops under these conditions. In this context, black gram has been found to be an ideal crop for machine-harvested rice fields. Sowing on the day of rice harvest resulted in mechanical dibbling with high germination, which is effective for both below- and above-ground growth and development. An increased seed rate of 20% is required to compensate for the mechanical damage caused by machine harvesting under fallow conditions. Black gram sown with a 20% (36 kg ha^{-1}) increase in seed rate on the day of rice harvest was found to be the best combination for rice fallow crops in machine-harvested rice fields. The same approach can be recommended for delta areas where rice fallow crops are part of the traditional system. The inclusion of pulses in cereal-based crop rotations enhances input use efficiency and is considered a resource conservation technology.

Data availability statement

The original contributions presented in the study are included in the article/supplementary material, further inquiries can be directed to the corresponding authors.

Author contributions

DJ: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project

administration, Resources, Software, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing. SE: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing, Funding acquisition. AP: Data curation, Writing – review & editing, Conceptualization, Investigation, Methodology, Supervision. GA: Data curation, Validation, Writing – review & editing. BB: Project administration, Validation, Writing – review & editing. SG: Writing – review & editing. JK: Writing – review & editing. SA: Investigation, Resources, Supervision, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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References

- Ali, M. (2015). Improving productivity of pulses in Rice fallows. *Ind. Farm.* 63, 17–19.
- Ali, M., Ghosh, P., and Hazra, K. (2014). "Resource conservation technologies in rice fallow" in Resource conservation technology in pulses, eds P. K. Ghosh, N. Kumar, M. S. Venkatesh, K. K. Hazra and N. Nadarajan (India: Scientific publishers), 83–88.
- Amuthaselvi, G., Dhanushkodi, V., and Eswaran, S. (2019). Performance of zero till seed drill in raising blackgram under rice fallow. *J. crop weed*, 15, 195–197.
- Bandyopadhyay, P., Singh, K., Mondal, K., Nath, R., Ghosh, P., Kumar, N., et al. (2016). Effects of stubble length of rice in mitigating soil moisture stress and on yield of lentil (*Lens culinaris Medik*) in rice-lentil relay crop. *Agric. Water Manag.* 173, 91–102. doi: 10.1016/j.agwat.2016.05.009
- Black, C. A., Evans, D., White, J., Ensminger, L., and Clarke, F. (1965). Methods of soil analysis, vol. I. Madison, Wisconsin: ASA, 1–770.
- Chandrasekaran, B., Annadurai, K., and Somasundaram, E. (2010). A textbook of agronomy. New Age International (P) Limited: New Delhi, 182.
- Dwivedi, B., Singh, V., Shekhawat, K., Meena, M. C., and Dey, A. (2017). Enhancing use efficiency of phosphorus and potassium under different cropping systems of India. *Indian J. Fertil* 13, 20–41.
- Gangopadhyay, S., Banerjee, R., Batabyal, S., Das, N., Mondal, A., Pal, S. C., et al. (2022). Carbon sequestration and greenhouse gas emissions for different rice cultivation practices. *Sustain. Prod. Consum.* 34, 90–104. doi: 10.1016/j.spc.2022.09.001
- Gautam, P., Lal, B., Panda, B., Bihari, P., Chatterjee, D., Singh, T., et al. (2021). Alteration in agronomic practices to utilize rice fallows for higher system productivity and sustainability. *Field Crop Res.* 260:108005. doi: 10.1016/j.fcr.2020.108005
- Geethika, J. D., Subramanian, E., Gurusamy, A., Arunachalam, P., Saliha, B. B., and Kumar, A. S. (2024). Sustainable Rice fallow crop production challenges and opportunities: an overview. *Curr Agri Res.* 12, 530–544. doi: 10.12944/CARJ.12.2.04

- Gomez, K. A., and Gomez, C. M. (1984). Statistical procedures for agricultural research. New York: John Wiley and Sons Inc.
- Gull, R., Bhat, T. A., Sheikh, T. A., Wani, O. A., Fayaz, S., Nazir, A., et al. (2020). Climate change impact on pulse in India-a review. *J Pharmacogn Phytochem.* 9, 3159–3166.
- Hariharan, G., Abhayapala, R., Karunarathna, B., and Zakeel, M. C. M. (2022). “Efficient utilization of rice fallow through pulse cultivation” in *Advances in Legumes for Sustainable Intensification* (Cambridge, Massachusetts: Academic Press).
- Hazra, K., and Bohra, A. (2021). Increasing relevance of pulse crops to sustainable intensification of Indian agriculture. *Springer* 44, 1–3. doi: 10.1007/s40009-020-00948-6
- Kar, G., and Kumar, A. (2009). Evaluation of post-rainy season crops with residual soil moisture and different tillage methods in rice fallow of eastern India. *Agric. Water Manag.* 96, 931–938. doi: 10.1016/j.agwat.2009.01.002
- Kumari, N., and Rahaman, S. (2021). Rice-fallows: a Destiny or opportunity to farmers from Bhagalpur District of Bihar
- Olsen, S. R. (1954). Estimation of available phosphorus in soils by extraction with sodium bicarbonate: US Department of Agriculture.
- Prasad, R., and Nagarajan, S. (2004). Rice–wheat cropping system–food security and sustainability. *Curr. Sci.* 87, 1334–1335.
- Subrahmaniyan, K., Kumar, G. S., Subramanian, E., Raju, M., Veeramani, P., and Ravi, V. (2023). Crop establishment methods and moisture mitigation practices in rice fallow blackgram for productivity enhancement in Cauvery delta zone of Tamil Nadu. *Legume Res. Int. J.* 46, 502–505. doi: 10.18805/LR-4364
- Umamageswari, C., Manimaran, R., and Iyanar, K. (2019). Impact of improved production technologies on yield of rice fallow pulses in Cauvery delta zone. *J Pharmacogn Phytochem.* 8, 963–967.



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Boosting resource use efficiency, soil fertility, food security, ecosystem services, and climate resilience with legume intercropping: a review

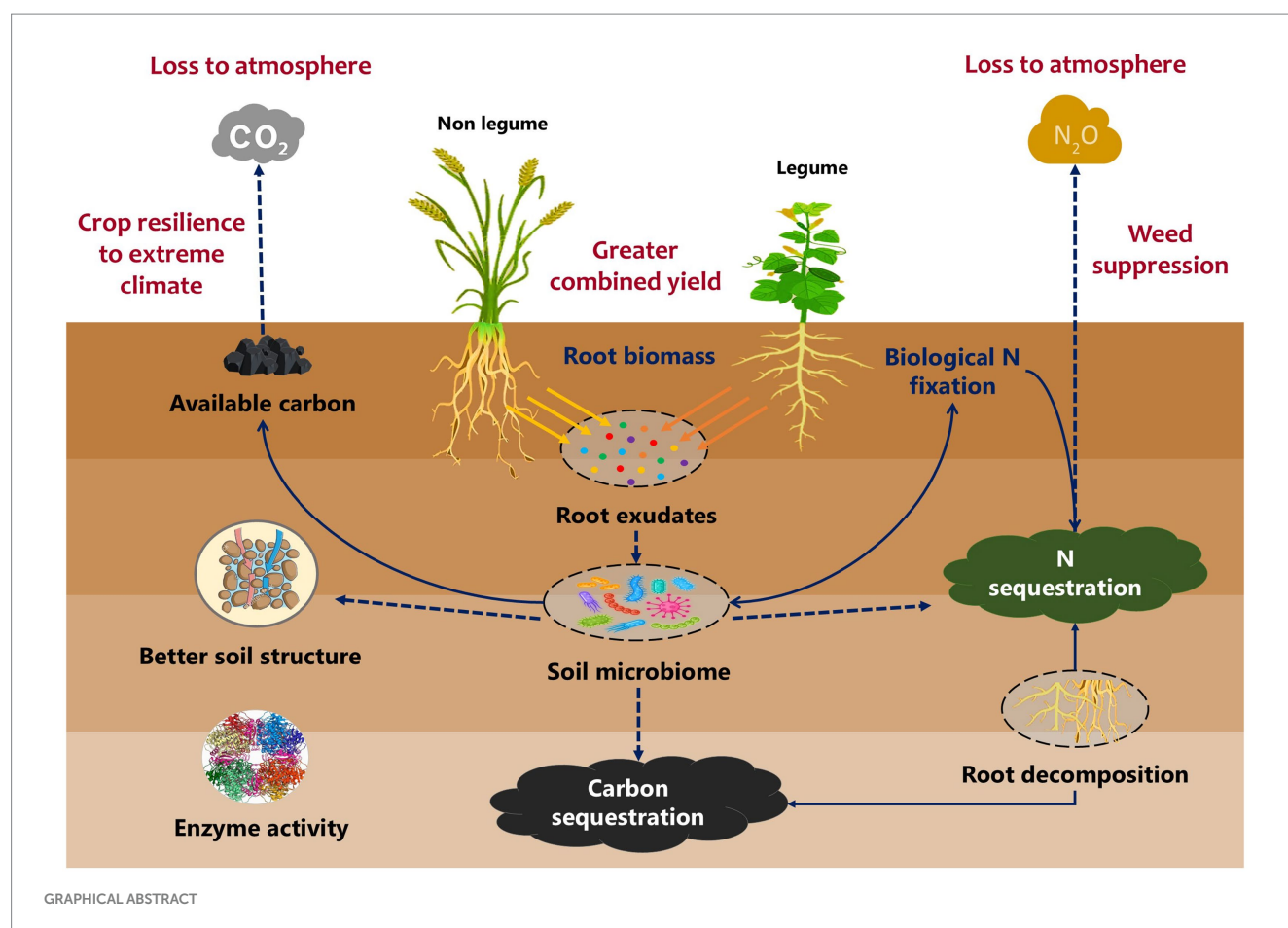
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Adopting sustainable agricultural practices that enhance productivity while preserving ecosystem services is essential to ensure food security for a growing global population and address environmental challenges. This review examines the impact of legume intercropping on nitrogen (N) fixation, soil physio-chemical properties, water retention, pest and disease control, and crop yield across diverse agro-climatic zones and cropping systems. The findings consistently demonstrate that integrating legumes into the cropping system improves soil health by reducing bulk density, breaking up hardpan layers, reducing erosion, increasing soil organic matter, and fixing atmospheric nitrogen (~125 kg N/ha/season) reducing the need for inorganic N fertilizers. It boosts crop yields by 30–35% (in terms of main crop equivalent yield) and land productivity per unit area and time, mitigates total crop loss, and promotes biodiversity. It also improves water use efficiency by 20–25% and enhances nutrient use efficiency by 25–30%. Additionally, legume intercropping reduces yield losses from pests and diseases by 20–25% compared to sole cropping systems. The practice bolsters crop resilience through ecological processes like bio-littering, bio-ploughing, bio-irrigation, and bio-pumping (the “4Bs”), which are valuable for adapting to climate variability. However, research gaps remain, particularly in the optimal selection of legume species for specific regions, suitable agronomic practice for each system, and addressing socio-economic barriers to widespread adoption.

KEYWORDS

intercropping, nutrient cycling, resource utilization, climate resilience, pulses



1 Introduction

The Food and Agriculture Organization (FAO) estimates that by 2050, food production must grow by 70% from 2005 to feed a population of 9.7 billion (Falcon et al., 2022). The modern input-intensive monoculture has boosted food production and self-sufficiency (Belete and Yadete, 2023) but it relies heavily on synthetic fertilizers and pesticides, leading to declining soil health, groundwater depletion, pest and disease outbreaks, environmental problems like eutrophication, greenhouse gas (GHG) emissions, and biodiversity loss (Mrabet, 2023; Ahmed et al., 2022). These challenges, compounded by increasing climate vulnerability, further threaten sustainability. Therefore, sustainable farming strategies are critically needed to increase food production while minimizing environmental harm.

In response to these challenges, researchers and practitioners are advocating for a transition to more resilient and efficient cropping systems that ensure long-term food security without harming the ecosystem (Glaze-Corcoran et al., 2020). Crop diversification, through the introduction of various crops in temporal and spatial arrangements, has emerged as a promising strategy for enhancing agroecosystem health and sustainability (Stomph et al., 2020). Cover crops are plants grown between main crops to improve soil health and protect the land from soil erosion during the off-season. These crops are not harvested for profit. Crop rotation is the practice of planting different crops in the same field in successive growing seasons. Intercropping is the cultivation of more than one crop simultaneously on the same piece of land with a defined row pattern. Intercrops

provide benefits like additional income and insurance against total crop failure. Agroforestry is a land-use management system that combines agricultural crops with trees and shrubs.

Practices like cover cropping, crop rotation, intercropping, and agroforestry significantly improve ecosystem services, such as enhancing soil fertility, increasing water infiltration, reducing erosion, sequestering carbon, and supporting biodiversity (Barman et al., 2022). These practices also conserve soil moisture, reduce synthetic nitrogen (N) fertilizer requirements, lower fossil energy consumption, and suppress weeds and pests (Duchene et al., 2017; Bybee-Finley and Ryan, 2018; Stomph et al., 2020). All these benefits are derived mainly by incorporating legumes in cropping systems. Among crop diversification methods, legume intercropping has garnered significant attention due to its numerous ecological and economic advantages. Legume symbiosis with rhizobial bacteria converts atmospheric nitrogen (N₂) into plant-available forms such as ammonium (NH₄⁺) and nitrate (NO₃⁻), enriching soil N levels and reducing the need for external N inputs (Bybee-Finley and Ryan, 2018). This natural process lowers the environmental impact of agriculture and enhances soil fertility besides promoting sustainability (Stagnari et al., 2017). In addition to N fixation, legumes contribute to improving soil health through various mechanisms. These mechanisms are classified into four 'B's viz., bio-littering, bio-ploughing, bio-irrigation, and bio-pumping (Delaquis et al., 2018).

Bio-littering refers to the accumulation of organic residues like leaves and stems on the soil surface. As these residues gradually decompose, they enrich the soil with nutrients and organic matter, thereby improving its fertility. Bio-ploughing occurs when deep-rooted

plants loosen and aerate compacted soil layers, enhancing root penetration and water infiltration. Similarly, bio-irrigation improves soil water availability by facilitating water movement, ensuring optimal moisture distribution in the soil. Finally, bio-pumping allows deep-rooted plants to draw nutrients and water from the subsoil, redistributing them to the topsoil to benefit companion crops. While the benefits of legume intercropping are well-documented, its adoption remains limited in many regions due to a range of technical, socio-economic, and policy-related challenges (Delaquis et al., 2018).

Overcoming these barriers requires a multifaceted approach that includes improving farmer access to knowledge, resources, and support systems. Providing region-specific guidance on legume intercropping techniques, tailored to local soil and environmental conditions, can help maximize its effectiveness. Additionally, fostering collaboration between researchers, policymakers, and farmers can address socio-economic and policy constraints, creating an enabling environment for wider adoption (Kumawat et al., 2022). This review evaluates the role of legume intercropping in improving soil health, resource use efficiency, and crop productivity across diverse agro-ecological conditions, positioning legume intercropping as a “win-win solution” to address the challenges of food security, environmental sustainability, and climate change. It also explores optimal crop combinations and socio-economic barriers to its broader adoption and recommends suitable interventions to overcome existing barriers.

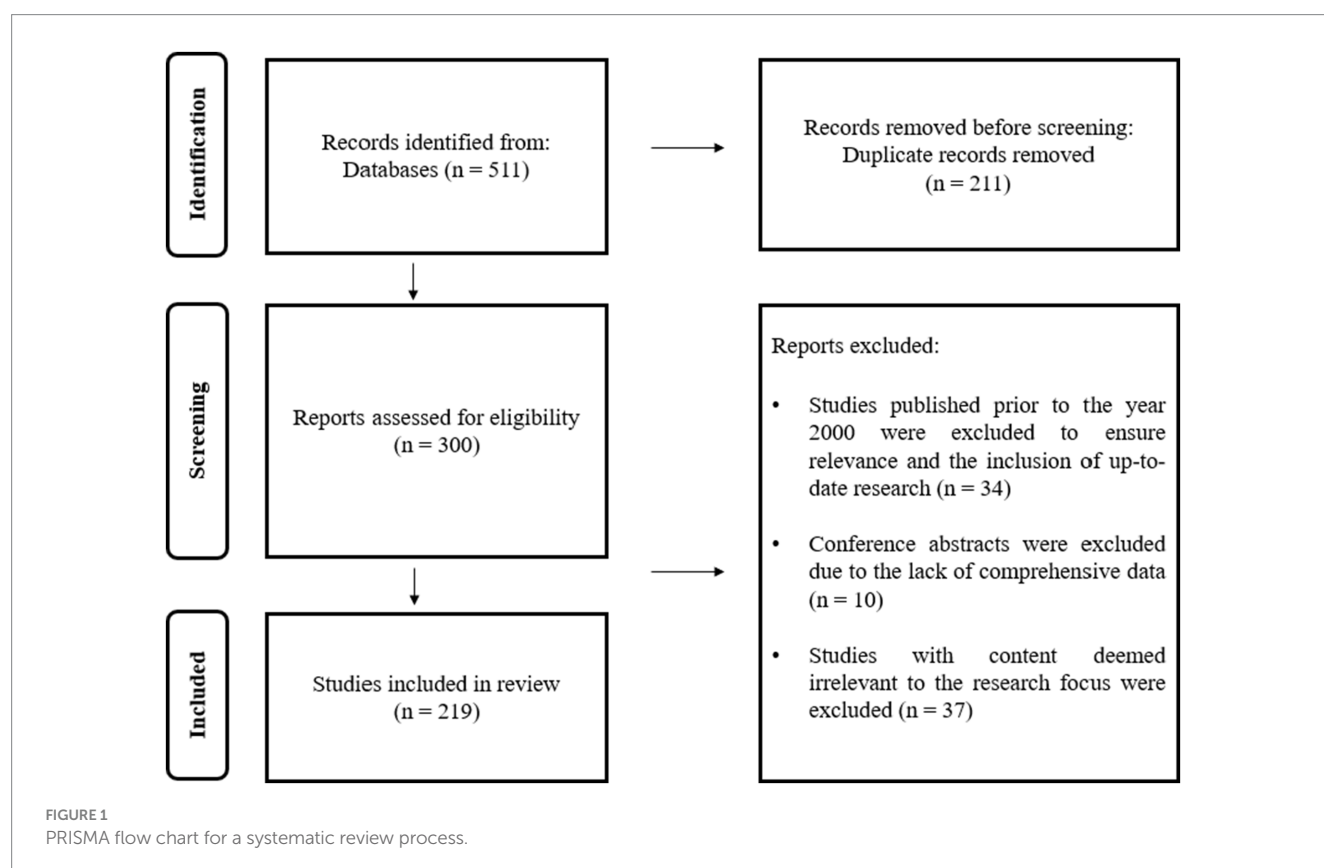
2 Selection of literature

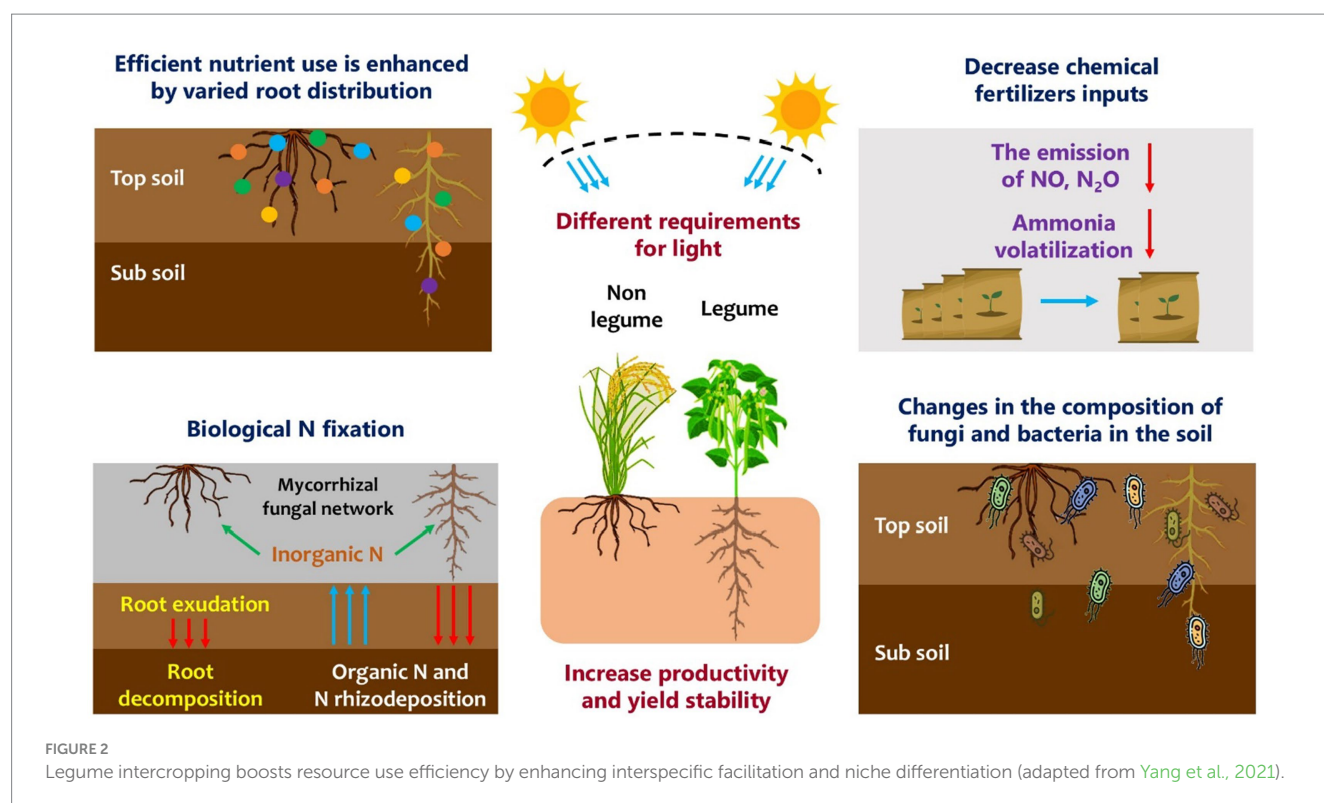
For this review, 511 research articles and book chapters on legume intercropping were gathered from the Web of Science using

keywords such as intercropping, N fixation, nutrient cycling, resource utilization, soil conservation, and climate change resilience. Articles unrelated to climate change resilience, those lacking a focus on N fixation, and certain book chapters were excluded, reducing the pool to 300. A detailed examination of 240 articles followed, specifically focusing on biological nitrogen fixation (BNF) and its role in environmental stability and sustainability. Figure 1 presents the PRISMA flow chart illustrating the systematic review process.

3 Improving resource use efficiency through legume intercropping

Legume intercropping enhances climate resilience by improving resource efficiency and natural suppression of pests, pathogens, and weeds, which in turn boost farm profitability despite increased management complexity and labor needs (Stomph et al., 2020). Intercrops occupy different spatial niches and achieve higher combined productivity than monocultures, resulting in greater yield and economics per unit area (Ahmed et al., 2022). Efficient intercrops often have complementary solar radiation needs, for example, shade-tolerant plants thrive beneath shade-intolerant crops, optimizing space (Sahoo et al., 2023). Intercropping maize and peanuts helps to augment the yield up to 44% more than their respective monocultures. Maize initially outcompetes peanuts, but peanuts recover yield potential after maize harvest. Plants with different root structures utilize various soil layers for nutrients and water, reducing weed pressure and management needs and further decreasing land requirements





compared to separate monocultures at similar densities (Temesgen et al., 2016). Figure 2 illustrates how legume intercropping enhances resource use efficiency by promoting interspecific facilitation and niche differentiation.

3.1 Pest and pathogen suppression

Intercropping typically reduces pest pressure compared to monocultures by hindering pests ability to locate a host plant. Intercrops obstruct pest foraging, camouflage crops, and mask plant odors, making it harder for pests to find targets. For example, when peas and wheat were intercropped, the visual consistency of the wheat field was broken by the contrasting leaves of peas. The pests like wheat aphids found it more difficult to find and target the wheat as a result of this visual disturbance (Aziz et al., 2015). Aerial pests are more likely to land on unsuitable plants in diverse intercrops, reducing their search efficiency and increasing the likelihood of predation before finding a suitable host (Mir et al., 2022). When maize is intercropped with *Desmodium* and napier grass is planted around the field, it repels maize stem borer (*Busseola fusca*). The stemborer moths often land on the *Desmodium* plants, which are unsuitable hosts, thereby delaying their search for maize plants. This delay increases their exposure to natural predators (Rahman, 2021). Similarly, perennial peanuts and coriander lower whitefly populations and reduce yellow mottle virus in tomato crops.

Intercropping reduces disease incidence by altering microclimates, suppressing virus vectors, diluting host plant pools, and fostering plant–soil feedbacks that inhibit them (Huss et al., 2022). For example,

living mulches like buckwheat or white clover between squash rows enhance natural enemies and reduce aphid and whitefly colonization, limiting pathogen spread (Razze et al., 2016). Meta-analyses by Li et al. (2023) showed that legume/grain intercropping reduces pathogen incidence by 34%. Besides harboring pathogens, oilseed/legume intercrops also suppress soil fungi, nematodes, and weeds through allelopathy. Allelopathic chemicals produced by legumes, such as phenolic acids and flavonoids, suppress weed germination and growth. Groundnut (*Arachis hypogaea*) residues have been shown to reduce weed density in intercropping systems by releasing phenolic compounds, including p-coumaric acid, ferulic acid, and caffeic acid, into the soil (Prasad et al., 2020).

A meta-analysis by Chadfield et al. (2022) revealed that intercropping reduces plant-parasitic nematode damage by 40% and disease incidence by 55% by influencing factors like fertilization and crop family. Despite yield reductions from intercrop competition, nematode control offset losses, making intercropping a viable strategy. By enhancing system resilience against biotic stresses, intercropping reduces yield losses by 40–55%, providing significant benefits for sustainable agriculture. This approach enhances biodiversity by supporting beneficial insects, birds, and soil organisms, which boosts ecosystem services and farming sustainability (Duru et al., 2015). Intercropping cowpea with cotton lowers sucking pests, and groundnut with upland rice minimizes stem borers (*Chilo zacconius*) and green stink bugs (*Nezara viridula*). Intercropping peanuts with beans cuts pest incidence of cotton jassid by 30 to 50%, and in soybean-maize intercropping, the incidence of *Spodoptera* in maize is reduced from 15 to 35% (Pierre et al., 2023). Table 1 displays the impact of intercropping on pest and disease control with associated yield increments.

TABLE 1 Impact of legume intercropping on pest and disease control with associated yield increments.

Primary crop	Intercrop	Pest/Disease controlled	Method of control	Yield gain (%)	References
Maize	Beans	Fall armyworm (P)	Disruption of pest movement	17%	Midega et al. (2018)
Groundnut	Sorghum	<i>Aphis craccivora</i> (P)	Natural pest repellence	13%	Balikai et al. (2020)
Cassava	Maize	Cassava mosaic virus (D)	Reduced virus spread due to mixed canopy	14%	Houngue et al. (2019)
Sunflower	Soybean	Sunflower helianthus rust (D)	Diversion of disease to non-economic plant	16%	Soto et al. (2020)
Wheat	Clover	Wheat aphid (P)	Biodiversity increases natural enemies	20%	Storkey et al. (2019)
Pearl millet	Groundnut	Downy mildew (D)	Improved air circulation reducing humidity	22%	Thakur et al. (2011)
Pea	Barley	Powdery mildew (D)	Physical barrier and habitat modification	14%	Devi et al. (2022)
Maize	Cowpea	Stem borer (P)	Disruption of pest habitat	15%	Mutyambai et al. (2022)
Cotton	Groundnut	Bollworm (P)	Groundnut attracts natural predators	25%	Rajendran et al. (2018)

P, Pest; D, Disease.

3.2 Improving water use efficiency

Incorporating legumes with cereals has been shown to enhance water use efficiency (WUE) by 25% over monocultures by optimizing water uptake and reducing soil evaporation, particularly during drought conditions (Fernández-Ortega et al., 2023). Mupangwa et al. (2021) demonstrated a 25% improvement in WUE in maize-groundnut intercropping systems compared to monoculture maize. This enhancement was attributed to the groundnut's shallow rooting pattern, which effectively utilized surface moisture, minimizing competition for subsoil water required by maize. Similarly, Dai et al. (2019) highlighted the benefits of sorghum-cowpea intercropping, where cowpea roots predominantly exploited surface moisture, allowing sorghum to access deeper soil water reserves. This complementary root system facilitated efficient water partitioning and significantly reduced competition between the crops. Venkatesh et al. (2010) reported that lucerne intercropped with maize lifted significant quantities of water from deeper soil horizons, which was subsequently utilized by maize during periods of limited rainfall.

Pulse crops, such as chickpeas and lentils in northern and central India, and mung bean, urd bean, cowpea, and lentil in southern, eastern, and northeastern India, are highly water-efficient. These crops thrive on residual soil moisture and typically require less irrigation than rice, which needs 5–6 irrigations in the same period (Kumar, 2023). Due to their distinct morphology and physiology, pulses not only have a lower water demand but also demonstrate a higher WUE compared to cereals and oilseeds. Additionally, deep-rooted legumes like lucerne and clovers effectively mitigate waterlogging by extracting moisture from deeper soil layers (Jordan, 2022). Among all pulses, dry peas exhibited the highest WUE ($8.3 \text{ kg ha}^{-1} \text{ mm}^{-1}$), whereas chickpeas showed the lower WUE ($5.62 \text{ kg ha}^{-1} \text{ mm}^{-1}$) (Wang et al., 2012). This hydraulic lift

mechanism of legumes, where deep-rooted plants like legumes redistribute water from deeper soil layers to drier topsoil at night, and nutrient-efficient intercropping, underscores the potential of leguminous systems to improve resource efficiency, optimize water use, and enhance crop performance, particularly in low-input and rainfed agriculture. The impact of legume intercropping on improving resource use efficiency is summarized in Table 2.

3.3 The four 'B's concept for leguminous crops

The concept of the four 'B's viz., bio-littering, bio-ploughing, bio-irrigation, and bio-pumping provides an innovative framework for understanding the benefits of leguminous crops in sustainable agriculture. Legumes, offer multiple harvests, improve soil fertility, and enhance nutrient and moisture levels in the soil. Known for their high drought tolerance and biomass productivity, these crops serve as an excellent source of fodder and soil enrichers, thereby supporting soil health and promoting sustainable farming practices amid climate variability and drought conditions (Chitraputhirapillai et al., 2022). Figure 3 demonstrates the four 'B's concept, illustrating how leguminous crops enhance resource use efficiency.

Among these practices, bio-ploughing is an effective soil structure improvement technique in which the deep-rooting abilities of leguminous crops such as pigeon pea (*Cajanus cajan*) and cowpea (*Vigna unguiculata*) alleviate the problem of soil compaction (Chitraputhirapillai et al., 2022). By penetrating compacted soil layers, these crops create micropores that enhance water infiltration and improve soil structure (Dugassa, 2023). Bio-ploughing not only loosens the soil but also reduces soil erosion by increasing infiltration rates (Priori et al., 2020). Additionally, intercropping leguminous crops like

TABLE 2 The influence of legume intercropping on improving resource use efficiency.

Intercropping	WUE under monocropping (%)	WUE undue intercropping (%)	NUE under monocropping (%)	NUE under intercropping (%)	Bio-ploughing	Bio-littering	Bio-irrigation	Bio-pumping	% yield over monocropping	References
Maize + Cowpea	15.4%	20%	20%	25%	Enhances root penetration	Increases OM	Improves water infiltration	Recycles deep N	30%	Tamta et al. (2019)
Wheat + Chickpea	18.7%	22%	22%	28%	Loosens compact soil	Boosts soil fertility	Reduces evaporation	Makes P bioavailable	32%	Betencourt et al. (2012)
Sorghum + Pigeon pea	20%	25%	25%	30%	Breaks up soil compaction	Adds N-rich litter	Deep roots enhance water retention	Accesses deep nutrients	35%	Phiri and Njira (2023)
Barley + Lentil	16.0%	18%	20%	22%	Improves aeration of soil	Improves SOC	Reduces water stress	Pumps up micronutrients	28%	Tosti et al. (2023)
Rice + Mung bean	18.2%	23%	24%	29%	Enhances water percolation	Increases litterfall	Conserves soil moisture	Improves K availability	33%	Li et al. (2009)
Cotton + Groundnut	19.1%	24%	22%	26%	Enhances soil tilth	Recycles crop residue nutrients	Enhances capillary rise of water	Mobilizes P and zinc	34%	Reddy and Mohammad (2009)
Pearl millet + Cowpea	21.5%	27%	25%	30%	Facilitates soil aeration	Improves nutrient cycling	Improves water availability	Increases N uptake	36%	Indoria et al. (2016)
Sugarcane + Soybean	20.7%	25%	23%	28%	Enhances subsoil porosity	Adds OM	Reduces water loss	Brings up micronutrients	35%	Singh (2008)
Maize + Groundnut	17.0%	22%	21.0%	27%	Enhances nutrient mobility	Adds N and carbon to soil	Prevents erosion	Pumps deep minerals like Mg and P	31%	Mubarak et al. (2002)
Wheat + Pea	16.7%	20%	19%	23%	Breaks hardpan	Contributes to N build-up	Retains soil moisture	Increases nutrient availability	30%	Rathi et al. (2024)
Finger millet + Cowpea	18.0%	24%	23%	29%	Increases root penetration	Enhances nutrient recycling	Promotes water storage	Enhances P and K	33%	Peter et al. (2024)
Sunflower + Chickpea	16.0%	21%	20%	26%	Increases soil porosity	Adds organic residues	Retains water in dry periods	Pumps essential nutrients	34%	Shatkovskiy et al. (2022)
Maize + Soybean	19.3%	26%	22%	28%	Loosens soil	Returns high N litter	Improves soil moisture	Mobilizes deep soil N	35%	Ning et al. (2022)
Sorghum + Groundnut	16.6%	22%	23%	30%	Reduces soil compaction	Recycles OM	Reduces water requirements	Pumps P from deeper layers	33%	Mohanty et al. (2024)
Barley + Faba bean	18.5%	23%	22%	28%	Enhances root depth	Improves N availability	Enhances water retention	Pumps up nutrients	32%	Fouda et al. (2022)

(Continued)

TABLE 2 (Continued)

Intercropping	WUE under monocropping (%)	WUE undue intercropping (%)	NUE under monocropping (%)	NUE under intercropping (%)	Bio-ploughing	Bio-littering	Bio-irrigation	Bio-pumping	% yield over monocropping	References
Rice + Soybean	17.9%	24%	21%	27%	Improves soil structure	Adds OM	Improves water percolation	Brings nutrients to surface	34%	Suntoro et al. (2020)
Cotton + Mung bean	18.5%	25%	23%	30%	Increases subsoil aeration	Residue and nutrient recycling	Retains moisture	Mobilizes deep nutrients	35%	Liang et al. (2020)
Wheat + Lupin	16.2%	20%	19%	24%	Increases soil pore space	Increases N reserves	Reduces drought stress	Pumps deep nutrients	31%	Lalotra et al. (2022)
Maize + Lentil	17.0%	23%	22%	29%	Improves root penetration	Returns high N residues	Improves moisture retention	Enhances micronutrient availability	36%	Venkatesh et al. (2014)
Finger millet + Groundnut	19.4%	26%	23%	30%	Increases subsoil fertility	Recycles crop litter	Increases soil water retention	Pumps N and K	34%	Ramachandra et al. (2023)

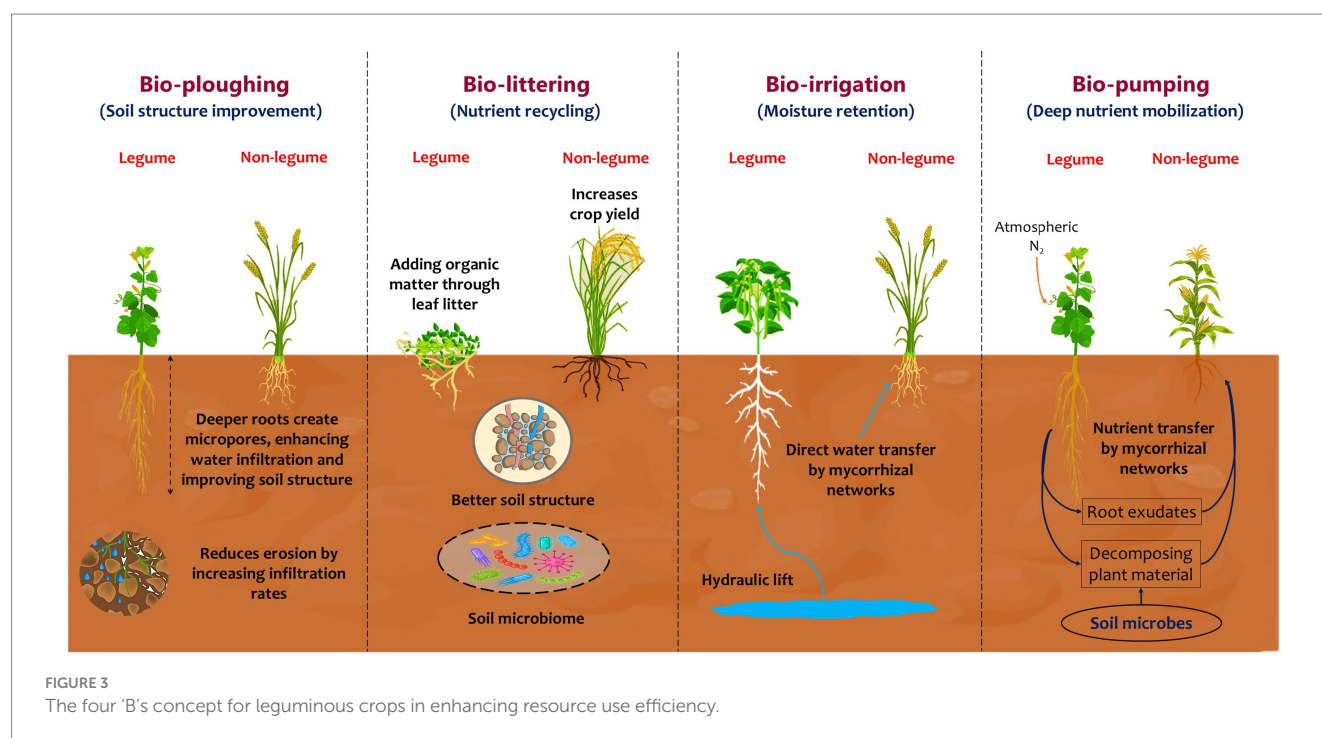
N, Nitrogen; P, Phosphorus; K, Potassium; WUE, Water use efficiency; NUE, Nutrient use efficiency; OM, Organic matter; SOC, Soil organic carbon.

faba bean (*Vicia faba*), clover (*Trifolium* spp.), and pigeon pea (*Cajanus cajan*) with mustard (*Brassica* spp.), rye (*Secale cereale*), and oats (*Avena sativa*) and organic amendments addition has shown to increase soil health and resilience by approximately 35% (Raihan, 2023). This approach reduces the need for mechanical tillage, which in turn lowers fuel consumption and GHG emissions while also supporting sustained improvements in soil organic carbon (SOC) and microbial biomass over multiple cropping seasons (Kumar, 2023). Therefore, bio-ploughing offers a sustainable alternative to conventional soil management methods by enhancing soil structure, water infiltration, and overall agricultural sustainability under legume intercrop systems.

Bio-littering, another beneficial practice, enhances soil health and agricultural productivity by providing a renewable source of organic matter (OM) and nutrients, thereby reducing the reliance on synthetic fertilizers (Mugi-Ngenga et al., 2022). This practice supports sustainable agriculture by fostering soil fertility, promoting environmental sustainability, enhancing nutrient cycling, and reducing GHG emissions (Tahat et al., 2020). Bio-littering of legumes adds OM to the soil through leaf litter and root residues, which increases SOC and N levels and supports higher yields for subsequent non-leguminous crops in rotational systems. Moreover, legume crop litter significantly contributes to nutrient levels in the soil. For instance, Hu et al. (2023) reported that alfalfa (*Medicago sativa*) litter supplies approximately 35 kg N ha⁻¹, while Jensen et al. (2020) reported a N contribution of up to 85 kg ha⁻¹ from faba bean (*Vicia faba*) and clover (*Trifolium* spp.) litter. In total, N from legume litter, stems, and seeds can reach up to 150 kg ha⁻¹, with about 30% of this N returned to the soil (Wang J. et al., 2024).

Pulse crop residues supply between 20 and 80 kg N ha⁻¹, accounting for around 70% of biologically fixed N, depending on the crop and environmental conditions (Lal, 2017). Sequential cropping systems with a preceding pulse crop can add between 18 to 70 kg N ha⁻¹ to the soil, reducing fertilizer needs by 25–30% (Kaur and Singh, 2022). Specifically, faba beans and lentils contribute around 39 kg N ha⁻¹ and 40 kg N ha⁻¹, respectively, through their residues, further improving soil fertility (Lalotra et al., 2022). Intercropping legumes such as chickpeas with cereals like durum wheat has been shown to lower soil pH, enhancing phosphorus (P) solubility and availability (Sharma et al., 2023). Studies have reported a 28.5% increase in available P in the rhizosphere of intercropped systems compared to monocultures (Souid et al., 2024). Additionally, intercropping legumes with cereals is associated with higher biomass production and improved grain yields.

Bio-irrigation and pumping, facilitated by the hydraulic lift mechanism in deep-rooted leguminous crops, offer additional benefits in intercropping systems, particularly in semi-arid or rainfed conditions. The hydraulic lift can provide an additional 25–40 mm of water to the topsoil during dry periods, benefiting shallow-rooted companion crops in intercrop systems (Caldwell and Richards, 1989; Fenta et al., 2022; Kumar and Boraiah, 2022). A study conducted on hydraulic lift in *Cullen pallidum* and *Medicago sativa* showed an improvement in water availability and survival of interplanted *Trifolium subterraneum* under dry topsoil conditions. *T. subterraneum* maintained similar or slower declines in leaf water potential compared to well-watered plants, depending on the interplanted species. Despite alleviated water stress, nutrient uptake in *T. subterraneum* was not enhanced by hydraulic lift (Pang et al., 2013). Research indicates that alfalfa's hydraulic lift can increase upper soil moisture by up to 15% (Wang Y. et al., 2024), while deep-rooted legumes can boost water



availability for neighboring finger millet by approximately 20% (Singh et al., 2020).

4 Nitrogen fixation through legume intercropping

Nitrogen is vital for plant growth and productivity, with most research focusing on BNF in grain legumes, as they obtain up to 75% of their N needs from atmospheric sources (Zhao et al., 2022). Cereal + legume intercropping systems often enhance nutrient dynamics by improving N uptake and overall nutrient status. In these systems, legumes fix atmospheric N_2 , which benefits nearby cereal crops through mechanisms like root interactions, root exudation, and mycorrhizal associations, ultimately increasing N efficiency (Lan et al., 2023). By fixing atmospheric N_2 , legumes contribute to soil N replenishment and nutrient recycling, thriving under low inputs and adverse conditions (Kebede, 2021). For example, wheat + soybean, maize + faba bean, barley + pea, and sorghum + soybean intercropping systems show significant N acquisition improvements compared to sole cropping. Faba bean + maize intercropping showed a 72% increase in N acquisition, underscoring its efficiency in N assimilation (Zhao et al., 2022).

Globally, BNF in cereal-based cropping systems contributes around 50 teragram (Tg) of annual N fixation, with 34.4 Tg originating from grain legumes and 15.6 Tg from non-symbiotic sources (de Moissac, 2020). Legume intercropping systems are valuable for soil fertility, fixing around 150 tons of atmospheric N_2 annually and enhancing soil conservation through increased ground cover compared to monocultures (Ananthi and Parasuraman, 2021). BNF converts atmospheric N_2 into ammonia (NH_3) with the help of rhizobia, meeting up to 80% of the legume N needs (Guo K. et al.,

2023) and reducing synthetic N inputs by 70–90%, thereby promoting sustainable agriculture (Ladha et al., 2022). This process also enhances soil N retention in maize-legume intercropping systems and reduces N leaching by 30% (Gardarin et al., 2022). Similarly, in pulse-wheat rotations, pulses supply 20–40% of the N needed by wheat, showcasing their role in improving N cycling and soil fertility, though the exact N transfer remains challenging to quantify (Tripathi et al., 2021). Overall, BNF not only reduces the reliance on chemical N inputs but also enhances fertilizer efficiency and mitigates environmental impacts. These systems also contribute to reducing nitrate leaching by 10–16% compared to monocultures (Hauggaard-Nielsen et al., 2009).

Research utilizing techniques like ^{15}N labeling has illustrated the direct transfer of N from legumes to neighboring cereals, through root exudation, where nitrogenous compounds like amino acids are released into the soil. Additionally, rhizodeposition of decayed root nodules, and shared mycorrhizal networks facilitate nutrient exchange, enhancing overall N uptake and boosting yield (Raza et al., 2023). However, the spatial arrangement is crucial, as excessive distance between legumes and non-legumes can hinder N transfer. Many findings signified that N competition in legume-cereal mixtures may intensify due to the N-fixing activity of legumes (Kebede, 2021). The effectiveness of legume intercropping depends on factors such as species selection, crop morphology, plant density, cultivation practices, and N-fixing capacity. Legumes adjust the carbon-nitrogen (C:N) ratio and boost soil enzyme activity, which enhances nutrient conversion efficiency. Key legume crops like soybean, common bean, cowpea, lablab, and groundnuts play crucial roles in BNF. Soybeans, for example, can meet 50–60% of their N needs through BNF, highlighting their importance in sustainable N management (Lai et al., 2022).

The symbiotic relationship between legumes and rhizobia is crucial for BNF, a process in which rhizobia infects legume roots to form nodules where N fixation occurs. Well-nodulated legumes can

fix over 250 kg N ha⁻¹ year⁻¹, significantly enhancing plant growth and soil fertility (Fahde et al., 2023). Under optimal conditions, N fixation rates can reach up to 300 kg N ha⁻¹ year⁻¹ (Zhang et al., 2021). The efficiency of N fixation varies among the different species, wherein soybean fixes between 60 and 300 kg N ha⁻¹ year⁻¹, while crops like alfalfa and clover can fix as much as 150–500 kg N ha⁻¹ year. Factors such as soil pH, texture, and OM content have a significant impact on the efficiency of BNF (Issah et al., 2020). Soil pH significantly influences N fixation efficiency in legumes. Soybean had optimal nodulation and N fixation in slightly acidic to neutral soils (pH 6.0–7.0) (Nakei et al., 2023). Similarly, mung beans (pH 6.0–6.5) and alfalfa (pH 6.5–7.5) performed best in slightly acidic to neutral soils, indicating the importance of maintaining optimal soil pH for maximizing BNF.

For example, in a study comparing *Dolichos lablab* + maize (LM), fodder soybean + maize (FM), and maize monoculture (M), the application of 240 kg N ha⁻¹ to the *Dolichos lablab* + maize system increased dry biomass yield and forage quality, achieving a nitrogen use efficiency (NUE) of 59.5% (Zhang et al., 2022). Additionally, maize + legume intercropping saved 25% of N (37.5 kg ha⁻¹) needed for the subsequent wheat crops, indicating that this strategy could improve soil N fertilizer usage and reduce reliance on synthetic N fertilizers by approximately 26% (Nasar et al., 2023). Crops like pigeon pea and chickpea, when intercropped with cereals such as sorghum or maize, can increase soil fertility and N fixation by 30–50% (Chamkhi et al., 2022). These intercropping systems not only boost soil N levels but also enhance microbial diversity in the rhizosphere, supporting nutrient cycling and overall soil health (Solomon et al., 2023). Table 3 represents the pulse intercropping on N fixation in different crops.

Furthermore, excess N fertilizer application poses environmental risks, contributing to nitrate contamination in groundwater and nitrous oxide emissions. Legume intercropping can mitigate these

issues by enhancing resource use efficiency, reducing ammonia volatilization, and lowering nitrous oxide emissions (Hassan et al., 2022). In cereal-legume systems, the competitive N uptake by cereals prompts legumes to fix more atmospheric N₂, indirectly reducing the reliance on synthetic fertilizers, thereby decreasing environmental pollution and nitrate concentrations in the soil and surrounding ecosystems (Grzebisz et al., 2022). Shifting a portion of global cereal cropland to cereal-legume intercropping systems could potentially lower N fertilizer use by 26%, significantly reducing agriculture's carbon footprint.

4.1 Nutrient improvement of legume intercropping beyond nitrogen and phosphorus

Legume intercropping is renowned for enhancing N and P availability via BNF and improved P solubility. Beyond these, it also benefits the cycling and availability of essential macro- and micronutrients such as potassium (K), calcium (Ca), magnesium (Mg), zinc (Zn), iron (Fe), and boron (B) through root exudation, microbial activity, and enhanced soil organic matter. These nutrients are vital for plant growth, productivity, and soil health, making legume intercropping an effective tool for addressing nutrient deficiencies. Intercropping legumes with cereals enhances K availability through root exudation of organic acids, releasing K from non-exchangeable reserves. Maize + legume intercropping has shown a 15–20% increase in soil exchangeable K compared to monocropping (Wang et al., 2014). Deep-rooting legumes like pigeon pea access subsoil K and recycle them to the topsoil through leaf litter and root turnover. Maize + soybean intercropping enhances K uptake and nutrient accumulation in roots and green biomass by 20% with optimal K application (80:60 kg ha⁻¹) compared to no K application (Ahmed et al., 2020). In soybean-based systems, K uptake primarily occurs from shallow soil layers, while intercropping improves K cycling and efficiency (Maciel de Oliveira et al., 2020). Additionally, legumes like alfalfa excrete organic acids that mobilize less-available K forms, benefiting both intercrop species (Gao et al., 2022). This reduces reliance on K fertilizers, especially in K-deficient soils.

Legume intercropping also improves Ca and Mg availability, essential for cell wall stability, enzymatic functions, and photosynthesis. Ca-rich leaf litter from legumes like cowpea and groundnut enriches soil Ca upon decomposition, benefiting associated crops like maize and millet. Legume root exudates solubilize Mg from soil minerals, improving its availability (Sardans et al., 2023). Furthermore, legume intercropping enhances micronutrient bioavailability, such as Zn, Fe, and B, through rhizosphere interactions and microbial activity, promoting enzymatic functions and stress resistance. For example, chickpea + maize intercropping systems increased soil Zn availability by 25% due to microbial solubilization (Kumar et al., 2022). Legume roots release organic acids and phytosiderophores, chelating Zn and making it more accessible to companion crops. Similarly, wheat + lentil intercropping increased Fe uptake by 30%, facilitated by root exudates and microbial siderophores (Siddiqui et al., 2021), benefiting high-pH soils. Additionally, peanut + sorghum systems showed a 15% increase in soil B availability, boosting sorghum grain quality and yield through root-mediated organic compound release (Patel et al., 2019). Targeted management

TABLE 3 Pulse intercropping on N fixation in different crops.

Primary crop	Legume crop	N fixation (kg ⁻¹ ha ⁻¹ year ⁻¹)	References
Maize	Common bean	50–150	Nassary et al. (2020)
Maize, Sorghum	Soybean	100–200	Nakei et al. (2023)
Millet, Sorghum	Cowpea	50–200	Nair et al. (2018)
Maize, Millet	Pigeon pea	50–300	Lavanya et al. (2019)
Wheat	Chickpea	60–120	Koul et al. (2022)
Barley, Wheat	Lentil	50–150	Singh et al. (2022)
Barley, Oats	Pea	70–150	Baxevanos et al. (2017)
Wheat, Barley	Faba bean	150–300	Stagnari et al. (2017)
Rice	Mung bean	50–100	Mutti et al. (2019)
Wheat, Barley	Lupin	100–200	Schreuder (2021)

strategies can optimize these benefits, promoting sustainable agriculture while enhancing soil health and ecosystem resilience.

5 Soil response to legume intercropping

Soil nutrient content is a very good indicator of soil fertility, with crop yield serving as a direct measure of soil health. Legume intercropping has emerged as one of the key strategies for sustainable intensification, providing greater stability in soil fertility and environmental health compared to sole cropping systems. Low soil fertility can limit crop production, but incorporating legumes into cropping systems has been shown to improve soil's physical, chemical, and biological properties by fixing atmospheric N₂, leaf shedding, and mobilizing insoluble nutrients, which in turn enhances nutrient

availability and use efficiency (Table 4). Over a five-year study, Tang et al. (2021) found that intercropping legumes with cereals increased soil OM by 20%, total N by 15%, and available P by 10%, indicating enhanced soil fertility and nutrient availability. Figure 4 illustrates the physiological mechanisms driving interspecific facilitation in the acquisition of N, P, and water in intercropping systems.

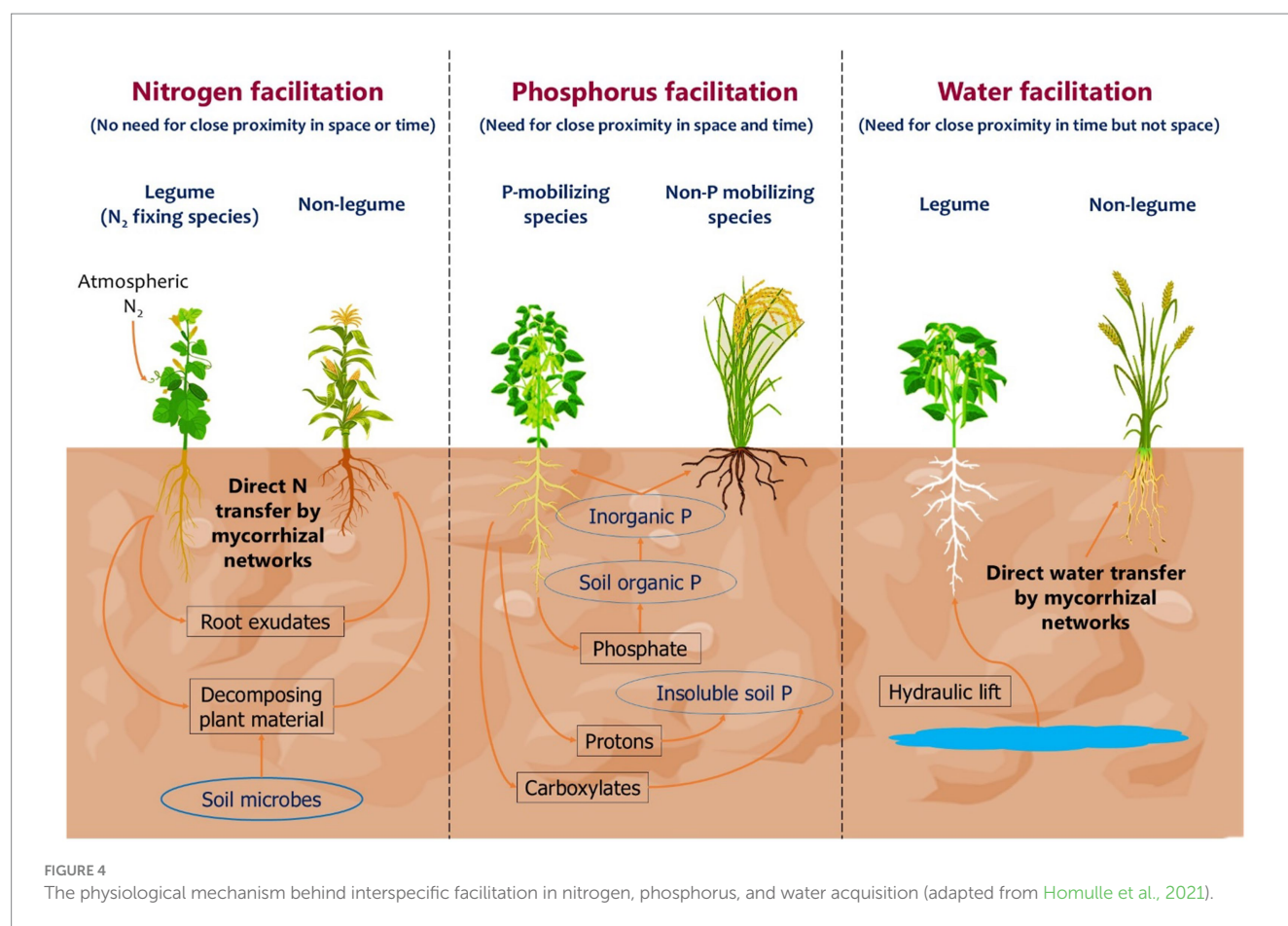
5.1 Physical properties

Legumes play a significant role in enhancing soil physical properties, including bulk density, saturated hydraulic conductivity, and the stability of cracking clay. Legume intercropping systems increase the proportion of macro- and micro-aggregates by 52 and 111%, respectively, compared to sole crops (Garland et al., 2017). This structural improvement helps to reduce soil erosion. For example,

TABLE 4 Impact of legume intercropping on soil physical, chemical, and biological properties.

Intercropping system	Soil physical properties	Soil chemical properties	Soil biological properties	References
Finger millet + Groundnut	Increased water retention	35% higher N content	Increased AMF colonization	Srinivasarao et al. (2012)
Sorghum + Pigeon pea	Enhanced soil aggregation	Boosted soil N by 40%	Increased microbial biomass carbon (MBC)	Weldeslassie et al. (2016)
Pearl millet + Cowpea	Improved infiltration rates	Boosted soil N by 38%	Enhanced rhizosphere microbial activity	Siébou et al. (2019)
Maize + Cowpea	Increased soil porosity and root penetration	Increased soil N by 35%	Increased rhizobia population for N fixation	Eze et al. (2020)
Barley + Lentil	Better moisture retention	Increased cation exchange capacity (CEC)	Improved N-fixing bacteria	Rajpoot et al. (2020)
Cotton + Groundnut	Improved capillary rise of water	30% increase in organic matter	Increased beneficial nematode populations	Chi et al. (2019)
Wheat + Chickpea	Reduced compaction	30% increase in soil organic carbon (SOC)	Increased enzyme activity for nutrient cycling	Mbanyele et al. (2024)
Sugarcane + Soybean	Reduced soil crusting	Balanced pH levels	Enhanced microbial biomass nitrogen (MBN)	Morsy et al. (2017)
Barley + Faba bean	Increased root penetration	31% increase in N content	Enhanced microbial community structure	Dordas et al. (2019)
Wheat + Pea	Reduced soil compaction	28% increase in soil N	Increased fungal diversity	Longepierre et al. (2022)
Rice + Mung bean	Reduced soil erosion	Improved soil pH balance	Enhanced root exudates promoting microbial growth	Papong and Cagasan (2020)
Finger millet + Cowpea	Increased porosity	34% higher N content	Increased beneficial fungi	Peter et al. (2024)
Maize + Groundnut	Reduced bulk density	Improved N (36%) availability	Higher rhizobia populations	Ajayi (2015)
Sunflower + Chickpea	Enhanced water infiltration	Increased N by 32%	Increased enzymatic activity	Ullah et al. (2018)
Sorghum + Groundnut	Enhanced moisture retention	Increased N by 39%	Increased AMF colonization	Watts-Williams et al. (2022)
Maize + Soybean	Better root structure	Boosted N and SOC levels	Increased microbial biomass	Bawa et al. (2019)
Cotton + Mung bean	Enhanced root proliferation	33% increase in soil N	Increased rhizobia activity	Ali et al. (2020)
Rice + Soybean	Increased soil aggregation	Increased N and P levels	Increased root-associated microbes	Nascente and Stone (2018)
Maize + Lentil	Enhanced root penetration	Increased N by 38%	Increased fungal and bacterial diversity	Razavi et al. (2016)
Wheat + Lupin	Increased porosity	Increased soil N (27%)	Increased enzyme activities	Esnarriaga et al. (2020)

N, Nitrogen; P, Phosphorus.



sorghum + cowpea intercropping decreased runoff by 20–30% compared to sole sorghum and by 45–55% compared to monocropped cowpea, resulting in a 50% reduction in soil loss. Intercropping systems, particularly with maize and soybean or legumes and cereals, enhance soil structure, increasing aggregate stability by 20% and reducing bulk density by 12% over 3 years (Bhattacharyya et al., 2023). Similarly, Rajanna et al. (2022) reported that intercropping systems increased aggregate stability by 15% and reduced bulk density by 10% over 3 years, enhancing water infiltration and aeration. As anchor crops, legumes effectively enhance soil structure and water infiltration, particularly under semiarid and rainfed conditions, making them ideal for intercropping with fast-growing, shallow-rooted crops. In pigeon pea + maize intercropping, root interactions, and biochemical activities improve soil structure and nutrient storage, especially in P-sorbing soils. This raised organic P storage in micro-aggregates to 84 mg P kg⁻¹ in intercrop versus 29 mg P kg⁻¹ in sole maize (Chamkhi et al., 2022).

5.2 Chemical properties

In semi-arid areas, legumes such as lablab and soybean increase soil OC, available P, and total N while simultaneously reducing exchangeable cations and C:N ratios compared to weedy fallows (Nigussie et al., 2021). Cuartero et al. (2022) reported that melon + cowpea intercropping increased total soil carbon by 25% and total N by 18% compared to mono-cropping due to higher populations of

nutrient-cycling bacteria like rhizobia. Similarly, Cong et al. (2015) found that intercropping maize with wheat or faba bean raised SOC by 4% and organic N by 11%, with carbon and N sequestration rates of 184 kg ha⁻¹ yr⁻¹ and 45 kg N ha⁻¹ yr⁻¹, respectively. Hussain et al. (2024) found a 20% rise in SOC over 3 years when intercropping soybeans with maize, compared to monoculture maize. Similarly, Virk et al. (2021) observed a 15% increase in SOC over 4 years with clover or vetch in maize + wheat systems, due to increased residue and microbial activity.

Furthermore, legume + cereal intercropping significantly enhances P availability and uptake. A meta-analysis by Tang et al. (2021) on P efficiency in cereal + legume intercrops found a significant increase in P absorption and a soil equivalent ratio for P uptake averaging 1.24. The net effect for P uptake was 3.67 ± 1.00 kg ha⁻¹, with an absolute gain of 6.87 kg ha⁻¹ due to intercropping, demonstrating improved P use efficiency and reduced fertilizer need compared to sole crops. In northwest China, intercropping systems like maize + turnip, maize + faba bean, maize + chickpea, and maize + soybean showed higher P acquisition than monocultures, with faba bean's P uptake increasing by 42.4% at flowering. Fertilizer P recovery in intercropping improved from 6 to 30% at 40 kg ha⁻¹ and from 5 to 14% at 80 kg ha⁻¹ (Yang et al., 2021). Betencourt et al. (2012) found increased P availability in durum wheat + chickpea intercrops due to root-induced alkalization and exudation. Similarly, Guo L. et al. (2023) showed soybean root exudates boost N mineralization by 30% and P availability by 25%. Legumes improve P availability through root exudates like piscidic acid, which releases P from iron-phosphate

complexes (Sugihara et al., 2021). Their deep root systems offer drought tolerance and access nutrients from deeper soil layers reducing dependence on synthetic fertilizers and promoting sustainability (Shoaib et al., 2022).

5.3 Biological properties

A study comparing a 30-year maize monoculture with intercropping systems found *Sphingomonas* resistant to monoculture effects, while *Massilia* and *Haliangium* served as sensitive bacterial indicators, highlighting intercropping's role in enhancing soil health and biodiversity (Wolińska et al., 2022). Field experiments with maize + sesame, maize + peanut, maize + soybean, and maize + sweet potato intercropping showed increased microbial diversity, particularly fungi and bacteria, measured by species richness, Shannon index, and evenness. Notably, maize + peanut intercropping yielded the highest bacterial species richness (Xiao et al., 2023).

Legume intercropping significantly enhances soil properties by increasing microbial diversity, which improves nutrient cycling, OM turnover, nitrification, and soil structure. These microbial changes boost plant growth and health, highlighting the benefits of diverse soil bacterial communities in legume intercropping systems. Work done by Song et al. (2007) found that intercropping systems like wheat + faba bean, wheat + maize, and maize + bean increased soil microbial biomass and C: N ratios compared to monocultures. This indicates that intercrops with higher OM foster diverse and active microbial communities, enhancing soil enzymatic activities such as dehydrogenase, urease, and phosphatase. Additionally, Hao et al. (2022) found that maize root exudates increased microbial diversity and biomass by 20%, showing the impact of specific crops on microbial communities. Soil microbial community composition is influenced by environmental factors, fertilization practices, agricultural practices, and planting patterns, which account for around 26.7% of bacterial community variation.

Intercropping impacts microbial community structure, affecting soil P and carbon cycling through changes in microbial biomass phosphorus (MBP) and carbon (MBC). Legume intercropping enhances crop productivity by increasing the presence of N-fixing bacteria like *Bradyrhizobium* and *Skermanella* (Yang et al., 2019). Molecular methods reveal that intercropping enhances rhizosphere bacterial diversity compared to monocropping, increasing the abundance of ammonia-oxidizing bacteria (AOB), ammonia-oxidizing archaea (AOA), and nitrite-oxidizing bacteria (NOB), which are crucial for nitrification. Intercropping with rhizobium inoculation boosts the abundance of total bacteria, archaea, AOB, and AOA, potentially reducing nitrification in the rhizosphere. Therefore, legume intercropping represents an effective strategy to optimize beneficial rhizobacterial colonization, offering a sustainable alternative to chemical fertilizers by naturally enhancing soil health and nutrient cycling.

Legumes play a critical role in altering soil-borne pathogens and reducing pathogenic microbial loads through mechanisms such as biological control and soil health enhancement. Their interactions with beneficial microorganisms, including actinobacteria and rhizobia, significantly contribute to disease suppression and improved crop productivity. For example, *Streptomyces* strains have proven effective in controlling soil-borne pathogens that affect legumes like

chickpea and pigeonpea, which are often susceptible to diseases such as wilt and collar rot (Gopalakrishnan and Srinivas, 2019). Similarly, *Sinorhizobium saheli* has demonstrated the ability to suppress root pathogens in arid legumes, enhancing root nodulation and achieving seed yields of up to 1,325 kg ha⁻¹ when co-inoculated with other beneficial microbes (Gautam et al., 2015). In addition to pathogen suppression, legumes improve soil fertility through BNF, fostering microbial communities that compete with pathogens for resources (Kalyan et al., 2024). However, the effectiveness of legumes in managing pathogens is influenced by soil conditions and competing microbial communities, which underscores the importance of understanding these dynamics for sustainable agriculture. Despite their benefits, legumes remain vulnerable to specific root diseases, potentially limiting their effectiveness in certain conditions (Pilet-Nayel et al., 2024). Therefore, integrated disease management strategies are essential to balance the benefits and vulnerabilities of leguminous crops, ensuring their success in diverse agricultural systems.

5.4 Soil conservation through legume intercropping

Soil conservation is essential for adapting to climate change, ensuring soil health, and supporting crop growth by providing crucial minerals. However, extreme weather events, such as heavy rainfall and strong winds, can worsen soil erosion. In semiarid regions, practices, like tree planting and establishing hedgerows, help combat wind erosion, while in humid and coastal areas, vegetation cover, contour ploughing, and contour hedgerows are commonly adopted to control soil erosion. Intercropping has proven to be an effective solution to these challenges, especially when combined with conservation practices like cover cropping and mulching, which can reduce erosion by up to 50% (Lal, 2018), thus improving soil integrity and environmental resilience. For example, intercropping cowpeas with maize (two rows of maize with one row of cowpea) reduced runoff by 10% and soil loss by 28% compared to maize monoculture. Similarly, barnyard millet showed the lowest runoff (36% of rainfall), followed by soybean and maize at 37 and 42%, respectively (Tiwareti et al., 2023).

In drylands, intercrops like soybean, groundnut, or cowpea with maize, sorghum, or pearl millet have been effective at controlling soil erosion. In mountainous regions like the Himalayas, vegetative barriers have proven to be effective, reducing runoff by 18–21% and soil loss by 23–68% on slopes of 2–8%. Barriers made from pigeon pea, with its dense canopy cover of 95–98%, reduced runoff by 28–29% and soil loss by 2.1 to 2.6 tons per hectare in a sequence with finger millet, kodo millet, and lentil. Converting just 10% of a field to native perennial vegetation can cut sediment runoff by up to 95% and reduce P and N losses by over 85% (Tiwareti et al., 2023). Greater plant species diversity enhances soil carbon and N stocks through greater root biomass, improving carbon storage and potentially displacing fossil fuel use. Long-term field experiments conducted since 2003 showed that intercropping systems, such as maize + wheat, maize + rapeseed, and maize + pea, have higher SOC and N compared to monocultures (Wu et al., 2024). These intercropping systems not only yield more grain but also emit 50% less carbon per hectare per millimeter of water than maize monoculture. Furthermore, maize

silage intercropped with forage sorghum has demonstrated a 7.3% lower global warming potential compared to maize silage alone.

Intercropping also helps address soil contamination. For example, faba bean intercropped with *Sedum alfredii* and inoculated with a plant growth-promoting endophyte showed improved biomass production and enhanced removal of heavy metals like cadmium (Cd) and lead (Pb) from soils. This improvement is attributed to the synergistic interaction between the legume and the endophyte, which collectively enhanced the plant's ability to tolerate and uptake heavy metals. This intercropping system successfully reduced the concentrations of Cd and Pb in faba beans and maintained its concentration within permissible limits ($0\text{--}0.2\text{ mg kg}^{-1}$), making it a viable solution for managing soil contamination (Rezende et al., 2020). Thus, intercropping not only enhances soil health and fertility but also plays a crucial role in climate change mitigation, erosion control, and addressing soil contamination, contributing to sustainable agricultural systems.

6 Yield response to legume intercropping

Legume intercropping has gained recognition for its ability to enhance yields compared to traditional monocultures (Glaze-Corcoran et al., 2020). Intercropping has been consistently shown to improve land-use efficiency (more yield per unit area compared to monocultures), as demonstrated by enhanced Land Equivalent Ratios (LERs). Supporting this, a meta-analysis of 126 studies across 41 countries revealed that intercrops produced 38% more biomass on average, with a mean LER of 1.38, highlighting their superior productivity and resource-use efficiency. Similarly, Feng et al. (2021) observed that maize + peanut and maize + soybean intercropping systems improved land-use efficiency, with LERs increasing by 20–30%, reflecting better resource utilization due to the differing root depths and growth habits of these crops.

Vertical stratification in intercropping systems reduces competition for resources like light and nutrients, enhancing overall productivity. However, the effectiveness of intercropping can vary with soil conditions, and initial root competition may hinder early growth, as seen in pea + barley systems, where pea plants experienced a 15–20% reduction in shoot dry matter (Giuliani et al., 2024). Nevertheless, promising combinations such as N-fixing legumes, deep-rooted species like lucerne, and autumn-sown oilseeds and cereals have shown significant potential. For instance, mean LER values for barley + faba bean intercropping ranged from 1.05 to 1.23 (Salinas-Roco et al., 2024). In sub-Saharan Africa, maize + common bean intercrops achieved LERs of 1.48 to 1.55 (Gidey et al., 2024).

In northwest China, intercropping systems involving faba bean + maize, chickpea + maize, and soybean + maize significantly increased grain yields by 24, 45, and 39%, respectively, illustrating the role of intercropping in boosting productivity while supporting sustainable intensification (Nasar et al., 2024). Biodiversity within intercropping systems also enhances the temporal stability of biomass production (Markos and Yoseph, 2024). Kahrarian et al. (2021) found that optimal intercropping ratios of barley and vetch improved both grain yield and forage quality. In conservation agriculture systems, maize yields ranged from 2,800 to 3,000 kg ha⁻¹ under sole cropping conditions. However, when intercropped with legumes, yields

significantly improved, reaching 3,609 kg ha⁻¹ with groundnut and 3,307–3,576 kg ha⁻¹ with common bean (Mupangwa et al., 2021; Dai et al., 2019). Crop complementarity in intercropping systems capitalizes on the unique traits of each species to boost productivity (Pelzer et al., 2020).

Intercropping maize with short-grain cereals or legumes, which have distinct growth periods from maize, results in higher absolute gains compared to monocultures (Kakraliya et al., 2018). In China, high-input intercropping systems with multi-row configurations have achieved yields approximately four times higher than low-input strategies. Both high- and low-input intercropping conserve 16–29% of land and 19–36% of fertilizer compared to monocultures. These gains result from enhanced resource efficiency, nutrient uptake, optimized light interception, and improved water use, along with reduced pest pressure and healthier soils (Yu et al., 2022). Economically, intercropping benefits farmers through reduced input costs, diversified income streams, and access to premium markets. Legume intercropping alone can lower fertilizer costs by 25% and pesticide costs by 30% (Raza et al., 2023). Furthermore, sustainably produced products often command a 10 to 30% price premium, providing economic stability by mitigating risks from fluctuating input prices and market volatility (USDA Economic Research Service, 2023). Table 5 summarizes the distribution and LER figure of the main intercropping systems of selected countries. Through careful crop selection and spatial arrangement, intercropping offers significant environmental and economic benefits, ensuring long-term productivity and resilience.

Optimal spatial arrangements and planting densities are critical for maximizing resource use and yield stability (Gaikwad et al., 2022). For example, planting legumes in wide rows or alternating them with cereals like maize or sorghum enhances sunlight interception and soil nutrient utilization, directly contributing to improved crop productivity (Toker et al., 2024). Feng et al. (2022) demonstrated that spatial configurations like narrow-wide-row relay-intercropping improve light interception and photosynthesis, reinforcing intercropping as an effective strategy for enhancing yields and maintaining ecosystem health. Row intercropping reduces light competition and pest incidence, resulting in healthier crops and higher yields. Similarly, strip intercropping facilitates efficient mechanical operations and optimizes resource distribution, further enhancing yield potential. Mixed intercropping, by creating diverse microhabitats, promotes plant growth and resilience, enabling crops to better withstand environmental stresses and achieve greater productivity (Benmrid et al., 2023). Effective spatial arrangements, such as row and strip intercropping, have been shown to increase yields by 10 to 20% (Liu et al., 2017). Recent studies have also emphasized the potential of soil amendments such as N fertilization and biochar to enhance yield and nutrient efficiency in intercropping systems (Hu et al., 2021; Wang et al., 2023).

6.1 Economics and cost benefit of legume intercropping

Intercropping has consistently demonstrated its ability to improve economic efficiency and deliver greater benefits compared to monocropping across various agricultural systems. This sustainable practice optimizes land and resource utilization, leading to higher

TABLE 5 Distribution and land equivalent ratio (LER) of different intercropping systems in selected countries.

Continent	Country	Intercropping system	LER	References
Africa	Ethiopia	Wheat + Faba bean	1.03–1.17	Maalouf et al. (2022)
	Mozambique	Maize + Cowpea	1.53–1.91	Dimande et al. (2024)
Asia	China	Maize + Soybean	1.33	Nasar et al. (2023)
		Maize + Soybean	1.91–2.13	Chen et al. (2019)
		Maize + Faba bean	0.94–1.47	Xia et al. (2013)
	India	Maize + Soybean	1.1–1.6	Banik and Sharma (2009)
		Rice + Peanut	1.66	Sarkar and Pal (2004)
	Iran	Sunflower + Soybean	0.82–1.28	Hamzei and Seyyedi (2016)
Europe	England	Maize + Faba bean	1.02–1.23	Barker and Dennett (2013)
	Italy	Ryegrass + Clover	1.1–1.2	Giambalvo et al. (2011)
North America	Canada	Pea + Barley	1.13–1.31	Kwabiah (2005)
		Pea + Oat	1.13–1.29	
Oceania	Australia	Wheat + Chickpea	0.97–1.10	Jahansooz et al. (2007)
South America	Brazil	Cowpea + Beet	1.05–1.11	Chaves et al. (2020)

yields and profitability. For instance, maize + soybean strip intercropping has proven highly lucrative, with ideal configurations yielding 23,965 CNY ha⁻¹ (Kou et al., 2024). Similarly, in Ethiopia, eucalyptus + maize intercropping outperformed monoculture systems by achieving a land expectation value (LEV) of \$3,677.5 USD at a 15% interest rate (Belay and Melka, 2024). Moreover, vegetable intercropping, such as kale with carrots and mustard, enhanced land use efficiency by 184%, surpassing monoculture profitability (Parajara et al., 2024).

Additionally, a meta-analysis by Mudare et al. (2022) highlighted the economic advantages of maize and grain legume intercropping, revealing gross incomes of US\$ 3,188 ha⁻¹ in China and US\$ 1,519 ha⁻¹ in Africa, significantly higher than the US\$ 1946 ha⁻¹ and US\$948 ha⁻¹ generated by monocropping in these regions, respectively. Among maize-legume systems, maize + soybean intercropping in China delivered the highest gross income of US\$ 4,124 ha⁻¹, while in Africa, maize + common bean intercropping with US\$ 1932 ha⁻¹. Furthermore, Singh et al. (2021), explored chickpea (*Cicer arietinum* L.) and lentil (*Lens culinaris* Medik.) intercropping with linseed (*Linum usitatissimum* L.) and Indian mustard (*Brassica juncea* L.). Their study found that chickpea and Indian mustard intercropped in a 4:2 ratio yielded the highest net return of Rs. 81,168 ha⁻¹. Similarly, Meena et al. (2024) reported that the chickpea + mustard system (6:2 ratio) in southeastern Rajasthan achieved the best net returns of Rs. 93,681 ha⁻¹, with a benefit–cost (B:C) ratio of 3.11. Despite these advantages, challenges such as management complexity and potential yield reductions must be addressed for optimal decision-making.

7 Potential risks of legume intercropping and possible solutions

Despite their benefits, legume intercropping systems face limitations, often confined to mixed farms or collaborations for

biomass supply. Legume intercropping presents several challenges due to its complexity, as it involves growing multiple crops simultaneously in the same field. Challenges, such as nutrient management, difficulties in establishing crops and maintaining optimal legume proportions, increased labor requirements, production costs, etc., hinder widespread adoption (Burgess et al., 2022).

7.1 Complexity in management

Intercropping encounters complexity in various aspects of planting, management, and harvesting, leading to higher labor costs and difficulties in scaling up mechanized farming. Farmers must carefully determine optimal seeding rates, sowing depths, compatible plant combinations, equipment use, herbicide applications, harvesting stage, and marketing options. For example, intercropping large-seeded peas with small-seeded canola involves precise seeding rates, planting depths, and fertilizer placement to effectively capture soil moisture. The multiple passing of seeders results in seedbed compaction and increased labor demands. However, innovations like affordable multi-crop seeders allow single-pass planting of multiple species, while ensuring precision sowing depths, making legume intercropping more feasible (Madsen et al., 2022).

Harvesting intercrops also poses challenges as the crops mature at different times and require multiple harvests. The introduction of a second crop disrupts rotation schedules, adding complexity to farm operations. Harvesting crops with different maturities requires specialized equipment, which may not be accessible to resource-limited farmers. In contrast, strip intercropping, where crops are grown in wider bands, allows for separate harvesting if the strips are wide enough to accommodate existing machinery. However, this method often increases labor demands for managing weeds, fertilizer application, and crop care, increasing production costs and making it less profitable. Grain separation is another significant challenge in intercropping when crops have similar grain sizes, necessitating

careful crop combination selection. Farmers have addressed this issue by calibrating combine rotors and fans or developing custom seed separation systems. While effective, these solutions increase labor and equipment costs, highlighting the need for further research to optimize profitability.

To better support legume intercropping, several advancements are necessary. These include developing suitable herbicides for mixed cropping systems, grain separation facilities, and studies on intercropping's impact on crop rotations. Policy measures such as carbon credits and expanded crop insurance options could further encourage adoption. Additionally, farmers need intercropping practices tailored to local conditions, including climate, soil type, and production goals, to optimize productivity (Brandmeier et al., 2021). Overall, while legume intercropping promotes sustainable agriculture and resource efficiency, it requires innovative management strategies, technological advances, and policy support to overcome inherent challenges.

7.2 Complexity in yields

Legume intercropping offers benefits such as weed, pest, and pathogen suppression, but yields vary based on context. Additive intercrops, planted between existing crop rows, can reduce yields due to heightened competition, especially in non-legume systems. In contrast, substitutive intercrops, where a portion of the main crop is replaced to limit competition, can improve per-capita crop yields but may lower overall yield per area. Although legume intercropping generally increases LER and ecosystem benefits, these advantages do not always result in yield gains. Suggesting competition may limit productivity more than pest pressure (Shanmugam et al., 2022).

In semiarid regions, legumes compete with cereals for water, negatively affecting yields. For instance, faba beans reduced soil water availability for intercropped maize, increasing kernel abortion rates and lowering yields (Wang M. et al., 2024). Legumes may also compete for N, inhibiting their N fixation capabilities. High soil N levels reduce legume's ability to fix atmospheric N, impacting growth and yield (Salinas-Roco et al., 2024). In olive agroforestry systems, legume intercropping caused yield reductions of approximately 33% for legumes and 47% for cereals compared to sole cropping, indicating potential negative impacts on associated crops (Amassaghrou et al., 2023). Additionally, grain quality can decline, as seen in pea-canola intercrops, which showed a 6–9% decrease in protein content compared to monocrops (Liu et al., 2024). Despite these challenges, intercropping enhances biodiversity and soil health, indicating a complex relationship between intercropping practices and productivity.

Intercropping systems incur higher costs due to the need for regionally adapted management practices to balance light and water competition effectively. Selecting drought-resistant varieties is crucial for realizing efficient water-use, but may be inaccessible to low-income farmers. Yield benefits are limited in nutrient-rich environments or without drought conditions. Relay intercropping and optimizing strip widths can reduce competition, but these complex systems often deter adoption. Identifying intercrop combinations with complementary architecture and resource needs is essential to enhance productivity and profitability (Seleiman et al., 2021).

7.3 Complexity in other resources

Legume intercropping offers ecological and soil health benefits but faces several challenges that can limit its efficiency and sustainability (Zhu et al., 2023). A major issue is resource competition, as both legumes and companion crops compete for sunlight, water, and nutrients. This competition can be particularly challenging in densely planted, nutrient-deficient systems, often reducing legume productivity. Uneven resource distribution further exacerbates the problem, negatively affecting both legumes and companion crops in intercropped fields (Ananthi and Parasuraman, 2020). Pests and diseases also pose significant challenges. While intercropping can disrupt some pest life cycles, it can also create opportunities for others. Additionally, legumes are vulnerable to various soil-borne pathogens, increasing the risk of disease in mixed cropping systems and complicating pest and disease management (Islam and Ashilenje, 2018). Intercropping requires high labor inputs, including precise planning, staggered planting, and multiple harvests. Mechanization is often difficult due to the diversity of crops used, limiting the efficiency gains typically achieved with machinery (Zhu et al., 2023). Environmental stress factors such as drought, salinity, and soil acidity further hinder legume intercropping by reducing yields and increasing resource competition (Ananthi and Parasuraman, 2020). Despite these challenges, effective management practices and leveraging biological interactions can improve soil health and biodiversity, enhancing the resilience and sustainability of legume intercropping systems.

8 The role of legume intercropping under climate resilience

Intercropping helps create microclimates that reduce soil and canopy temperatures, shielding crops from heat stress. For example, Molla et al. (2023) reported a 2–3°C decrease in canopy temperatures and a 10% yield boost under heat stress in maize + cowpea intercropping. Similarly, Murphy et al. (2021) found pigeon pea intercropping yielded 15% more than monocultures under high temperatures. Diverse rotations in intercropping systems also enhance maize yield and resilience, reducing drought-year losses by 14–89% (Bowles et al., 2020). Intercropping is increasingly recognized as a form of “insurance” against extreme weather and pest pressures due to its ability to enhance system resilience. By combining crops of different growth habits, root systems, and resource requirements, intercropping minimizes the risk of total crop failure during droughts, floods, or temperature extremes (Loreau et al., 2021). When one crop fails due to environmental stressors, disease, or pests, the remaining crops can utilize freed-up resources to offset yield losses (Boincean and Dent, 2019).

Competitive legume intercrops can fill gaps left by failed crops, suppress weeds, and stabilize yields. This resilience has been demonstrated in both irrigated and arid climates, supporting stable agricultural productivity amid climate variability (Ebbisa, 2023). However, the success of intercropping depends on precise management tailored to regional conditions to mitigate competition for light, water, and nutrients (Kremsa, 2021). The success of intercropping under drought conditions often depends on using drought-resistant crop varieties, a challenge for low-income farmers with limited access to such resources. In nutrient-rich or non-drought

environments, the yield advantages of intercrops adapted to extreme climates can be minimal, underscoring the importance of selecting appropriate crop combinations based on local conditions (Renwick et al., 2020; Singh et al., 2020). Climate-resilient intercropping systems offer additional benefits, such as reducing reliance on fossil fuel-intensive inputs (Tang et al., 2021) and stabilizing production (Paut et al., 2020) while lowering environmental impacts. However, farmers often face concerns about perceived risks of crop failure and higher implementation costs.

Effective intercropping requires initial experimentation tailored to local conditions, such as climate, farm size, and soil. Technical support and local expertise, based on local data, are crucial (Noy and Jabbour, 2020). To improve adoption, outreach efforts should integrate farmers' perspectives (Snapp et al., 2019). Peer mentoring by early adopters and information networks can help share successes, address challenges, and provide guidance (Bressler et al., 2021). Federal incentive programs could reduce economic risks and support experimentation with intercropping. Cost-share programs help offset initial diversification costs but may involve logistical challenges. Special crop insurance programs could ensure competitive payments during the trial-and-error phase of intercropping adoption (Lithourgidis et al., 2011). While intercropping provides a resilient approach to climate adaptation, its widespread adoption depends on addressing economic and logistical barriers, tailoring strategies to local conditions, and integrating farmer perspectives into outreach and support frameworks. Table 5 depicts the response of legume intercropping across various countries, offering insights into trial methods and climate characteristics.

9 Prospects

To effectively compete with large-scale monocultures, optimizing resource use and crop yield in intercropping systems is essential. This involves a thorough understanding of agronomic practices, including tillage methods, seed rates, crop combinations, plant nutrition, and harvesting techniques, as well as alignment with market demand for simultaneous harvests. Further research on crop genotype and species interactions, focusing on resource availability through niche complementarity, is necessary to refine intercropping practices. This is especially relevant as intercropping enhances agricultural resilience and stability by leveraging context-dependent interactions, pest and disease suppression, system linkages, and microtopographic variations.

Despite extensive research, more studies are needed to explore current trends and integrate findings into practical applications, particularly through on-farm testing. This is especially crucial for intercropping systems involving legumes, which play an important role in sustainable agriculture by efficiently managing N, benefiting non-legume crops in mixed systems. Past research conducted on small plots should be validated through collaboration between researchers and producers to facilitate real-world application and encourage adoption. In evaluating the impact of intercropping on crop rotations, it is essential to assess how these systems affect subsequent productivity, disease management, and soil health. Additionally, integrating diverse climate, soil, crop species, and genotype data into models could better illustrate interspecific interactions under varying conditions, which is vital for assessing

productivity, sustainability, and resource efficiency on larger scales. Such approaches provide critical insights needed to optimize intercropping systems and foster resilience in sustainable agriculture.

10 Conclusion

Intensive agriculture, characterized by monocultures, heavy reliance on fertilizers and pesticides, and excessive groundwater withdrawal, results in higher production costs, significant environmental challenges, and long-term threats to sustainability. In contrast, integrating legumes into cropping systems enhances food and livelihood security, reduces environmental impact, and promotes sustainability by improving resource use efficiency, suppressing weed growth, increasing the productivity of non-legume crops, and fixing atmospheric nitrogen, soil carbon sequestration, climate adaptation, and biodiversity enhancement. Although intercropping is more labor-intensive and less mechanized than monocropping, it is particularly well-suited to regions like Asia and Africa, where farms are small, cropping systems are diverse, and a substantial agricultural workforce is available. In these regions, intercropping provides food and nutritional security, helps meet most family needs through family farming, offers insurance against crop failures, and creates employment opportunities. Meanwhile, in developed countries, legume intercropping reduces input requirements such as herbicides, fungicides, insecticides, and fertilizers, improves soil health by sequestering carbon, fixing atmospheric nitrogen, breaking hardpan layers, enhancing porosity, increasing water infiltration, and boosts overall resource use efficiency. Successful adoption of legume intercropping requires collaboration among policymakers, researchers, advisors, and farmers. As the challenges of food security and climate change continue to grow, legume intercropping aligns with the principles of sustainable intensification, blending natural crop synergies with local knowledge and creating resilient, productive agricultural systems.

Data availability statement

The original contributions presented in the study are included in the article/supplementary material, further inquiries can be directed to the corresponding authors.

Author contributions

KA: Writing – original draft. PP: Resources, Supervision, Writing – review & editing. KP: Writing – original draft, Writing – review & editing, Supervision, Resources, Conceptualization. SV: Writing – original draft, Writing – review & editing, Conceptualization, Methodology, Visualization, Data curation, Supervision, Formal analysis. KT: Data curation, Writing – original draft. MM: Writing – review & editing, Visualization, Methodology, Formal analysis. SR: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration,

Resources, Software, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing. AC: Data curation, Formal analysis, Visualization, Writing – review & editing.

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References

- Ahmed, A., Aftab, S., Hussain, S., Nazir Cheema, H., Liu, W., Yang, F., et al. (2020). Nutrient accumulation and distribution assessment in response to potassium application under maize–soybean intercropping system. *Agronomy* 10:725. doi: 10.3390/agronomy10050725
- Ahmed, M., Asim, M., Ahmad, S., and Aslam, M. (2022). “Climate change, agricultural productivity, and food security” in *Global agricultural production: Resilience to climate change*. ed. M. Ahmed (Cham: Springer International Publishing), 31–72.
- Ajayi, A. S. (2015). The effects of tillage methods and intercropping on soil water characteristics, growth and grain yield of maize (*Zea mays* L.) and groundnut (*Arachis hypogaea*, L.) on an alfisol in south west, Nigeria. *Afr. J. Agric. Res.* 10, 2866–2874. doi: 10.5897/AJAR2015.9964
- Ali, H., Sarwar, N., Ahmad, S., Farooq, O., Nahar, K., and Hasanuzzaman, M. (2020). “Cotton-based intercropping systems” in *Cotton production and uses: Agronomy, crop protection, and postharvest technologies*. eds. S. Ahmad and M. Hasanuzzaman (Cham: Springer), 321–340.
- Amassaghrou, A., Barkaoui, K., Bouaziz, A., Alaoui, S. B., Fatemi, Z. E. A., and Daoui, K. (2023). Yield and related traits of three legume crops grown in olive-based agroforestry under an intense drought in the South Mediterranean. *Saudi J. Biol. Sci.* 30:103597. doi: 10.1016/j.sjbs.2023.103597
- Ananthi, K., and Parasuraman, P. (2020). Assessment of morphological, physiological and yield response of Varagu with legume intercropping planting system. *Int. J. Curr. Microbiol. App. Sci.* 9, 3295–3301. doi: 10.20546/ijcmas.2020.905.391
- Ananthi, K., and Parasuraman, P. (2021). Physiological and biochemical evaluation of varagu with blackgram intercropping competition and yield advantage. *Int. J. Plant Sci.* 16, 147–154. doi: 10.15740/HAS/IJPS/16.2/147-154
- Aziz, M., Mahmood, A., Asif, M., and Ali, A. (2015). Wheat-based intercropping: a review. *JAPS* 25, 896–907.
- Balikai, R. A., Madhurima, V., and Desai, S. (2020). Non-chemical approaches for the management of insect pests in Agri-horti crops and storage. *J. Eco Friendly Agric.* 15, 95–111. doi: 10.5958/2582-2683.2020.00013.1
- Banik, P., and Sharma, R. C. (2009). Yield and resource utilization efficiency in baby corn—legume-intercropping system in the eastern plateau of India. *J. Sustain. Agric.* 33, 379–395. doi: 10.1080/10440040902834970
- Barker, S., and Dennett, M. D. (2013). Effect of density, cultivar and irrigation on spring sown monocrops and intercrops of wheat (*Triticum aestivum* L.) and faba beans (*Vicia faba* L.). *Eur. J. Agron.* 51, 108–116. doi: 10.1016/j.eja.2013.08.001
- Barman, A., Saha, P., Patel, S., and Bera, A. (2022). “Crop diversification an effective strategy for sustainable agriculture development” in *Sustainable crop production-recent advances* (London: IntechOpen). doi: 10.5772/intechopen.102635
- Bawa, S. I., Quansah, C., Tuffour, H. O., Abubakari, A., and Melenya, C. (2019). Root growth responses of maize (*Zea mays* L.) and soybean (*Glycine max* L.) to soil compaction and fertilization in a ferric Acrisol. *J. Exp. Agric. Int* 35, 1–11. doi: 10.9734/JEAI/2019/v35i330207
- Baxevanos, D., Tsialtas, I. T., Vlachostergios, D. N., Hadjigeorgiou, I., Dordas, C., and Lithourgidis, A. (2017). Cultivar competitiveness in pea-oat intercrops under Mediterranean conditions. *Field Crop Res.* 214, 94–103. doi: 10.1016/j.fcr.2017.08.024
- Belay, Y. B., and Melka, Y. (2024). Comparative profitability analysis of monoculture and intercropping land-use systems: the case of smallholder farmers in North-Western Ethiopia. *Int. J. For. Res.* 2024:6322124. doi: 10.1155/2024/6322124
- Belete, T., and Yadete, E. (2023). Effect of mono cropping on soil health and fertility Management for Sustainable Agriculture Practices: a review. *J. Plant Sci.* 11, 192–197. doi: 10.11648/j.jps.20231106.13
- Benmrid, B., Ghoulam, C., Zeroual, Y., Kouisni, L., and Bargaz, A. (2023). Bioinoculants as a means of increasing crop tolerance to drought and phosphorus deficiency in legume-cereal intercropping systems. *Commun. Biol.* 6:1016. doi: 10.1038/s42003-023-05399-5
- Betencourt, E., Duputel, M., Colomb, B., Desclaux, D., and Hinsinger, P. (2012). Intercropping promotes the ability of durum wheat and chickpea to increase rhizosphere phosphorus availability in a low P soil. *Soil Biol. Biochem.* 46, 181–190. doi: 10.1016/j.soilbio.2011.11.015
- Bhattacharyya, R., Bhatia, A., Chakrabarti, B., Saha, N. D., Pramanik, P., Ghosh, A., et al. (2023). Elevated CO₂ alters aggregate carbon and microbial community but does not affect total soil organic C in the semi-arid tropics. *Appl. Soil Ecol.* 187:104843. doi: 10.1016/j.apsoil.2023.104843
- Boincean, B. P., and Dent, D. L. (2019). “Tillage and conservation agriculture” in *Farming the black earth: Sustainable and climate-smart management of chernozem soils*. eds. B. Boincean and D. Dent, Cham: Springer Nature Switzerland AG. 125–149. doi: 10.1007/978-3-030-22533-9_6
- Bowles, T. M., Pritchard, D., and Haider, Z. (2020). Diverse crop rotations and maize yield resilience under drought conditions. *Agron. J.* 2, 284–293. doi: 10.1016/j.oneear.2020.02.007
- Brandmeier, J., Reininghaus, H., Pappagallo, S., Karley, A. J., Kiaer, L. P., and Scherber, C. (2021). Intercropping in high input agriculture supports arthropod diversity without risking significant yield losses. *Basic Appl. Ecol.* 53, 26–38. doi: 10.1016/j.baee.2021.02.011
- Bressler, R. M., Lichtenberg, E., and Browne, K. (2021). The role of peer mentoring and information networks in intercropping adoption. *J. Agric. Educ. Ext.* 27, 35–49.
- Burgess, A. J., Cano, M. E. C., and Parkes, B. (2022). The deployment of intercropping and agroforestry as adaptation to climate change. *Crop Environ.* 1, 145–160. doi: 10.1016/j.crope.2022.05.001
- Bybee-Finley, K. A., and Ryan, M. R. (2018). Advancing intercropping research and practices in industrialized agricultural landscapes. *Agriculture* 8:80. doi: 10.3390/agriculture8060080
- Caldwell, M. M., and Richards, J. H. (1989). Hydraulic lift: water efflux from upper roots improves effectiveness of water uptake by deep roots. *Oecologia* 79, 1–5. doi: 10.1007/BF00378231
- Chadfield, V. G., Hartley, S. E., and Redeker, K. R. (2022). Associational resistance through intercropping reduces yield losses to soil-borne pests and diseases. *New Phytol.* 235, 2393–2405. doi: 10.1111/nph.18302

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- Chamkhi, I., Cheto, S., Geistlinger, J., Zeroual, Y., Kouisni, L., Bargaz, A., et al. (2022). Legume-based intercropping systems promote beneficial rhizobacterial community and crop yield under stressing conditions. *Ind. Crop. Prod.* 183:114958. doi: 10.1016/j.indcrop.2022.114958
- Chaves, A. P., Bezerra, F., Lima, J. S., Silva, J. N., Nunes, R. L., Barros, A. P., et al. (2020). Cowpea and beet intercropping agro-economic dynamics under spatial arrangement and cowpea population density. *Hortic. Bras.* 38, 192–203. doi: 10.1590/S0102-053620200212
- Chen, P., Song, C., Liu, X. M., Zhou, L., Yang, H., Zhang, X., et al. (2019). Yield advantage and nitrogen fate in an additive maize-soybean relay intercropping system. *Sci. Total Environ.* 657, 987–999. doi: 10.1016/j.scitotenv.2018.11.376
- Chi, B., Zhang, Y., Zhang, D., Zhang, X., Dai, J., and Dong, H. (2019). Wide-strip intercropping of cotton and peanut combined with strip rotation increases crop productivity and economic returns. *Field Crop Res.* 243:107617. doi: 10.1016/j.fcr.2019.107617
- Chitraputhirapillai, S., Kannan, P., Krishnaprabu, N., and Yassin, M. M. (2022). Four 'Bio' Traits craft Pigeonpea (*Cajanus cajan* (L.) Millsp.) to survive in a dry soil environment under intercropping situation - A Review. *Int. J. Plant Env.* 8, 39–46. doi: 10.18811/ijpen.v8i03.05
- Cong, W. F., Hoffland, E., Li, L., Six, J., Sun, J. H., Bao, X. G., et al. (2015). Intercropping enhances soil carbon and nitrogen. *Glob. Chang. Biol.* 21, 1715–1726. doi: 10.1111/gcb.12738
- Cuartero, J., Pascual, J. A., Vivo, J. M., Özbolat, O., Sánchez-Navarro, V., Egea-Cortines, M., et al. (2022). A first-year melon/cowpea intercropping system improves soil nutrients and changes the soil microbial community. *Agric. Ecosyst. Environ.* 328:107856. doi: 10.1016/j.agee.2022.107856
- Dai, J., Qiu, W., Wang, N., Wang, T., Nakanishi, H., and Zuo, Y. (2019). From Leguminosae/Gramineae intercropping systems to see benefits of intercropping on iron nutrition. *Front. Plant Sci.* 10:605. doi: 10.3389/fpls.2019.00605
- de Moissac, L. R. (2020). Examining the effect of rotation sequence on biological nitrogen fixation of pulse crops. MSc Thesis. Saskatoon, SK, Canada: University of Saskatchewan. Available at: <https://harvest.usask.ca/handle/10388/12823>
- Delaquis, E., de Haan, S., and Wyckhuys, K. A. (2018). On-farm diversity offsets environmental pressures in tropical agro-ecosystems: a synthetic review for cassava-based systems. *Agric. Ecosyst. Environ.* 251, 226–235. doi: 10.1016/j.agee.2017.09.037
- Devi, J., Mishra, G. P., Sagar, V., Kaswan, V., Dubey, R. K., Singh, P. M., et al. (2022). Gene-based resistance to Erysiphe species causing powdery mildew disease in peas (*Pisum sativum* L.). *Genes* 13:316. doi: 10.3390/genes13020316
- Dimande, P., Arrobas, M., and Rodrigues, M. A. (2024). Intercropped maize and cowpea increased the land equivalent ratio and enhanced crop access to more nitrogen and phosphorus compared to cultivation as sole crops. *Sustain. For.* 16:1440. doi: 10.3390/su16041440
- Dordas, C. A., Lithourgidis, A. S., and Galanopoulou, K. (2019). Intercropping of faba bean with barley at various spatial arrangements affects dry matter and N yield, nitrogen nutrition index, and interspecific competition. *Not. Bot. Horti Agrobot. Cluj Na.* 47, 1116–1127. doi: 10.15835/nbha47411520
- Duchene, O., Vian, J. F., and Celette, F. (2017). Intercropping with legume for agroecological cropping systems: complementarity and facilitation processes and the importance of soil microorganisms. A review. *Agric. Ecosyst. Environ.* 240, 148–161. doi: 10.1016/j.agee.2017.02.019
- Dugassa, M. (2023). The role of cereal legume intercropping in soil fertility management: review. *J. Agric. Aquac.* 5, 1–8.
- Duru, M., Therond, O., Martin, G., Martin-Clouaire, R., Magne, M. A., Justes, E., et al. (2015). How to implement biodiversity-based agriculture to enhance ecosystem services: a review. *Agron. Sustain. Dev.* 35, 1259–1281. doi: 10.1007/s13593-015-0306-1
- Ebbisa, A. (2023). "Application of crop modeling in multi-cropping Systems for Maximize Production and Build Resilient Ecosystem Services" in Resource Management in Agroecosystems. eds. G. Ondrasek and L. Zhang (London: IntechOpen). doi: 10.5772/intechopen.110742
- Esnaarriaga, D. N., Mariotti, M., Cardelli, R., and Arduini, I. (2020). The importance of root interactions in field bean/triticale intercrops. *Plan. Theory* 9:1474. doi: 10.3390/plants9111474
- Eze, S., Dougill, A. J., Banwart, S. A., Hermans, T. D., Ligowe, I. S., and Thierfelder, C. (2020). Impacts of conservation agriculture on soil structure and hydraulic properties of Malawian agricultural systems. *Soil Tillage Res.* 201:104639. doi: 10.1016/j.still.2020.104639
- Fahde, S., Boughribil, S., Sijilmassi, B., and Amri, A. (2023). Rhizobia: a promising source of plant growth-promoting molecules and their non-legume interactions: examining applications and mechanisms. *Agriculture* 13:1279. doi: 10.3390/agriculture13071279
- Falcon, W. P., Naylor, R. L., and Shankar, N. D. (2022). Rethinking global food demand for 2050. *Popul. Dev. Rev.* 48, 921–957. doi: 10.1111/padr.12508
- Feng, C., Sun, Z., Zhang, L., Feng, L., Zheng, J., Bai, W., et al. (2021). Maize/peanut intercropping increases land productivity: a meta-analysis. *Field Crop Res.* 270:108208. doi: 10.1016/j.fcr.2021.108208
- Feng, L., Yang, W., Tang, H., Huang, G., and Wang, S. (2022). Bandwidth row ratio configuration affect interspecific effects and land productivity in maize-soybean intercropping system. *Agronomy* 12:3095. doi: 10.3390/agronomy12123095
- Fenta, H. M., Hussein, M. A., Tilahun, S. A., Nakawuka, P., Steenhuis, T. S., Barron, J., et al. (2022). Berken plow and intercropping with pigeon pea ameliorate degraded soils with a hardpan in the Ethiopian highlands. *Geoderma* 407:115523. doi: 10.1016/j.geoderma.2021.115523
- Fernández-Ortega, J., Álvaro-Fuentes, J., Talukder, R., Lampurlanés, J., and Cantero-Martínez, C. (2023). The use of double-cropping in combination with no-tillage and optimized nitrogen fertilization improve crop yield and water use efficiency under irrigated conditions. *Field Crop Res.* 301:109017. doi: 10.1016/j.fcr.2023.109017
- Fouda, S. E., El-Saadony, F. M., Saad, A. M., Sayed, S. M., El-Sharnouby, M., El-Tahan, A. M., et al. (2022). Improving growth and productivity of faba bean (*Vicia faba* L.) using chitosan, tryptophan, and potassium silicate anti-transpirants under different irrigation regimes. *Saudi J. Biol. Sci.* 29, 955–962. doi: 10.1016/j.sjbs.2021.10.007
- Gaikwad, D. D., Pankhaniya, R. M., Singh, B., Patel, K. G., and Viridia, H. M. (2022). Studies on growth and productivity of maize-cowpea intercropping system under different spatial arrangements and nutrient levels. *Pharm. Innov.* 12, 2506–2512.
- Gao, H., Zhang, C., van der Werf, W., Ning, P., Zhang, Z., Wan, S., et al. (2022). Intercropping modulates the accumulation and translocation of dry matter and nitrogen in maize and peanut. *Field Crop Res.* 284:108561. doi: 10.1016/j.fcr.2022.108561
- Gardarin, A., Celette, F., Naudin, C., Piva, G., Valantin-Morison, M., Vignon-Brenas, S., et al. (2022). Intercropping with service crops provides multiple services in temperate arable systems: a review. *Agron. Sustain. Dev.* 42:39. doi: 10.1007/s13593-022-00771-x
- Garland, G., Bünemann, E. K., Oberson, A., Frossard, E., and Six, J. (2017). Plant-mediated rhizospheric interactions in maize-pigeon pea intercropping enhance soil aggregation and organic phosphorus storage. *Plant Soil* 415, 37–55. doi: 10.1007/s11104-016-3145-1
- Gautam, R., Singh, S. K., and Sharma, V. (2015). Suppression of soil-borne root pathogens of arid legumes by *Sinorhizobium saheli*. *SAARC J. Agri.* 13, 63–74. doi: 10.3329/sja.v13i1.24181
- Giambalvo, D., Ruisi, P., Di Miceli, G., Frenda, A. S., and Amato, G. (2011). Forage production, N uptake, N₂ fixation, and N recovery of berseem clover grown in pure stand and in mixture with annual ryegrass under different managements. *Plant Soil* 342, 379–391. doi: 10.1007/s11104-010-0703-9
- Gidey, T., Berhe, D. H., Birhane, E., Gufi, Y., and Haileslassie, B. (2024). Intercropping maize with Faba bean improves yield, income, and soil fertility in semiarid environment. *Scientifica* 2024, 2552695–2552698. doi: 10.1155/2024/2552695
- Giuliani, L. M., Hallett, P. D., and Loades, K. W. (2024). Effects of soil structure complexity to root growth of plants with contrasting root architecture. *Soil Tillage Res.* 238:106023. doi: 10.1016/j.still.2024.106023
- Glaze-Corcoran, S., Hashemi, M., Sadehghpour, A., Jahanzad, E., Afshar, R. K., Liu, X., et al. (2020). Understanding intercropping to improve agricultural resiliency and environmental sustainability. *Adv. Agron.* 162, 199–256. doi: 10.1016/bs.agron.2020.02.004
- Gopalakrishnan, S., and Srinivas, V. (2019). Management of soil-borne diseases of grain legumes through broad-spectrum actinomycetes having plant growth-promoting and biocontrol traits. A. Varma, S. Tripathi and R. Prasad (eds) Plant Microbe Interface, Springer, Cham pp.129–144.
- Grzebisz, W., Niewiadomska, A., and Przygocka-Cyna, K. (2022). Nitrogen hotspots on the farm - a practice-oriented approach. *Agronomy* 12:1305. doi: 10.3390/agronomy12061305
- Guo, K., Yang, J., Yu, N., Luo, L., and Wang, E. (2023). Biological nitrogen fixation in cereal crops: Progress, strategies, and perspectives. *Plant Commun.* 4:100499. doi: 10.1016/j.xplc.2022.100499
- Guo, L., Yu, Z., Li, Y., Xie, Z., Wang, G., Liu, J., et al. (2023). Stimulation of primed carbon under climate change corresponds with phosphorus mineralization in the rhizosphere of soybean. *Sci. Total Environ.* 899:165580. doi: 10.1016/j.scitotenv.2023.165580
- Hamzei, J., and Seyyedi, M. (2016). Energy use and input-output costs for sunflower production in sole and intercropping with soybean under different tillage systems. *Soil Tillage Res.* 157, 73–82. doi: 10.1016/j.still.2015.11.008
- Hao, C., Dungait, J. A., Wei, X., Ge, T., Kuzyakov, Y., Cui, Z., et al. (2022). Maize root exudate composition alters rhizosphere bacterial community to control hotspots of hydrolase activity in response to nitrogen supply. *Soil Biol. Biochem.* 170:108717. doi: 10.1016/j.soilbio.2022.108717
- Hassan, M. U., Aamer, M., Mahmood, A., Awan, M. I., Barbanti, L., Seleiman, M. F., et al. (2022). Management strategies to mitigate N₂O emissions in agriculture. *Life* 12:439. doi: 10.3390/life12030439
- Hauggaard-Nielsen, H., Gooding, M., Ambus, P., Corre-Hellou, G., Crozat, Y., Dahlmann, C., et al. (2009). Pea-barley intercropping and short-term subsequent crop effects across European organic cropping conditions. *Nutr. Cycl. Agroec.* 85, 141–155. doi: 10.1007/s10705-009-9254-y
- Homulle, Z., George, T. S., and Karley, A. J. (2021). Root traits with team benefits: understanding belowground interactions in intercropping systems. *Plant Soil* 471, 1–26. doi: 10.1007/s11104-021-05165-8

- Houngue, J. A., Pita, J. S., Ngalle, H. B., Zandjanakou-Tachin, M., Kuate, A. F., Cacaï, G. H. T., et al. (2019). Response of cassava cultivars to African cassava mosaic virus infection across a range of inoculum doses and plant ages. *PLoS One* 14:e0226783. doi: 10.1371/journal.pone.0226783
- Hu, A., Huang, D., Duan, Q., Zhou, Y., Liu, G., and Huan, H. (2023). Cover legumes promote the growth of young rubber trees by increasing organic carbon and organic nitrogen content in the soil. *Ind. Crop. Prod.* 197:116640. doi: 10.1016/j.indcrop.2023.116640
- Hu, Y., Sun, B., Wu, S., Feng, H., Gao, M., Zhang, B., et al. (2021). After-effects of straw and straw-derived biochar application on crop growth, yield, and soil properties in wheat (*Triticum aestivum* L.)-maize (*Zea mays* L.) rotations: a four-year field experiment. *Sci. Total Environ.* 780:146560. doi: 10.1016/j.scitotenv.2021.146560
- Huss, C. P., Holmes, K. D., and Blubaugh, C. K. (2022). Benefits and risks of intercropping for crop resilience and pest management. *J. Econ. Entomol.* 115, 1350–1362. doi: 10.1093/jeec/toac045
- Hussain, A., Elkmarmout, A. F., Mansour, E. Z., Awais, M., Usman, M., Ahmad, H., et al. (2024). An environment friendly practice, the climate smart agriculture crop production and soil management systems: a review. *J. Sustain. Agric. Environ. Sci.* 3, 101–124.
- Indoria, A. K., Sharma, K. L., Reddy, K. S., and Rao, C. S. (2016). Role of soil physical properties in soil health management and crop productivity in rainfed systems–II. Management technologies and crop productivity. *Curr. Sci.* 110, 320–328. doi: 10.18520/cs/v110/i3/320-328
- Islam, M. A., and Ashilenje, D. S. (2018). Understanding species traits and Biodiversity indices to solve problems associated with legume persistence in cropping systems. In *Legume Crops and Their Interactions with Environment and Agro-Ecosystems*. London: IntechOpen. doi: 10.5772/intechopen.7652
- Issah, G., Schoenau, J. J., Lardner, H. A., and Knight, J. D. (2020). Nitrogen fixation and resource partitioning in alfalfa (*Medicago sativa* L.), cicer milkvetch (*Astragalus cicer* L.) and sainfoin (*Onobrychis viciifolia* Scop.) using ¹⁵N enrichment under controlled environment conditions. *Agronomy* 10:1438. doi: 10.3390/agronomy10091438
- Jahansooz, M. R., Yunusa, I. A. M., Coventry, D. R., Palmer, A. R., and Eamus, D. (2007). Radiation-and water-use associated with growth and yields of wheat and chickpea in sole and mixed crops. *Eur. J. Agron.* 26, 275–282. doi: 10.1016/j.eja.2006.10.008
- Jensen, E. S., Carlsson, G., and Hauggaard-Nielsen, H. (2020). Intercropping of grain legumes and cereals improves the use of soil N resources and reduces the requirement for synthetic fertilizer N: a global-scale analysis. *Agron. Sustain. Dev.* 40:5. doi: 10.1007/s13593-020-0607-x
- Jordan, L. (2022). Responses to drought stress and water logging of 12 diverse pastoral lines in pakihī podzol soil. Lincoln, New Zealand: Lincoln University.
- Kahrarian, B., Farahvash, F., Mohammadi, S., and Mirshekari, B. (2021). Evaluation of yield, yield components and nutritive value in intercropping of barley with vetch. *Plant Sci. Today* 8, 373–379. doi: 10.14719/pst.2021.8.2.871
- Kakraliya, S. K., Jat, H. S., Singh, I., Sapkota, T. B., Singh, L. K., Sutaliya, J. M., et al. (2018). Performance of portfolios of climate smart agriculture practices in a rice-wheat system of western indo-Gangetic plains. *Agric. Water Manag.* 202, 122–133. doi: 10.1016/j.agwat.2018.02.020
- Kalyan, K., Deshray, G., Bijendra, B., and Tammineni, V. K. (2024). The role of grain legumes in enhancing soil health and promoting sustainable agricultural practices: a review. *J. Exp. Agric. Int.* 46, 344–354. doi: 10.9734/jeai/2024/v46i82712
- Kaur, J., and Singh, B. (2022). Nitrogen management for wheat (*Triticum aestivum* L.) intercropped with variable aged poplar (*Populus deltoides* Bartr.) plantations in North-Western India. *J. Plant Nutr.* 45, 686–702. doi: 10.1080/01904167.2021.1949463
- Kebede, E. (2021). Contribution, utilization, and improvement of legumes-driven biological nitrogen fixation in agricultural systems. *Front. Sustain. Food Syst.* 5:767998. doi: 10.3389/fsufs.2021.767998
- Kou, H., Liao, Z., Zhang, H., Lai, Z., Liu, Y., Kong, H., et al. (2024). Grain yield, water-land productivity and economic profit responses to row configuration in maize-soybean strip intercropping systems under drip fertigation in arid Northwest China. *Agric. Water Manag.* 297:108817. doi: 10.1016/j.agwat.2024.108817
- Koul, B., Sharma, K., Sehgal, V., Yadav, D., Mishra, M., and Bharadwaj, C. (2022). Chickpea (*Cicer arietinum* L.) biology and biotechnology: from domestication to biofortification and biopharming. *Plan. Theory* 11:2926. doi: 10.3390/plants11212926
- Kremsa, V. Š. (2021). “Sustainable management of agricultural resources (agricultural crops and animals)” In *Sustainable resource management: Modern Approaches and Contexts*. LaFleur, M. (Ed.), (Amsterdam: Elsevier), 99–145.
- Kumar, N. (2023). “Advances in pulses production technologies: a holistic approach for new millennium” In *Advances in crop production and climate change*. eds. A. S. Yadav, N. Kumar, S. Arora, D. S. Srivastava and H. Pant (Boca Raton: CRC Press), 111–141. doi: 10.1201/9781003281948-5
- Kumar, R. M., and Boraiah, B. (2022). Bio-irrigation: a drought alleviation strategy through induced hydro-parasitization under bi-cropping practices of rainfed agro-ecosystem: a review. *Agric. Rev.* 43, 211–216. doi: 10.18805/ag.R-2139
- Kumar, G., Kumari, R., Shambhavi, S., Kumar, S., Kumari, P., and Padbhushan, R. (2022). Eight-year continuous tillage practice impacts soil properties and forms of potassium under maize-based cropping systems in inceptisols of eastern India. *Commun. Soil Sci. Plant Anal.* 53, 602–621. doi: 10.1080/00103624.2021.2017961
- Kumawat, A., Bamboriya, S. D., Meena, R. S., Yadav, D., Kumar, A., Kumar, S., et al. (2022). “Legume-based inter-cropping to achieve the crop, soil, and environmental health security” In *Advances in legumes for sustainable intensification*. eds. R. S. Meena and S. Kumar (London: Academic Press), 307–328.
- Kwabiha, A. B. (2005). Biological efficiency and economic benefits of pea-barley and pea-oat intercrops. *J. Sustain. Agric.* 25, 117–128. doi: 10.1300/J064v25n01_09
- Ladha, J. K., Peoples, M. B., Reddy, P. M., Biswas, J. C., Bennett, A., Jat, M. L., et al. (2022). Biological nitrogen fixation and prospects for ecological intensification in cereal-based cropping systems. *Field Crop Res.* 283:108541. doi: 10.1016/j.fcr.2022.108541
- Lai, H., Gao, F., Su, H., Zheng, P., Li, Y., and Yang, H. (2022). Nitrogen distribution and soil microbial community characteristics in a legume–cereal intercropping system: a review. *Agronomy* 12:1900. doi: 10.3390/agronomy12081900
- Lal, R. (2017). Improving soil health and human protein nutrition by pulses-based cropping systems. *Adv. Agron.* 145, 167–204. doi: 10.1016/bs.agron.2017.05.003
- Lal, R. (2018). Sustainable intensification of China's agroecosystems by conservation agriculture. *Int. Soil Water Conserv. Res. ISWCR* 6, 1–12. doi: 10.1016/j.iswcr.2017.11.001
- Lalotra, S., Kumar, S., Meena, R. S., and Kumar, V. (2022). Sustainable intensification in cropping systems through inclusion of legumes. In *Meena, R. S., and Kumar, S. Advances in legumes for sustainable intensification*. 27–50. London: Academic Press.
- Lan, Y., Zhang, H., He, Y., Jiang, C., Yang, M., and Ye, S. (2023). Legume-bacteria-soil interaction networks linked to improved plant productivity and soil fertility in intercropping systems. *Ind. Crop. Prod.* 196:116504. doi: 10.1016/j.indcrop.2023.116504
- Lavanya, K. R., Kadalli, G. G., Patil, S., Jayanthi, T., Naveen, D. V., and Channabasavogowda, R. (2019). Sulphur fractionation studies in soils of long-term fertilizer experiment under finger millet-maize cropping sequence. *Int. J. Curr. Microbiol. Appl. Sci* 8, 1334–1345. doi: 10.20546/ijcma.2019.809.153
- Li, Y., Ran, W., Zhang, R., Sun, S., and Xu, G. (2009). Facilitated legume nodulation, phosphate uptake and nitrogen transfer by arbuscular inoculation in an upland rice and mung bean intercropping system. *Plant Soil* 315, 285–296. doi: 10.1007/s11104-008-9751-9
- Li, C., Stomph, T. J., Makowski, D., Li, H., Zhang, C., Zhang, F., et al. (2023). The productive performance of intercropping. *Proc. Natl. Acad. Sci.* 120:e2201886120. doi: 10.1073/pnas.2201886120
- Liang, J., He, Z., and Shi, W. (2020). Cotton/mung bean intercropping improves crop productivity, water use efficiency, nitrogen uptake, and economic benefits in the arid area of Northwest China. *Agric. Water Manag.* 240:106277. doi: 10.1016/j.agwat.2020.106277
- Lithourgidis, A. S., Dordas, C. A., Damalas, C. A., and Vlachostergios, D. O. (2011). Annual intercrops: an alternative pathway for sustainable agriculture. *Aust. J. Crop. Sci.* 5, 396–410.
- Liu, K., Choo-Foo, K., Wen, G., Schoenau, J., and Knight, J. D. (2024). Assessing crop productivity, grain quality, and soil labile carbon and nitrogen in pea-based intercrops under low nitrogen input. *Can. J. Plant Sci.* 105, 1–21. doi: 10.1139/cjps-2024-0136
- Liu, X., Rahman, T., Song, C., Su, B., Yang, F., Yong, T., et al. (2017). Changes in light environment, morphology, growth and yield of soybean in maize-soybean intercropping systems. *Field Crop Res.* 200, 38–46. doi: 10.1016/j.fcr.2016.10.003
- Longepierre, M., Feola Conz, R., Barthel, M., Bru, D., Philippot, L., Six, J., et al. (2022). Mixed effects of soil compaction on the nitrogen cycle under pea and wheat. *Front. Microbiol.* 12:822487. doi: 10.3389/fmicb.2021.822487
- Loreau, M., Isbell, F., and Biodiversity, A. (2021). Intercropping as an insurance policy in the face of climate change. *Nat. Ecol. Evol.* 5, 345–357.
- Maalouf, F., Abou Khater, L., Kumar, S., Hejjajou, K., Morda, W., Hayek, P., et al. (2022). Experimental on-farm trials data of faba bean and wheat intercropping field validation in Lebanon and Morocco. *Data Brief* 42:108098. doi: 10.1016/j.dib.2022.108098
- Maciel de Oliveira, S., Dias, D. S., Reis, A. F. D. B., Cruz, S. C. S., and Favarin, J. L. (2020). Vertical stratification of K uptake for soybean-based crop rotation. *Nutr. Cycl. Agroecosyst.* 117, 185–197. doi: 10.1007/s10705-020-10059-9
- Madsen, I. J., Parks, J. M., Friesen, M. L., and Clark, R. E. (2022). Increasing biodiversity and land-use efficiency through pea (*Pisum aestivum*)-canola (*Brassica napus*) intercropping (peaola). *Front. Soil Sci.* 2:818862. doi: 10.3389/fsoil.2022.818862
- Markos, D., and Yoseph, T. (2024). Revitalizing maize production through managing biological N fixation, soil acidification and nitrous oxide emission from legumes in tropics. *Afr. J. Environ. Sci. Technol.* 18, 21–40. doi: 10.5897/AJEST2023.3245
- Mbanyele, V., Enesi, R. O., Shaw, L., and Gorim, L. Y. (2024). A review of intercropping systems in Western Canada. *Agron. J.* 116, 2089–2108. doi: 10.1002/agi.2.21622
- Meena, S., Meena, L., Yadav, S., Jadon, C., Dhakad, U., Lal, M., et al. (2024). Chickpea (*Cicer arietinum*)-based intercropping systems in Rajasthan's Hadoti region: productivity and economic viability. *Indian J. Agron.* 69, 54–60. doi: 10.59797/ija.v69i1.5482

- Midega, C. A., Pittchar, J. O., Pickett, J. A., Hailu, G. W., and Khan, Z. R. (2018). A climate-adapted push-pull system effectively controls fall armyworm, *Spodoptera frugiperda* (JE smith), in maize in East Africa. *Crop Prot.* 105, 10–15. doi: 10.1016/j.cropro.2017.11.003
- Mir, M. S., Saxena, A., Kanth, R. H., Raja, W., Dar, K. A., Mahdi, S. S., et al. (2022). Role of intercropping in sustainable insect-pest management: a review. *Int. J. Environ. Clim.* 12, 3390–3404. doi: 10.9734/IJECC/2022/v12i111390
- Mohanty, L. K., Singh, N. K., Raj, P., Prakash, A., Tiwari, A. K., Singh, V., et al. (2024). Nurturing crops, enhancing soil health, and sustaining agricultural prosperity worldwide through agronomy. *J. Exp. Agric. Int.* 46, 46–67. doi: 10.9734/jeai/2024/v46i22308
- Molla, M. S. H., Kumdee, O., Worathongchai, N., Khongchiu, P., Ali, M. A., Anwar, M. M., et al. (2023). Efforts to stimulate Morpho-physio-biochemical traits of maize for efficient production under drought stress in tropics field. *Agronomy* 13:2673. doi: 10.3390/agronomy13112673
- Morsy, A. S., Elwan, A., and Eissa, N. (2017). Studies on intercropping soybean with sugar cane under different nitrogen levels. *Egypt. J. Agron.* 39, 221–237. doi: 10.21608/agro.2017.848.1061
- Mrabet, R. (2023). “Sustainable agriculture for food and nutritional security” in Sustainable agriculture and the environment. eds. M. Farooq, N. Gogoi and M. Pisante (London: Academic Press), 25–90.
- Mubarak, A. R., Rosenani, A. B., Anuar, A. R., and Siti Zaayah, D. (2002). Effect of incorporation of crop residues on a maize–groundnut sequence in the humid tropics. I. Yield and nutrient uptake. *J. Plant Nutr.* 26, 1841–1858. doi: 10.1081/PLN-120023287
- Mudare, S., Kanomanyanga, J., Jiao, X., Mabasa, S., Lamichhane, J. R., Jing, J., et al. (2022). Yield and fertilizer benefits of maize/grain legume intercropping in China and Africa: a meta-analysis. *Agron. Sustain. Dev.* 42:81. doi: 10.1007/s13593-022-00816-1
- Mugi-Ngenga, E., Bastiaans, L., Anten, N. P. R., Zingore, S., and Giller, K. E. (2022). Immediate and residual-effects of sole and intercropped grain legumes in maize production systems under rain-fed conditions of northern Tanzania. *Field Crop Res.* 287:108656. doi: 10.1016/j.fcr.2022.108656
- Mupangwa, W., Nyagumbo, I., Liben, F., Chipindu, L., Craufurd, P., and Mkuhlani, S. (2021). Maize yields from rotation and intercropping systems with different legumes under conservation agriculture in contrasting agro-ecologies. *Agric. Ecosyst. Environ.* 306:107170. doi: 10.1016/j.agee.2020.107170
- Murphy, K. M., Shukla, R., and Kumar, S. (2021). The role of pigeon pea in intercropping systems under high-temperature conditions. *J. Crop. Sci. Biotechnol.* 24, 265–275.
- Mutti, N. K., Mahajan, G., Jha, P., and Chauhan, B. S. (2019). The response of glyphosate-resistant and glyphosate-susceptible biotypes of junglerice (*Echinochloa colona*) to mungbean interference. *Weed Sci.* 67, 419–425. doi: 10.1017/wsc.2019.12
- Mutyambai, D. M., Niassy, S., Calatayud, P. A., and Subramanian, S. (2022). Agronomic factors influencing fall armyworm (*Spodoptera frugiperda*) infestation and damage and its co-occurrence with stemborers in maize cropping systems in Kenya. *Insects* 13:266. doi: 10.3390/insects13030266
- Nair, N., Thangjam, B. C., Giri, U., and Debnath, M. R. (2018). “Pests of Leguminous” in Forage Crops of the World, Volume I: Major Forage Crops. eds. F. N. Nair, B. C. Thangjam, U. Giri and A. M. R. Debnath (Palm Bay: Apple Academic Press), 281–318.
- Nakei, M. D., Venkataramana, P. B., and Ndademi, P. A. (2023). Preliminary symbiotic performance of indigenous soybean (*Glycine max*)-nodulating rhizobia from agricultural soils of Tanzania. *Front. Sustain. Food Syst.* 6:1085843. doi: 10.3389/fsufs.2022.1085843
- Nasar, J., Ahmad, M., Gitari, H., Tang, L., Chen, Y., and Zhou, X. B. (2024). Maize/soybean intercropping increases nutrient uptake, crop yield and modifies soil physio-chemical characteristics and enzymatic activities in the subtropical humid region based in Southwest China. *BMC Plant Biol.* 24:434. doi: 10.1186/s12870-024-05061-0
- Nasar, J., Zhao, C. J., Khan, R., Gul, H., Gitari, H., Shao, Z., et al. (2023). Maize-soybean intercropping at optimal N fertilization increases the N uptake, N yield and N use efficiency of maize crop by regulating the N assimilatory enzymes. *Front. Plant Sci.* 13:1077948. doi: 10.3389/fpls.2022.1077948
- Nascente, A. S., and Stone, L. F. (2018). Cover crops as affecting soil chemical and physical properties and development of upland rice and soybean cultivated in rotation. *Rice Sci.* 25, 340–349. doi: 10.1016/j.rsci.2018.10.004
- Nassary, E. K., Baijuyka, F., and Ndademi, P. A. (2020). Assessing the productivity of common bean in intercrop with maize across agro-ecological zones of smallholder farms in the northern highlands of Tanzania. *Agriculture* 10:117. doi: 10.3390/agriculture10040117
- Nigussie, A., Haile, W., Aeggehu, G., and Kiflu, A. (2021). Grain yield and nitrogen uptake of maize (*zea mays* L.) as affected by soil management practices and their interaction on cambisols and chernozem. *Int. J. Res. Agron.* 2021:3411456. doi: 10.1155/2021/3411456
- Ning, T., Liu, Z., Hu, H., Li, G., and Kuzyakov, Y. (2022). Physical, chemical and biological subsoiling for sustainable agriculture. *Soil Tillage Res.* 223:105490. doi: 10.1016/j.still.2022.105490
- Noy, S., and Jabbour, N. (2020). The importance of local expertise in intercropping systems. *Agric. Econ.* 51, 835–846.
- Pang, J., Wang, Y., Lambers, H., Lambers, H., Tibbett, M., Siddique, K. H., et al. (2013). Commensalism in an agroecosystem: hydraulic redistribution by deep-rooted legumes improves survival of a droughted shallow-rooted legume companion. *Physiol. Plant.* 149, 79–90. doi: 10.1111/ppl.12020
- Papong, J., and Cagasan, U. (2020). Growth and yield performance of upland rice (*Oryza sativa* L. var. Zambales) intercropped with Mungbean (*Vigna radiata* L.) and peanut (*Arachis hypogaea* L.). *Int. J. Agric. For. Life Sci.* 4, 34–41.
- Parajara, M. D. C., Oliveira, F. L. D., Avelar, F. V., Oliveira, L. D. S., Carvalho, A. H. D. O., Lima, W. L. D., et al. (2024). Successive vegetable intercropping in organic system: agronomic and economic performance. *Hortic. Bras.* 42:e286663. doi: 10.1590/s0102-0536-2024-e286663
- Patel, P. R., Jain, S. K., Chauhan, R. M., and Patel, P. T. (2019). Stability analysis for fodder yield and its contributing traits in forage sorghum [*Sorghum bicolor* (L.) Moench] hybrids. *Electron. J. Plant Breed.* 10, 353–363. doi: 10.5958/0975-928X.2019.00045.0
- Paut, R., Sabatier, R., and Tchamitchian, M. (2020). Modelling crop diversification and association effects in agricultural systems. *Agric. Ecosyst. Environ.* 288:106711. doi: 10.1016/j.agee.2019.106711
- Pelzer, E., Bonifazi, M., Soulié, M., Guichard, L., Quinio, M., Ballot, R., et al. (2020). Participatory design of agronomic scenarios for the reintroduction of legumes into a French territory. *Agric. Syst.* 184:102893. doi: 10.1016/j.agry.2020.102893
- Peter, A., Indu, T., Singh, R., and Varsha, C. V. (2024). Response of intercropping finger millet on growth and yield of pulses. *J. Sci. Res. Rep.* 30, 449–455. doi: 10.9734/jsrr/2024/v30i72160
- Phiri, A. T., and Njira, K. O. W. (2023). Grain legume-based cropping systems’ effects on soil organic carbon and nutrient dynamics. *Agric. Res.* 12, 45–52. doi: 10.1007/s40003-022-00619-6
- Pierre, J. F., Jacobsen, K. L., Latournerie-Moreno, L., Torres-Cab, W. J., Chan-Canché, R., and Ruiz-Sánchez, E. (2023). A review of the impact of maize-legume intercrops on the diversity and abundance of entomophagous and phytophagous insects. *PeerJ* 11:e15640. doi: 10.7717/peerj.15640
- Pilet-Nayel, M. L., Coyne, C. J., Le May, C., and Banniza, S. (2024). Legume root diseases. *Front. Plant Sci.* 15:1393326. doi: 10.3389/fpls.2024.1393326
- Prasad, M., Yadav, R. S., and Saharan, B. (2020). Impact of weed management on weed dynamics and yield of rainy (Kharif) crops. *Indian J. Weed Sci.* 52, 391–395. doi: 10.5958/0974-8164.2020.00077.5
- Priori, S., Pellegrini, S., Vignozzi, N., and Costantini, E. A. (2020). Soil physical-hydrological degradation in the root-zone of tree crops: problems and solutions. *Agronomy* 11:68. doi: 10.3390/agronomy11010068
- Rahman, K. (2021). Cereal-legume intercropping: an eco-friendly land-use system for sustainable agriculture and pest management. *Int. J. Zool. Animal Biol.* 4:000325. doi: 10.23880/izab-16000325
- Raihan, A. (2023). A review of climate change mitigation and agriculture sustainability through soil carbon sequestration. *J. Agric. Sustain. Environ.* 2, 23–56. doi: 10.56556/jase.v2i2.783
- Rajanna, G. A., Dass, A., Suman, A., Babu, S., Venkatesh, P., Singh, V. K., et al. (2022). Co-implementation of tillage, irrigation, and fertilizers in soybean: impact on crop productivity, soil moisture, and soil microbial dynamics. *Field Crop Res.* 288:108672. doi: 10.1016/j.fcr.2022.108672
- Rajendran, T. P., Birah, A., and Burange, P. S. (2018). Insect pests of cotton. *Pests Manag.*, 361–411. Singapore: Springer. doi: 10.1007/978-981-10-8687-8_11
- Rajpoot, V. K., Awasthi, U. D., Ranjan, R., and Verma, A. K. (2020). Studies on barley based intercropping systems as influenced by integrated nutrient management on root development and consumptive use under moisture scarce condition. *J. Pharmacogn. Phytochem.* 9, 1995–1998.
- Ramachandra, C., Seenappa, C., and Rao, G. (2023). Influence of organic sources on growth and yield of finger millet in finger millet-groundnut cropping sequence. *Mysore journal of Agric. Sci.* 57:393.
- Rathi, A., Kumar, P., Nangla, S., Sharma, S., and Sharma, S. (2024). Soil restoration strategies for sustaining soil productivity: a review. *Asian Res. J. Agric.* 17, 33–48. doi: 10.9734/ARJA/2024/v17i1408
- Raza, M. A., Din, A. M. U., Zhiqi, W., Gul, H., Ur Rehman, S., Bukhari, B., et al. (2023). Spatial differences influence nitrogen uptake, grain yield, and land-use advantage of wheat/soybean relay intercropping systems. *Sci. Rep.* 13:16916. doi: 10.1038/s41598-023-43288-3
- Razavi, B. S., Zarebanadkouki, M., Blagodatkaya, E., and Kuzyakov, Y. (2016). Rhizosphere shape of lentil and maize: spatial distribution of enzyme activities. *Soil Biol. Biochem.* 96, 229–237. doi: 10.1016/j.soilbio.2016.02.020
- Razze, J. M., Liburd, O. E., and Webb, S. E. (2016). Intercropping buckwheat with squash to reduce insect pests and disease incidence and increase yield. *Agroecol. Sustain. Food Syst.* 40, 863–891. doi: 10.1080/21683565.2016.1205541
- Reddy, P. R. R., and Mohammad, S. (2009). Evaluation of cotton (*Gossypium hirsutum*)-based intercropping system through different approaches under rainfed conditions. *Indian J. Agric. Sci.* 79, 210–214.
- Renwick, L. L., Kimaro, A. A., Hafner, J. M., Rosenstock, T. S., and Gaudin, A. C. (2020). Maize-pigeonpea intercropping outperforms monocultures under drought. *Front. Sustain. Food Syst.* 4:562663. doi: 10.3389/fsufs.2020.562663

- Rezende, R. P. D., Golin, H. D. O., Abreu, V. L. D. S., Theodoro, G. D. F., Franco, G. L., Brumatti, R. C., et al. (2020). Does intercropping maize with forage sorghum effect biomass yield, silage bromatological quality and economic viability? *Res. Soc. Dev.* 9:e46942818. doi: 10.3344/rsd-v9i4.2818
- Sahoo, U., Malik, G. C., Maitra, S., Banerjee, M., Masina, S., Nath, S., et al. (2023). Intercropping system: a climate-smart approach for sustaining food security. *J. Appl. Biol. Biotechnol.* 10, 1–7. doi: 10.7324/JABB.2024.170871
- Salinas-Roco, S., Morales-González, A., Espinoza, S., Pérez-Díaz, R., Carrasco, B., Del Pozo, A., et al. (2024). N(2) fixation, N transfer, and land equivalent ratio (LER) in grain legume-wheat intercropping: impact of N supply and plant density. *Plant* 13:991. doi: 10.3390/plants13070991
- Sardans, J., Lambers, H., Preece, C., Alrefaei, A. F., and Penuelas, J. (2023). Role of mycorrhizas and root exudates in plant uptake of soil nutrients (calcium, iron, magnesium, and potassium): has the puzzle been completely solved? *Plant J.* 114, 1227–1242. doi: 10.1111/tpj.16184
- Sarkar, R. K., and Pal, P. K. (2004). Effect of intercropping rice (*Oryza sativa*) with groundnut (*Arachis hypogaea*) and pigeonpea (*Cajanus cajan*) under different row orientations on rainfed uplands. *Indian J. Agron.* 49, 147–150. doi: 10.59797/ija.v49i3.5181
- Schreuder, H. M. (2021). Fungal composition and mycotoxin contamination of commercial wheat in South Africa in association with climate and agronomic practices. Stellenbosch, South Africa: Stellenbosch University.
- Seleiman, M. F., Al-Suhaibani, N., Ali, N., Akmal, M., Alotaibi, M., Refay, Y., et al. (2021). Drought stress impacts on plants and different approaches to alleviate its adverse effects. *Plan. Theory* 10:259. doi: 10.3390/plants10020259
- Shanmugam, S., Hefner, M., Labouriau, R., Trinchera, A., Willekens, K., and Kristensen, H. L. (2022). Intercropping and fertilization strategies to progress sustainability of organic cabbage and beetroot production. *Eur. J. Agron.* 140:126590. doi: 10.1016/j.eja.2022.126590
- Sharma, J., Goyal, V., Dahiya, R., Kumar, M., and Dey, P. (2023). Response of long-term application of fertilizers and manure on P pools in Inceptisols. *Commun. Soil Sci. Plant Anal.* 54, 1042–1061. doi: 10.1080/00103624.2022.2137190
- Shatkovskiy, A. P., Hulenko, O. I., and Kalilei, V. V. (2022). Yield and energy assessment of chickpea and sunflower cultivation depending on the design of microirrigation systems. *Редукційна колекція* 13, 60–67. Series KB No. 25124-15064 PR. doi: 10.31548/agr.13(3).2022.60-67
- Shoaib, M., Banerjee, B. P., Hayden, M., and Kant, S. (2022). Roots' drought adaptive traits in crop improvement. *Plan. Theory* 11:2256. doi: 10.3390/plants11172256
- Siddiqui, N. A., Houson, H. A., Kamble, N. S., Blanco, J. R., O'Donnell, R. E., Hassett, D. J., et al. (2021). Leveraging copper import by yersiniabactin siderophore system for targeted PET imaging of bacteria. *JCI Insight* 6:880. doi: 10.1172/jci.insight.144880
- Siébou, P., Idriss, S., Sibiri Jean-Baptiste, T., Korodjouma, O., Stephen, C. M., and Adama, S. (2019). Pearl millet and cowpea yields as influenced by tillage, soil amendment and cropping system in the Sahel of Burkina Faso. *Int. J. Sci.* 8, 56–64. doi: 10.18483/ijSci.2136
- Singh, M. V. (2008). "Micronutrient deficiencies in crops and soils in India" in *Micronutrient deficiencies in global crop production*. ed. B. J. Alloway (Cham: Springer), 93–125.
- Singh, D., Mathimaran, N., Boller, T., and Kahmen, A. (2020). Deep-rooted pigeon pea promotes the water relations and survival of shallow-rooted finger millet during drought—despite strong competitive interactions at ambient water availability. *PLoS One* 15:e0228993. doi: 10.1371/journal.pone.0228993
- Singh, B., Padhy, A. K., Ambreen, H., Yadav, M., Bhardwaj, S., Singh, G., et al. (2022). "Understanding abiotic stress responses in lentil under changing climate regimes" in *Developing climate resilient grain and forage legumes*. eds. U. C. Jha, H. Nayyar, S. K. Agrawal and K. H. M. Siddique (Singapore: Springer Nature Singapore), 179–204.
- Singh, N. A., Sorokhaibam, S., Yumnam, S., and Konsam, J. (2021). Enhancing pulse productivity under rice based production system through chickpea and lentil based intercropping systems in north East India. *Legume Res.* 44, 215–220. doi: 10.18805/LR-4203
- Snapp, S., Gentry, L. E., and Ahl, K. (2019). Improving farmer adoption of intercropping through stronger integration of perspectives. *Agric. Hum. Values* 36, 549–560.
- Solomon, W., Janda, T., and Molnár, Z. (2023). Unveiling the significance of rhizosphere: implications for plant growth, stress response, and sustainable agriculture. *Plant Physiol. Biochem.* 206:108290. doi: 10.1016/j.plaphy.2023.108290
- Song, Y. N., Zhang, F. S., Marschner, P., Fan, F. L., Gao, H. M., Bao, X. G., et al. (2007). Effect of intercropping on crop yield and chemical and microbiological properties in rhizosphere of wheat (*Triticum aestivum* L.), maize (*Zea mays* L.), and faba bean (*Vicia faba* L.). *Biol. Fertil. Soils* 43, 565–574. doi: 10.1007/s00374-006-0139-9
- Soto, N., Hernández, Y., Delgado, C., Rosabal, Y., Ortiz, R., Valencia, L., et al. (2020). Field resistance to Phakopsora pachyrhizi and Colletotrichum truncatum of transgenic soybean expressing the NmDef02 plant defensin gene. *Front. Plant Sci.* 11:562. doi: 10.3389/fpls.2020.00562
- Soud, A., Hamdi, W., L'taief, B., Attallah, A., Hamdi, N., Alshaharni, M. O., et al. (2024). The potential of durum wheat–chickpea intercropping to improve the soil available phosphorus status and biomass production in a subtropical climate. *PLoS One* 19:e0300573. doi: 10.1371/journal.pone.0300573
- Srinivasarao, C., Venkateswarlu, B., Lal, R., Singh, A. K., Kundu, S., Vittal, K. P. R., et al. (2012). Long-term effects of crop residues and fertility management on carbon sequestration and agronomic productivity of groundnut–finger millet rotation on an Alfisol in southern India. *Int. J. Agric. Sustain.* 10, 230–244. doi: 10.1080/14735903.2012.662392
- Stagnari, F., Maggio, A., Galieni, A., and Pisante, M. (2017). Multiple benefits of legumes for agriculture sustainability: an overview. *Chem. Biol. Technol. Agric.* 4, 1–13. doi: 10.1186/s40538-016-0085-1
- Stomph, T., Dordas, C., Baranger, A., de Rijk, J., Dong, B., Evers, J., et al. (2020). Designing intercrops for high yield, yield stability and efficient use of resources: are there principles? *Adv. Agron.* 160, 1–50. doi: 10.1016/bs.agron.2019.10.002
- Storkey, J., Bruce, T. J., McMillan, V. E., and Neve, P. (2019). "The future of sustainable crop protection relies on increased diversity of cropping systems and landscapes." In: *Agroecosystem Diversity: Reconciling Contemporary Agriculture and Environmental Quality*. eds. G. Lemaire, P. C. de Faccio Carvalho, S. Kronenberg and S. Recous (Cambridge: Academic Press), 199–209. doi: 10.1016/B978-0-12-811050-8.00014-4
- Sugihara, S., Kawashita, T., Shitindi, M., Massawe, B., and Tanaka, H. (2021). Dynamics of fractionated rhizosphere soil P and plant P uptake under maize/P-mobilizing legumes intercropping in strongly weathered soil of Tanzania. *Soil Sci. Plant Nutr.* 67, 312–322. doi: 10.1080/00380768.2021.1911589
- Suntoro, S., Mujiyo, M., Widjanto, H., and Herdiansyah, G. (2020). Cultivation of Rice (*Oryza sativa*), corn (*Zea mays*) and soybean (*Glycine max*) based on land suitability. *J. Sett. Spat. Plan.* 11, 9–16. doi: 10.24193/JSSP.2020.1.02
- Tahat, M. M., Alananbeh, M. K., Othman, A. Y., and Leskovar, I. D. (2020). Soil health and sustainable agriculture. *Sustain. For.* 12:4859. doi: 10.3390/su12124859
- Tamta, A., Kumar, R. A. K. E. S. H., Ram, H. A. R. D. E. V., Meena, R. K., Kumar, U., Yadav, M. R., et al. (2019). Nutritional portfolio of maize and cowpea fodder under various intercropping ratio and balanced nitrogen fertilization. *Indian J. Anim. Sci.* 89, 276–280. doi: 10.56093/ijans.v89i3.88041
- Tang, X., Zhang, C., Yu, Y., Shen, J., van der Werf, W., and Zhang, F. (2021). Intercropping legumes and cereals increases phosphorus use efficiency: a meta-analysis. *Plant Soil* 460, 89–104. doi: 10.1007/s11104-020-04768-x
- Temesgen, A., Fukai, S., and Rodriguez, D. (2016). Intercropping in sustainable maize cultivation. Cambridge, UK: Burleigh Dodds Science Publishing. doi: 10.19103/AS.2016.0014.20
- Thakur, R. P., Sharma, R., and Rao, V. P. (2011). Screening techniques for pearl millet diseases. Information Bulletin No. 89. Patancheru, Andhra Pradesh, India: International Crops Research Institute for the Semi-Arid Tropics.
- Tiwari, H., Singh, P. K., Naresh, R. K., Islam, A., Kumar, S., Singh, K. V., et al. (2023). Millets based integrated farming system for food and nutritional security, constraints and agro-diversification strategies to fight global hidden hunger: a review. *Int. J. Plant Sci.* 35, 630–643. doi: 10.9734/IJPSS/2023/v35i193593
- Toker, P., Canci, H., Turhan, I., Isci, A., Scherzinger, M., Kordrostami, M., et al. (2024). The advantages of intercropping to improve productivity in food and forage production—a review. *Plant Prod. Sci.* 27, 155–169. doi: 10.1080/1343943X.2024.2372878
- Tosti, G., Falcinelli, B., and Guiducci, M. (2023). Lentil–cereal intercropping in a Mediterranean area: yield, pests and weeds. *Agron. J.* 115, 2570–2578. doi: 10.1002/agj.21413
- Tripathi, S. C., Venkatesh, K., Meena, R. P., Chander, S., and Singh, G. P. (2021). Sustainable intensification of maize and wheat cropping system through pulse intercropping. *Sci. Rep.* 11:18805. doi: 10.1038/s41598-021-98179-2
- Ullah, R., Aslam, Z., Khaliq, A., and Zahir, Z. A. (2018). Sunflower residue incorporation suppresses weeds, enhances soil properties and seed yield of spring-planted mung bean. *Planta Daninha* 36:e018176393. doi: 10.1590/S0100-83582018360100057
- USDA Economic Research Service. (2023). USDA ERS - land use and land cover estimates for the United States. Available at: <https://www.ers.usda.gov/about-ers/partnerships/strengthening-statistics-through-the-icars/land-use-and-land-cover-estimates-for-the-united-states/> (Accessed February 8, 2025).
- Venkatesh, M. S., Hazra, K. K., and Katiyar, R. (2014). "Nutrient acquisition and recycling through pulses" in *Resource conservation technology in pulses*. eds. P. K. Ghosh, N. Kumar and M. S. Venkatesh (Jodhpur: Scientific publishers), 190–198.
- Venkatesh, L., Policepath, A. S., Yogeeshappa, H., Manjunatha, B. N., Naveen, N. E., and Paramesh, V. (2010). Maize–Lucerne intercropping system in transitional tract of Karnataka. *Environ. Ecol.* 28, 1783–1786.
- Virk, A. L., Liu, W. S., Niu, J. R., Xu, C. T., Liu, Q. Y., Kan, Z. R., et al. (2021). Effects of diversified cropping sequences and tillage practices on soil organic carbon, nitrogen, and associated fractions in the North China plain. *J. Soil Sci. Plant Nutr.* 21, 1201–1212. doi: 10.1007/s42729-021-00433-z
- Wang, X., Gan, Y., Hamel, C., Lemke, R., and McDonald, C. (2012). Water use profiles across the rooting zones of various pulse crops. *Field Crop Res.* 134, 130–137. doi: 10.1016/j.fcr.2012.06.002

- Wang, Y., He, C., Meng, P., Sun, S., Zhang, J., Xue, P., et al. (2024). Effects of mowing frequency on the interspecific water relationships of a walnut (*Juglans regia* L.)-alfalfa (*Medicago sativa* L.) intercropping system. *Plant Soil*, 1–20. doi: 10.1007/s11104-024-06854-w
- Wang, Z. G., Jin, X., Bao, X. G., Li, X. F., Zhao, J. H., Sun, J. H., et al. (2014). Intercropping enhances productivity and maintains the most soil fertility properties relative to sole cropping. *PLoS One* 9:e113984. doi: 10.1371/journal.pone.0113984
- Wang, M., Shi, W., Kamran, M., Chang, S., Jia, Q., and Hou, F. (2024). Effects of intercropping and regulated deficit irrigation on the yield, water and land resource utilization, and economic benefits of forage maize in arid region of Northwest China. *Agric. Water Manag.* 298:108876. doi: 10.1016/j.agwat.2024.108876
- Wang, L., Yu, B., Ji, J., Khan, I., Li, G., Rehman, A., et al. (2023). Assessing the impact of biochar and nitrogen application on yield, water-nitrogen use efficiency and quality of intercropped maize and soybean. *Front. Plant Sci.* 14:1171547. doi: 10.3389/fpls.2023.1171547
- Wang, J., Zhang, X., Wang, H., Liu, T., Fayyaz, A., Gonzalez, N. C., et al. (2024). Leguminous crop restores the carbon flow attenuation from nitrogen loading within soil nematode food web in a *Camellia oleifera* plantation. *J. Environ. Manag.* 349:119580. doi: 10.1016/j.jenvman.2023.119580
- Watts-Williams, S. J., Gill, A. R., Jewell, N., Brien, C. J., Berger, B., Tran, B. T., et al. (2022). Enhancement of sorghum grain yield and nutrition: a role for arbuscular mycorrhizal fungi regardless of soil phosphorus availability. *Plants People Planet* 4, 143–156. doi: 10.1002/ppp3.10224
- Weldeslassie, T., Tripathi, R. P., and Ogbazghi, W. (2016). Optimizing tillage and irrigation requirements of sorghum in sorghum-pigeonpea intercrop in hamelmalo region of Eritrea. *J. Geosci. Environ. Prot.* 4, 63–73. doi: 10.4236/gep.2016.44009
- Wolińska, A., Kruczyńska, A., Podlewski, J., Słomczewski, A., Grządziel, J., Gałazka, A., et al. (2022). Does the use of an intercropping mixture really improve the biology of monocultural soils?—A search for bacterial indicators of sensitivity and resistance to long-term maize monoculture. *Agronomy*, 12:613. doi: 10.3390/agronomy12030613
- Wu, J., Bao, X., Zhang, J., Lu, B., Sun, N., Wang, Y., et al. (2024). Facilitation between intercropped species increases micronutrient acquisition and controls rust disease on maize. *Field Crop Res.* 307:109241. doi: 10.1016/j.fcr.2023.109241
- Xia, H. Y., Zhao, J. H., Sun, J. H., Bao, X. G., Christie, P., Zhang, F. S., et al. (2013). Dynamics of root length and distribution and shoot biomass of maize as affected by intercropping with different companion crops and phosphorus application rates. *Field Crop Res.* 150, 52–62. doi: 10.1016/j.fcr.2013.05.027
- Xiao, X., Han, L., Chen, H., Wang, J., Zhang, Y., and Hu, A. (2023). Intercropping enhances microbial community diversity and ecosystem functioning in maize fields. *Front. Microbiol.* 13:1084452. doi: 10.3389/fmicb.2022.1084452
- Yang, Y., Feng, X. M., Hu, Y. G., and Zeng, Z. H. (2019). The diazotrophic community in oat rhizosphere: effects of legume intercropping and crop growth stage. *Front. Agric. Sci. Eng.* 6, 162–171. doi: 10.15302/J-FASE-2018212
- Yang, H., Zhang, W., and Li, L. (2021). Intercropping: feed more people and build more sustainable agroecosystems. *Front. Agric. Sci. Eng.* 0–386. doi: 10.15302/J-FASE-2021398
- Yu, N., Ren, B., Zhao, B., Liu, P., and Zhang, J. (2022). Optimized agronomic management practices narrow the yield gap of summer maize through regulating canopy light interception and nitrogen distribution. *Europ. J. Agron.* 137:126520. doi: 10.1016/j.eja.2022.126520
- Zhang, J., He, P., Ding, W., Ullah, S., Abbas, T., Li, M., et al. (2021). Identifying the critical nitrogen fertilizer rate for optimum yield and minimum nitrate leaching in a typical field radish cropping system in China. *Environ. Pollut.* 268:115004. doi: 10.1016/j.envpol.2020.115004
- Zhang, H., Shi, W., Ali, S., Chang, S., Jia, Q., and Hou, F. (2022). Legume/maize intercropping and N application for improved yield, quality, water and n utilization for forage production. *Agronomy* 12:1777. doi: 10.3390/agronomy12081777
- Zhao, Y., Tian, Y., Li, X., Song, M., Fang, X., Jiang, Y., et al. (2022). Nitrogen fixation and transfer between legumes and cereals under various cropping regimes. *Rhizosphere* 22:100546. doi: 10.1016/j.rhisph.2022.100546
- Zhu, S. G., Zhu, H., Zhou, R., Zhang, W., Wang, W., Zhou, Y. N., et al. (2023). Intercrop overyielding weakened by high inputs: global meta-analysis with experimental validation. *Agric. Ecosyst. Environ.* 342:108239. doi: 10.1016/j.agee.2022.108239



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Effect of strip width in maize/ peanut intercropping on water use efficiency

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Introduction: Maize and peanut intercropping can optimize allocation of rainfall through crop canopies, enhancing crop resilience to drought. However, the mechanisms underlying this process remain unclear.

Methods: This study investigates the impact of strip width on rainfall redistribution to the soil in maize (MS) and peanut (PS) monoculture systems, as well as in intercropping systems with strip configurations of 2:2 (M2P2), 4:4 (M4P4), and 8:8 (M8P8).

Results and discussion: Results showed that maize/peanut intercropping consistently improved system water use efficiency (WUE) over the three-year experiment, with the M4P4 treatment maintaining the highest WUE throughout. Strip width significantly influenced stemflow and throughfall in maize rows, as well as throughfall in peanut rows, with maize plant height and leaf area playing key roles. Among the 17 rainfall events studied, maize rows in the M2P2, M4P4, and M8P8 treatments obtained 17.4%, 10.8%, and 5.4% more rainfall, respectively, compared to the MS. However, compared to PS, water captured by intercropped peanut rows decreased by 20.6%, 13.2%, and 7.1%, respectively. An edge effect was observed in the intercropping treatments, with stemflow in maize rows increasing by 23.7%, 17.8%, and 14.6%, and throughfall by 12.2% (M2P2), 10.6% (M4P4), and 8.6% (M8P8) compared to MS. Conversely, the M2P2, M4P4, and M8P8 treatments decreased throughfall in peanut by 20.6%, 18.0%, and 16.0%, respectively, compared with PS. Overall, our findings suggest that optimizing strip width in intercropping systems can improve both crop productivity and water management, offering insights for sustainable agricultural practices in regions with limited water resources.

KEYWORDS

intercropping, canopy, strip width, stemflow, throughfall, maize, peanut

1 Introduction

As global climate change intensifies, extreme weather events and natural disasters, such as droughts, are becoming more frequent and severe, posing significant challenges to agricultural production and farmer livelihoods (Lou et al., 2024). To ensure sustainable and stable agricultural systems, farming practices that can adapt to these adverse conditions are essential (Lou et al., 2024; Chimi et al., 2024). The relationship between biodiversity and ecosystem stability has been extensively studied following the development of the diversity-stability hypothesis (Odum, 1953; MacArthur, 1955). Intercropping—a practice where two or more crop species are grown together for all or part of their growing season—has gained attention as a strategy for increasing biodiversity in agricultural systems (Feng et al., 2021; Pelech et al.,

2023). By diversifying agricultural systems, intercropping can enhance crop production and improve resilience to stresses, such as drought, through optimizing resource use and system adaptability (Renwick et al., 2020; Nelson et al., 2022).

To maximize the benefits of intercropping, selecting appropriate crops and designing suitable intercropping configurations are essential (Brooker et al., 2015). Additionally, crop characteristics such as canopy structure (Chai et al., 2014), root system depth (shallow or deep) (Xia et al., 2013), and growth stages (Zhang et al., 2017) must also be considered. Recent research aimed at improving drought resistance and yield stability in intercropping systems has primarily focused on nutrient and water use (Feng et al., 2024; Zhang et al., 2024b; Ma et al., 2019). For instance, in maize/soybean intercropping systems, the root length density of both maize and soybean is higher than in monocultures, which enhances water uptake and improves drought resistance (Ren et al., 2017). However, there has been less focus on the impact of aboveground configurations on the water use efficiency of intercropping systems.

Rainfall is intercepted by the canopy and is then distributed as stemflow and throughfall into the soil (Nanko et al., 2016). Stemflow refers to the volume of water that flows down the plant stem to the roots after being captured by the plant canopy (Lamm and Manges, 2000). Throughfall, on the other hand, is the portion of rainfall that reaches the soil through gaps or complex structures in the canopy, representing a significant form of rainfall under crop canopies (Zhu et al., 2021; Guo et al., 2023). Thus, appropriately structured canopies can ensure drought resistance, stable yields, and efficient resource utilization (Yang et al., 2017; Nelson et al., 2018). The canopy, composed of stems, branches, and leaves, acts as the interface between the plant and its environment (Franco et al., 2018). Generally, in response to drought stress, crops modify their plant height, leaf area, number of branches or tillers, number of reproductive organs, growth period length, stomatal closure, direction of photosynthetic assimilate transport, enzyme composition, and genetic structure—collectively known as “growth redundancy” (Gao et al., 2020; Ye et al., 2020; Nehe et al., 2021). In intercropping systems, interactions between species can affect canopy development. For instance, intercropping maize and peanuts significantly alters the plant canopy structure compared to monocultures. Peanuts have abundant branches and leaves, shorter plant height, and better surface coverage (Tahir et al., 2016). This structure reduces the diffusion resistance of the boundary layer and minimizes soil moisture evaporation, facilitates airflow, and significantly improves the overall transpiration efficiency of both crops. While the relationship between canopy structure and drought resistance is better understood in monoculture systems, crops in intercropping systems exhibit similar adjustments.

A semi-arid region in northeastern China lies at the intersection of the Mongolian Plateau and Northeast Plain. This area receives annual precipitation ranging from 350 to 500 mm, though this amount fluctuates significantly from year to year, leading to low and variable crop yields (Lu and Shi, 2024). The main crops in this region are maize and peanuts (Feng et al., 2021). Maize, an essential food crop, has high water-use efficiency, but its tall stature and high rates of transpiration and evaporation result in substantial water demands. This increases the risk of poor harvests in the semi-arid region (Zhang et al., 2024a). In contrast, peanuts require less water than maize, and are more drought tolerant (Feng et al., 2021). Therefore, intercropping maize and peanut helps optimize the limited water supply in drylands and improve agricultural resistance to drought. Intercropping can also

block and reduce deep leakage and surface runoff of rainwater and irrigation water in maize and peanut canopy layers, improve usage of rainfall, and enhance soil water storage capacity, with significant economic benefits (Feng et al., 2016; Hamd-Alla et al., 2023). Additionally, Intercropping maize and peanut can also stagger critical periods of crop water demand and reduce interspecies competition, which is important for efficient water use in intercropping systems (Chauhan et al., 2015). However, little is known about how combining maize and peanut crops affects the passage of water flow into soils.

We investigated the impact of maize canopy structure and strip width on water flow in intercropped maize and peanut systems. Our objective was to evaluate whether intercropping could improve both agricultural stability and productivity in semi-arid, drought-prone regions, while also identifying more suitable planting patterns for these areas.

2 Methods

2.1 Experimental site

The experiment was conducted from 2021 to 2023 at the Jianping County Irrigation Experimental Station (41°47'18" N, 119°18'36" E, 512 m above sea level), located in Chaoyang City, Liaoning Province, China (Supplementary Figure S1). The site is situated in a transitional zone between arid and semi-arid climates and experiences a monsoon continental climate. The area has an average annual temperature of 7.1°C, a total effective accumulated temperature of 3,200°C, and a frost-free period of 125–133 days. Annual evaporation averages 1800 mm, while total annual precipitation is 451.2 mm. Rainfall exhibits significant interannual variability, with frequent droughts occurring in the spring. The dominant soil type is cinnamon soil with a sandy loam texture. The soil has a maximum field water-holding capacity of 25.4%, a bulk density of 1.4 g cm⁻³, and contains 1.21% organic matter, 320 mg kg⁻¹ total nitrogen, 13.6 mg kg⁻¹ Olsen phosphorus, and 110.1 mg kg⁻¹ available potassium. During the crop growth periods of 2021, 2022, and 2023, the total rainfall was 527 mm (wet year), 283.6 mm (normal year), and 233.7 mm (dry year), respectively (Supplementary Figure S2). The rainfall redistribution between maize and peanut was measured 17 times over three years: 2 times in 2021, 3 times in 2022, and 12 times in 2023.

2.2 Experiment design

Maize (“Zhengdan 958”) and peanut (“Baisha 1016”) varieties were grown under five different treatments: maize sole crop (MS); peanut sole crop (PS), intercropping with two rows of peanut and two rows of maize (M2P2), intercropping with four rows of peanut and four rows of maize (M4P4), and intercropping with eight rows of peanut and eight rows of maize (M8P8). Each treatment was replicated four times, with each plot measuring 10 × 20 m. Planting rows were oriented north–south, with a row spacing of 50 cm (Figure 1). The maize was planted at a density of 67,300 plants ha⁻¹ (plant spacing was 29.7 cm), while the peanut was planted at a density of 268,000 plants ha⁻¹ (hole spacing was 14.9 cm, 2 plants per hole). From 2021 to 2023, only basal fertilizer was applied during sowing, which was a compound fertilizer, consisting of 112 kg ha⁻¹ N, 112 kg ha⁻¹ P₂O₅ and 112 kg ha⁻¹ K₂O. Maize and peanut were sown simultaneously on May 12th, May 13th, and May 15th in

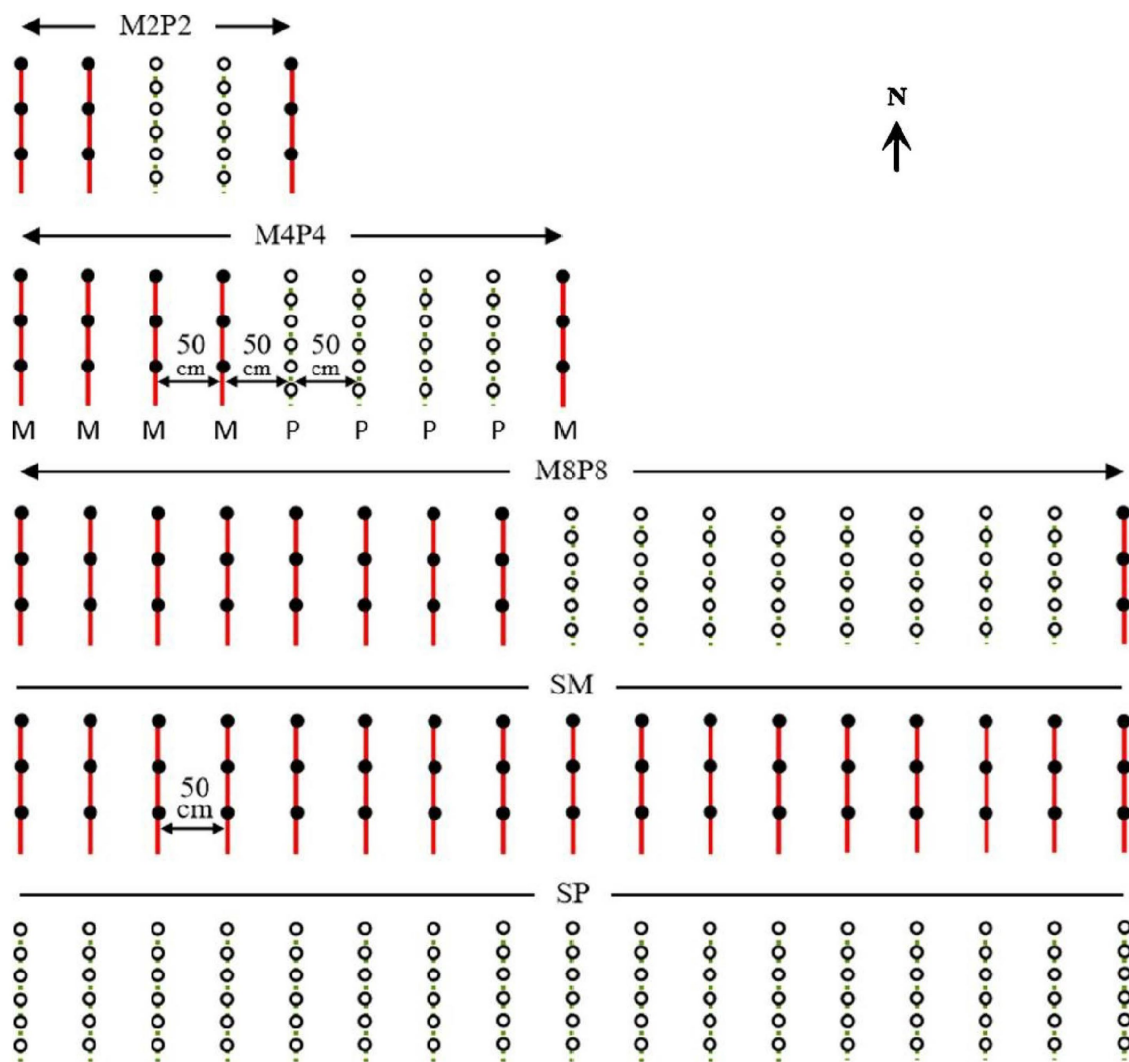


FIGURE 1
Layout of maize/peanut strip intercropping and sole systems. Solid circles in red lines represent maize plants and open circles in green dashed lines indicate peanut plants.

2021, 2022, and 2023, respectively, with harvesting occurring on September 30th, September 29th, and September 27th in the same years. Except during the spring drought in 2023, when crops were irrigated with 10 mm of water after sowing to ensure seedling emergence, no irrigation was applied during other growth periods.

2.3 Measurements

2.3.1 Rainfall

Real-time rainfall data were recorded using an automatic weather station (DZZ6, Zhong Huan Tig), installed in an open area approximately 10 meters from the experimental site. The experimental field has a flat terrain, and since it is an arid region, the runoff volume was not measured.

2.3.2 Stemflow

To measure stemflow, a funnel was attached to the base of selected maize stems, following a modification of the method

described by Lamm and Manges (2000). To ensure complete collection of the stemflow, a gap of more than 1 cm was kept between the top edge of the funnel and the maize stem. The bottom of the funnel was sealed to the maize stem using a mastic sealant to prevent any leakage. Eight guide pipes inserted into the bottom of the funnel connected to a water-collection bucket, which was covered to prevent any water other than stemflow from entering (Figure 2). Stemflow was standardized by dividing collected flow by the average area occupied by a single maize plant. Three measurement points were placed in parallel within each plot, with the distance between them exceeding 2 m.

Stemflow per plant was calculated as follows:

$$SF = \frac{SF_g / \rho}{A} \quad (1)$$

where SF is stemflow (mm), SF_g is stemflow mass (g), ρ is liquid density (g cm^{-3}), and A is canopy-occupied area by each maize plant (cm^2).

The stemflow rate is a ratio of stemflow to rainfall during a rainfall event, calculated as follows:

$$SR = SF / RF \quad (2)$$

Where SR is stemflow rate (%) and RF is rainfall during a rainfall event (mm).

2.3.3 Throughfall

For measuring throughfall, buckets of the same size as those used for stemflow measurements were placed on or in each ridge/furrow beneath the crop canopy (Figure 3). In the intercropping system, the maize canopy overlapped with the peanut canopy, meaning that the maize canopy influenced the throughfall in the peanut strips. Therefore, the rainfall that penetrated the peanut strips was also measured. Measurements were taken three times in parallel for each plot. The throughfall rate was calculated as the ratio of throughfall to total rainfall during a rainfall event, using the following formula:

$$TR = TF / RF \quad (3)$$

Where TR is throughfall rate (%) and RF is rainfall during a rainfall event (mm).

2.3.4 Plant height and leaf area

Plant height and leaf area were measured following each rainfall event. Five plants were randomly selected from each plot for these measurements. Plant height was measured from the ground to the highest point of the fully extended plant, while leaf area (including senescing leaves) was measured using a portable leaf area meter (YMJ-G, Laiyin Technology, Weifang, China).

2.3.5 Yields

After harvest, the crop yields from each plot were measured individually. The sampling area for yield measurement in each community was 10 m², and the yield of maize grains and peanut kernels was measured after air-drying.

2.3.6 Soil moisture content

Soil moisture content at different depths (from 10 cm to 100 cm) was measured before sowing and after harvest for each treatment. For the calculation of water consumption, soil volumetric moisture content was calculated based on the soil bulk density.

2.3.7 Land equivalent ratio

The Land equivalent ratio (LER) is used to assess the land utilization efficiency of intercropping (Feng et al., 2016), and was calculated as follows:

$$LER = LER_A + LER_B \frac{Y_{int, A}}{Y_{sole, A}} + \frac{Y_{int, B}}{Y_{sole, B}} \quad (4)$$

Where $Y_{int, A}$ and $Y_{int, B}$ represent the intercropping yields of crop A (maize) and crop B (peanut), respectively. $Y_{sole, A}$ and $Y_{sole, B}$ represent the sole crop yields of crop A and crop B, respectively. LER_A and LER_B are the partial land equivalent ratios of crop A and crop B. A LER greater than 1 indicates that the land utilization efficiency of the intercropping system is higher than that of sole cropping.

2.3.8 Water equivalent ratio

The water equivalent ratio (WER) is defined similarly to the LER (Feng et al., 2016). WER quantifies the amount of water that would be required in sole cropping to achieve the same yield as produced with one unit of water in an intercropping system. If the $WER > 1$, it indicates that the water utilization efficiency of intercropping is higher than that of sole.

$$WER = WER_A + WER_B \frac{(Y_{int, A} / WU_{int})}{(Y_{sole, A} / WU_{sole, A})} + \frac{(Y_{int, B} / WU_{int})}{(Y_{sole, B} / WU_{sole, B})} = \frac{WUE_{int, A}}{WUE_{sole, A}} + \frac{WUE_{int, B}}{WUE_{sole, B}} \quad (5)$$

Where $WUE_{sole, A}$ and $WUE_{sole, B}$ are the water use efficiencies of sole cropping for A and B. $WUE_{int, A}$ and $WUE_{int, B}$ are water use



FIGURE 2
Devices for measuring maize stemflow.



FIGURE 3
Devices for measuring the throughfall.

efficiencies of crops A and B in the intercropping system. These WUE values are calculated as the yield of crop A or B per unit of total water used in the intercropping system. Y is yield. WU_{int} is actual evapotranspiration of the entire intercropping system, $WU_{sole, A}$ and $WU_{sole, B}$ are the actual evapotranspiration values for crops A and B in sole cropping. The specific measurement method was the same as that described by Mao et al. (2012).

2.4 Statistical analysis

Data analysis (ANOVA) was performed using SPSS 19.0 (IBM Corporation), and regression equation simulation and plotting were conducted using Origin 2025.

3 Results

3.1 Crop productivity and water use efficiency

Results on crop yields from 2021 to 2023 showed that planting patterns significantly influenced crop yields (Table 1). Because maize-peanut intercropping was considered as a whole, the planting ratio of a certain crop in intercropping was lower than that in sole, so its yield was also lower than that of sole. The yield of intercropped maize increased as the strip width narrowed, while peanut yield showed year-to-year variability. The LER of maize-peanut intercropping was greater than 1, indicating that this intercropping system can enhance land productivity. Water utilization (WU) in intercropped maize was lower than in

MS, although the differences between treatments varied from year to year. While no significant difference was observed between intercropped and sole-cropped peanut. The water use efficiency (WUE) is a direct indicator of water use efficiency in intercropping systems. Since the LER of maize-peanut intercropping was greater than 1, it suggested that this system improved water use efficiency. The WER for M4P4 remained consistently high across the years, while that of M2P2 was relatively lower. In 2021, a wet year, and 2022, a normal year, no significant difference in WER was found between M4P4 and M8P8. However, in 2023, a dry year, M4P4 exhibited the highest water use efficiency.

3.2 Effects of strip width of intercropping on maize plant height and leaf area

The leaf area of intercropped maize was greater than that of sole-cropped maize, with the following ranking: M2P2 > M4P4 > M8P8 > MS (Figure 4A). Compared with sole-cropped maize, plant height was higher in 2022 (normal year) and 2023 (dry year) but lower in 2021 (wet year) (Figure 4B). These results indicated that both rainfall and planting patterns had a significant impact on plant height in this region.

3.3 Effect of width of intercropping on rainfall redistribution

To explore the impact of strip width on rainfall interception in intercropping systems, rainfall redistribution between maize

TABLE 1 Water use efficiency (WUE) and water equivalent ratio (WER).

Year	Treatment	Yield (g/m ²)		WU (mm)		WUE (g·m ⁻² ·mm ⁻¹)		LER	WER
		Maize	Peanut	Maize	Peanut	Maize	Peanut		
2021	M2P2	726b	158c	427.06b	415.79a	1.70b	0.38c	1.02b	1.07b
	M4P4	686c	212b	431.45b	424.00a	1.59c	0.50b	1.10a	1.14a
	M8P8	653d	216b	426.80b	423.53a	1.53c	0.51b	1.08a	1.12a
	Sole	1073a	456a	464.50a	410.81a	2.31a	1.11a	-	-
2022	M2P2	663b	110c	292.07b	282.05a	2.27b	0.39c	1.03b	1.13b
	M4P4	660b	135c	297.30b	281.25a	2.22b	0.48bc	1.09a	1.19a
	M8P8	572c	161b	299.48b	272.88a	1.91c	0.59b	1.07a	1.18a
	Sole	956a	333a	322.97a	308.33a	2.96a	1.08a	-	-
2023	M2P2	638b	102c	270.34b	261.54a	2.36b	0.39c	1.06b	1.05b
	M4P4	618c	134b	274.67b	262.75a	2.25b	0.51b	1.15a	1.10a
	M8P8	564d	143b	276.47b	264.81a	2.04c	0.54b	1.10b	1.06b
	Sole	861a	356a	282.30a	254.29a	3.05a	1.40a	-	-
Mean	M2P2	676b	123d	329.82b	319.79a	2.10b	0.39c	1.03b	1.08b
	M4P4	655c	160c	334.47b	322.67a	2.03b	0.50b	1.11a	1.14a
	M8P8	596d	173b	334.25b	320.41a	1.83c	0.52b	1.08a	1.12a
	Sole	963a	382a	356.59a	324.48a	2.78a	1.20a	-	-
P	Treatment	0.018	0.022	0.008	0.097	0.033	0.025	0.044	0.037
	Year	0.056	0.039	0.017	0.310	0.029	0.046	0.098	0.039
	Treatment×Year	0.408	0.211	0.160	0.385	0.143	0.185	0.462	0.232

The different lowercase letters indicate a significant difference among treatments of the same crop at 0.05 level.

and peanuts was measured 17 times between 2021 and 2023 (Not all rainfall events were measured during the three years). The results showed that strip width had a significant impact on stemflow in maize rows and throughfall in both maize and peanut rows (Table 2). The average stemflow in the maize rows of M2P2, M4P4, and M8P8 was 23.7, 14.2, and 5.6% higher than in MS across the 17 rainfall events, while the average throughfall in these maize rows was 12.2, 8.0, and 5.3% higher than in MS. Overall, maize rows in M2P2, M4P4, and M8P8 obtained, on average, 17.4, 10.8, and 5.4% more rainfall compared to MS. Conversely, the peanut rows in M2P2, M4P4, and M8P8 experienced a decrease in throughfall, with averages of 20.6, 13.2, and 7.1%, respectively, compared to PS.

3.4 Relationships between leaf area, plant height, and rainfall redistribution

Leaf area and plant height significantly influenced the redistribution of rainfall between crops (Figures 5, 6). For maize, stemflow rates increased with plant height and leaf area. These relationships were effectively modeled using linear regression (LR), polynomial regression (PR), and exponential regression (ER) equations. Among these, the ER equations exhibited higher R^2 values for the relationships between stemflow rates and both plant height and leaf area (Figures 5A,B). In contrast, throughfall

rates decreased as plant height and leaf area increased. The LR equations showed a high R^2 value for the relationship between throughfall rates and leaf area (Figure 5C), while PR and ER equations demonstrated high R^2 values for the relationship between throughfall rates and plant height (Figure 5D). Due to the shading effect of maize canopy on peanut in the intercropping systems, the throughfall rate for peanut decreased as maize height and leaf area increased (Figures 6A,B). PR and ER equations exhibited high R^2 values for the relationship between throughfall rate for peanut and maize leaf area, the ER equations showed a high R^2 value for the relationship between throughfall rate for peanut and plant height.

3.5 Edge effects of rainfall redistribution

The study examined the edge effects on rainfall redistribution in maize-peanut intercropping systems with different strip widths. Based on average data from 17 rainfall events, maize edge rows in the M2P2, M4P4, and M8P8 treatments increased stemflow by 23.7, 17.8, and 14.6%, respectively, compared to MS (Figure 7A). Throughfall increased by 12.2, 10.6, and 8.6%, respectively (Figure 7B). Overall, maize edge rows in M2P2, M4P4, and M8P8 obtained 17.4, 13.8, and 11.3% more rainfall than MS. Intercropping with peanuts significantly reduced throughfall, especially at the edge rows. Compared to PS,

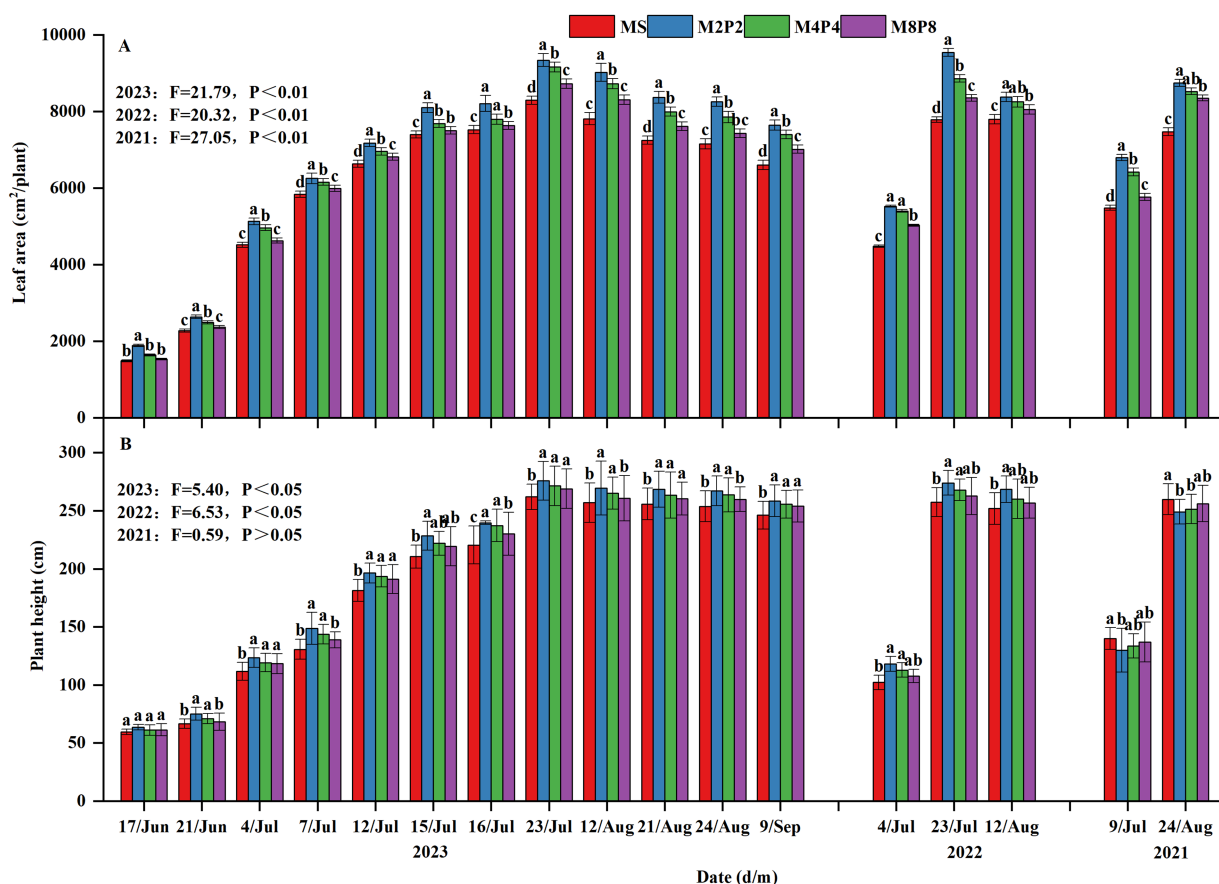


FIGURE 4

Leaf area (A) and plant height (B) of maize in different treatments. Lowercase letters indicate significant differences among treatments in the same year at $p < 0.05$ level.

throughfall in peanut edge rows in M2P2, M4P4, and M8P8 decreased by 20.6, 18.0, and 16.0%, respectively (Figure 7C).

4 Discussion

Our results indicate that narrower strip widths can increase maize leaf area, regardless of whether the growing season is in a wet or dry year. This suggests that light and space, rather than water availability, are the primary limiting factors for maize leaf extension in the maize-peanut intercropping system studied. Previous research has shown that intercropping with varying strip widths and canopy architectures creates spatial niche differentiation, alters light distribution, and affects yield (Wang et al., 2021; Yang et al., 2024). This suggests that the competitive relationship between intercrops in a specific strip intercropping system is regulated by width configuration (Abakumova et al., 2016). In the narrower strip width intercropping system, as shown in Figure 1, maize plants were less constrained by each other due to the presence of more edge rows. Fu et al. (2023) proposed that high N availability can enhance maize leaf extension in maize-legume intercropping systems. Given that strip width in maize-peanut intercropping has a significant impact on soil N availability and plant N uptake (Zhang et al., 2024c), this may influence maize

leaf area. In contrast to leaf area, plant height increased with narrower strip widths during normal and dry years but was not affected by strip width during the wet year. This indicates that water availability is the primary factor controlling plant height in this climate region. Similarly, a study in a high rainfall area by Zou et al. (2024) found that maize-peanut intercropping had no effect on maize height.

Through this experiment, it was found that intercropping can affect the allocation of rainfall between intercrops. Maize-peanut intercropping significantly increased stemflow and throughfall in maize rows, while it reduced throughfall in peanut rows. Maize obtained more rainfall than peanut due to its greater height and canopy, which overshadows the peanut rows. Due to this reason, in most cases, maize received more water than what was provided by rainfall in the maize-peanut intercropping system, with the excess water being taken from the peanut strips. Similar results have been observed in maize-soybean intercropping systems (Wang et al., 2024). We found a positive correlation between maize stemflow and both maize leaf area and plant height, whereas a negative relationship existed between maize and peanut throughfall and maize leaf area and plant height. These findings indicate that more rainfall is allocated to maize rows as maize leaf area and height increase, leading to higher water use efficiency (WUE) in maize and lower WUE in peanuts. This study was conducted in a semi-arid region where water availability is

TABLE 2 The impact of intercropping on rainfall distribution.

Year	Date	Rainfall (mm)	Stemflow of maize (mm)				Throughfall of maize (mm)				Throughfall of peanut (mm)			
			MS	M2P2	M4P4	M8P8	MS	M2P2	M4P4	M8P8	PS	M2P2	M4P4	M8P8
2021	9-Jul	21.52	9.46d	10.33a	9.87b	9.53c	10.32b	11.7a	11.53a	11.52a	19.32a	15.83d	16.65c	18.47b
	24-Aug	17.63	8.54d	10.27a	9.54b	8.9c	7.65c	8.7a	8.37ab	8.12b	16.08a	12.3d	13.84c	14.37b
2022	4-Jul	13.82	4.41b	5.69a	5.53a	4.56b	8.83b	9.32a	9.1a	8.86b	13.25a	10.68d	11.73c	12.45b
	23-Jul	13.50	6.28d	8.18a	7.79b	6.93c	5.92c	6.81a	6.65b	5.93c	11.98a	9.73d	10.42c	11.2b
	13-Aug	11.10	6.02d	6.93a	6.48b	5.89c	4.63b	5.01a	5.08a	4.92a	10.03a	8.34c	8.95c	9.73b
2023	17-Jun	3.32	0.45b	0.53a	0.43b	0.46b	2.73b	2.80a	2.85a	2.85a	3.24a	3.18a	3.20a	3.25a
	21-Jun	3.91	1.11c	1.29a	1.17b	1.13c	2.36c	2.59a	2.52a	2.41b	3.64a	3.16d	3.38c	3.50b
	4-Jul	30.56	9.94c	12.8a	12.49b	10.01c	19.79c	20.43a	19.91b	19.81c	29.52a	23.86d	26.17c	27.65b
	7-Jul	40.70	14.12d	18.99a	16.35b	15.94c	22.37c	24.98a	24.18ab	23.77b	36.93a	29.06c	31.70b	32.11b
	12-Jul	18.62	7.23d	8.99a	8.25b	7.51c	9.02c	10.18a	9.93b	9.93b	16.46a	13.70c	14.44b	16.08a
	15-Jul	5.51	2.74c	3.18a	2.87b	2.85b	2.28c	2.72a	2.67a	2.42b	5.01a	4.07d	4.38c	4.70b
	16-Jul	3.62	1.93c	2.18a	2.15a	2.11b	1.44c	1.71a	1.67ab	1.63b	3.36a	2.81c	2.94c	3.08b
	23-Jul	13.45	6.33d	8.16a	7.75b	6.8c	5.68d	6.96a	6.40b	5.87c	12.05a	9.58d	10.29c	11.34b
	12-Aug	9.02	4.87c	5.59a	5.32b	4.88c	3.76b	4.05a	4.04a	3.95a	8.22a	6.90c	7.37b	8.01a
	21-Aug	37.22	15.84d	20.37a	18.58b	17.76c	18.04d	20.53a	19.67b	19.04c	34.53a	26.42d	29.18c	31.87b
	24-Aug	25.28	12.37c	14.81a	12.98b	12.86bc	11.08c	12.69a	11.79b	11.89b	23.15a	17.81d	19.84c	20.76b
	9-Sep	13.09	5.83d	6.98a	6.61b	5.965c	6.82d	8.96a	7.84b	7.34c	11.98a	8.10d	10.18c	11.83b
Mean		16.52	6.91d	8.55a	7.89b	7.30c	8.40c	9.42a	9.07b	8.84b	15.22a	12.09d	13.22c	14.14b
P	Treatment		0.037				0.021				0.016			
	Year		0.135				0.297				0.096			
	Treatment×Year		0.624				0.870				0.261			

The different lower case letters indicate a significant difference among treatments of the same crop at 0.05 level.

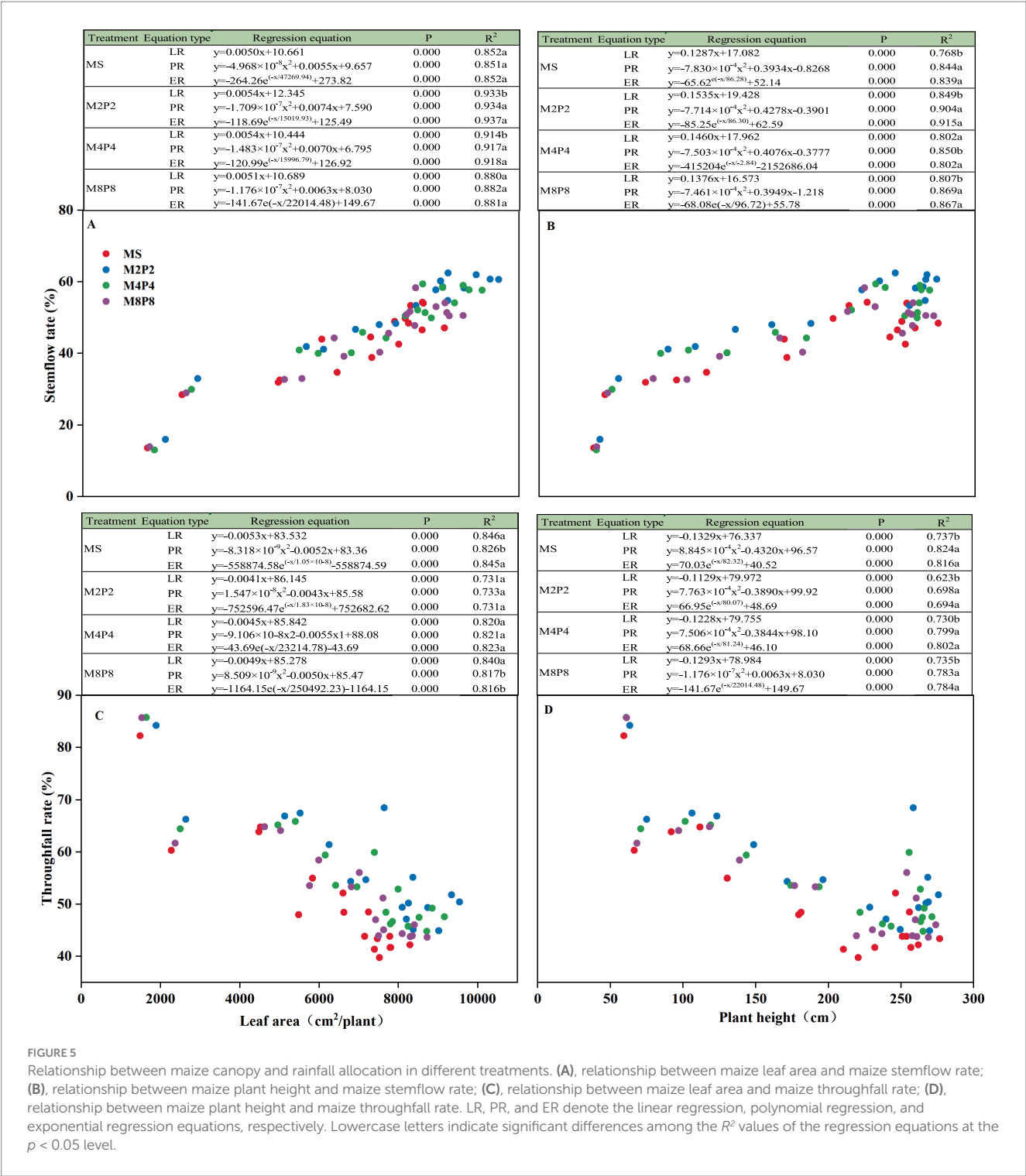


FIGURE 5 Relationship between maize canopy and rainfall allocation in different treatments. (A), relationship between maize leaf area and maize stemflow rate; (B), relationship between maize plant height and maize stemflow rate; (C), relationship between maize leaf area and maize throughfall rate; (D), relationship between maize plant height and maize throughfall rate. LR, PR, and ER denote the linear regression, polynomial regression, and exponential regression equations, respectively. Lowercase letters indicate significant differences among the R^2 values of the regression equations at the $p < 0.05$ level.

a key limiting factor for crop growth. Maize, being a high water-consuming crop, consistently shows increased WUE with higher water availability (Zhao et al., 2024). Our results support this, as maize WUE increased with narrower strip widths and higher rainfall allocation. However, for peanuts, due to their lower water consumption, no significant difference in WUE was observed between M4P4 and M8P8, regardless of whether it was a wet or dry year, even when rainfall allocation decreased.

In general, the water consumption of sole-cropped maize increases with plant height and leaf area. In intercropping systems, maize can not only capture more rainfall through its canopy but also extract water from peanut strips in the soil during drought periods. In this study, the water consumption of intercropped maize was estimated based on changes in soil moisture content within the intercropping strip. Therefore, it does not represent the actual water consumption of the maize itself. This explains why intercropped

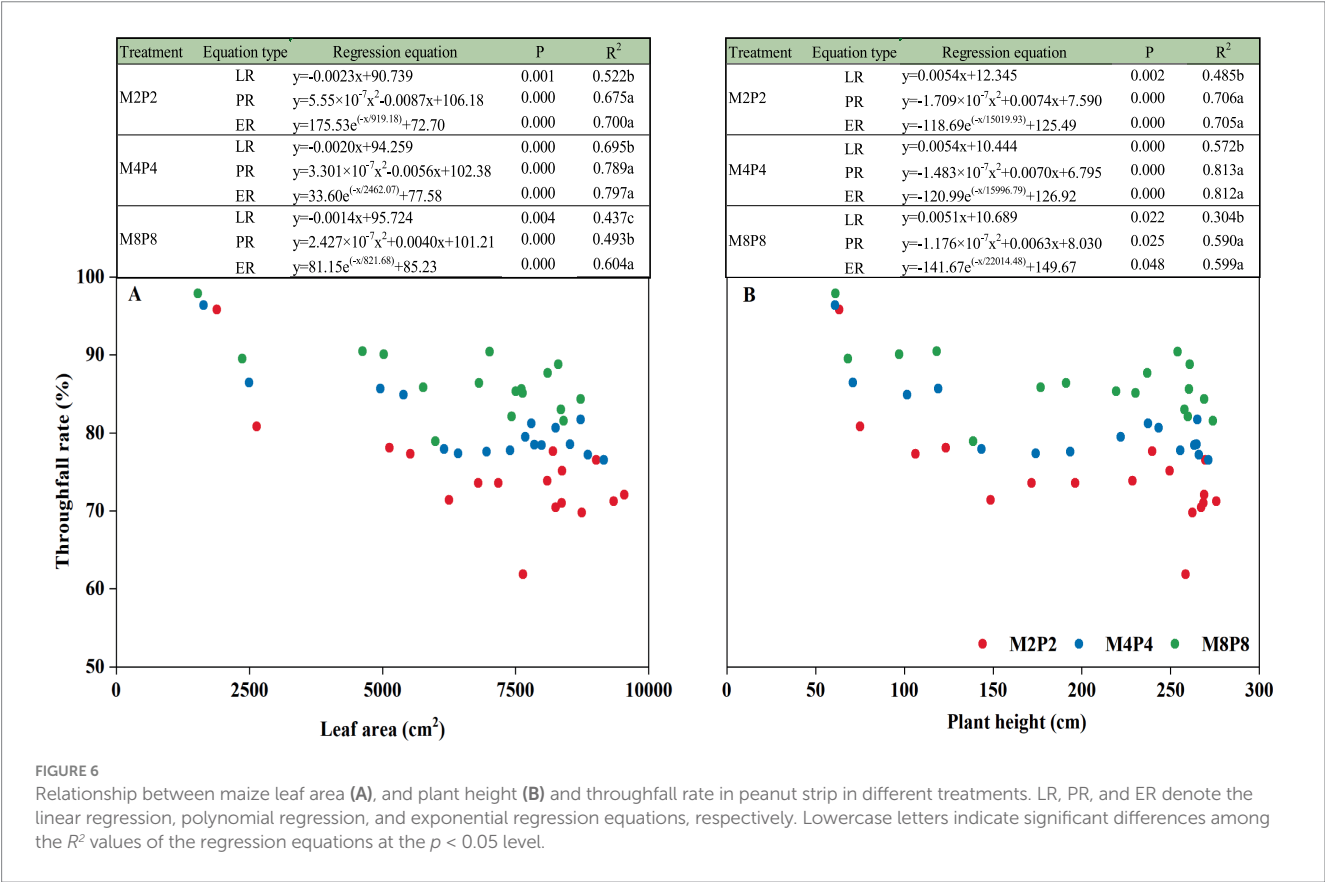


FIGURE 6 Relationship between maize leaf area (A), and plant height (B) and throughfall rate in peanut strip in different treatments. LR, PR, and ER denote the linear regression, polynomial regression, and exponential regression equations, respectively. Lowercase letters indicate significant differences among the R^2 values of the regression equations at the $p < 0.05$ level.

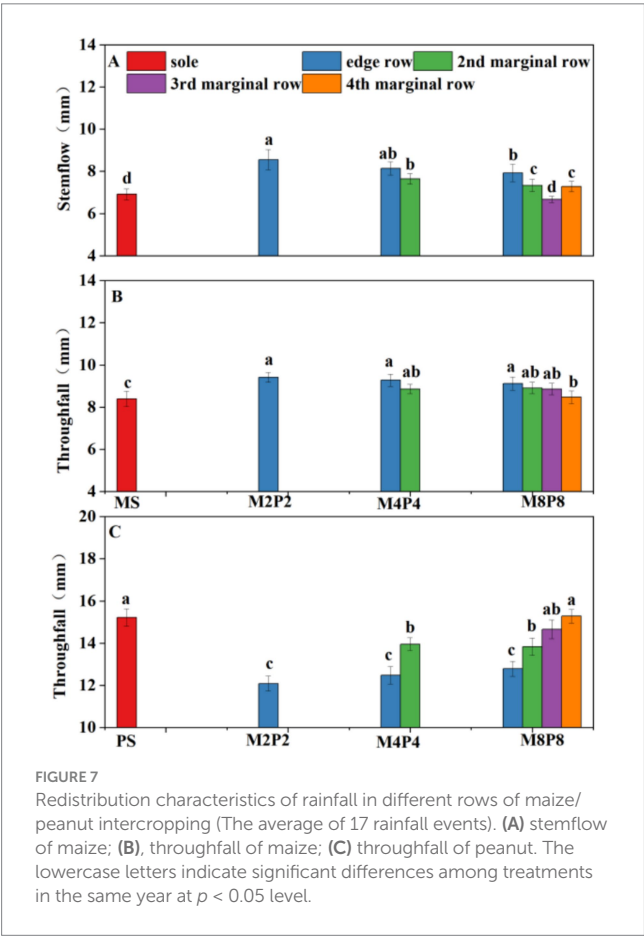
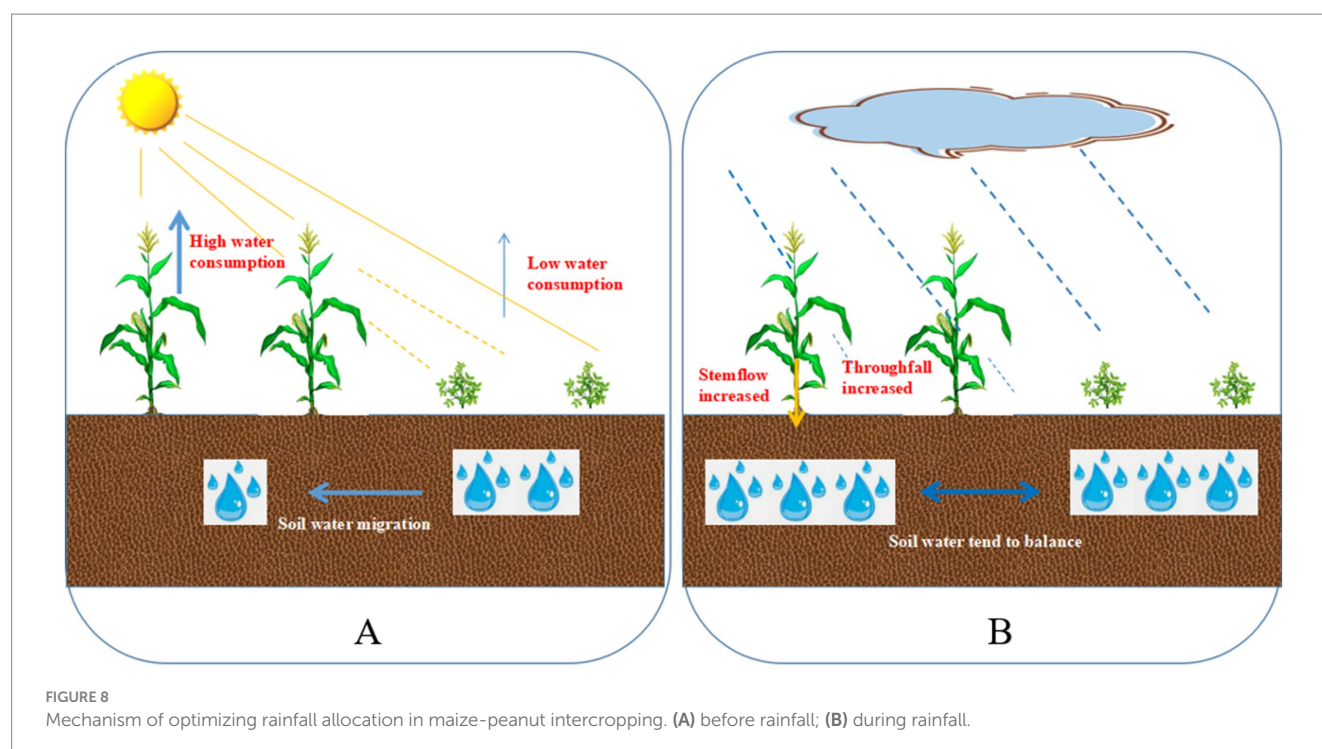


FIGURE 7 Redistribution characteristics of rainfall in different rows of maize/peanut intercropping (The average of 17 rainfall events). (A) stemflow of maize; (B), throughfall of maize; (C) throughfall of peanut. The lowercase letters indicate significant differences among treatments in the same year at $p < 0.05$ level.

maize in this study exhibited large plant height and leaf area but relatively low water consumption. However, relevant research is highly valuable for assessing the water use efficiency of maize-peanut intercropping systems. Mao et al. (2012) provided a detailed explanation of the methods for measuring WU, WUE, and WER (Equations 1–5) in intercropping systems, and their findings are consistent with the results of this study.

Comparing the different strip width treatments over the three years, we found that the M4P4 treatment exhibited the highest system WUE and crop productivity, as indicated by WER and LER. This suggests a balanced resource allocation between the maize and peanut strips. In the M4P4 treatment, approximately 27% of the rainfall from the peanut strip was allocated to the maize strip, resulting in a significant increase in maize yield with minimal impact on peanut yield (Table 1). Additionally, the relatively high WER and LER can be attributed to the edge effect. It is generally understood that the yield-enhancing effect of intercropping is largely due to the edge effect (Wang et al., 2017). Historically, positive edge effects in intercropping systems were thought to arise from differences in how the canopy influenced light interception and distribution (Wang et al., 2020; Zhang et al., 2020). Our research also identified an edge effect on rainfall redistribution within the intercropping system (Figure 8). Compared to M2P2 treatment, maize in the edge row of M4P4 received less water, while peanut rows received more. During drought periods, soil water could flow from the peanut rows to the maize rows, maintaining a steady water supply for maize. However, the long distance between the rows, such as M8P8, limited the movement of water from peanut to maize, while also increasing the potential for evaporation.



5 Conclusion

This study highlights the significant effects of strip width in maize-peanut intercropping systems on both crop productivity and water use efficiency (WUE). The M4P4 treatment demonstrated the highest system WUE and crop productivity, as evidenced by the higher values of the Land Equivalent Ratio (LER) and Water Equivalent Ratio (WER). The allocation of rainfall from the peanut strips to maize in the M4P4 treatment contributed to a notable increase in maize yield with minimal impact on peanut yield. This result suggests that intercropping with appropriate strip widths can optimize water redistribution, especially during drought periods, benefiting maize while maintaining peanut productivity. Furthermore, the edge effect played a significant role in enhancing yield and water use efficiency in the intercropping system. The maize rows at the edges benefited from the allocation of water, particularly during dry periods, while the peanut rows showed reduced throughfall, further supporting the positive effects of intercropping on water management. However, the long distance between rows in the M4P4 treatment also introduced some limitations, such as increased evaporation potential and restricted water movement between rows. These findings underscore the importance of strip width and edge effects in designing intercropping systems that maximize resource use and enhance crop productivity, particularly in semi-arid regions where water availability is a critical limiting factor.

Overall, the results of this study provide valuable insights for optimizing strip width configurations in intercropping systems. They demonstrate that careful management of spatial arrangements can improve both crop productivity and water use efficiency, with potential applications in sustainable agricultural practices.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary material, further inquiries can be directed to the corresponding author/s.

Author contributions

XS: Data curation, Formal analysis, Writing – original draft. YZ: Writing – review & editing. SZ: Writing – review & editing. NY: Writing – review & editing. GX: Supervision, Writing – review & editing. LF: Funding acquisition, Supervision, Writing – review & editing.

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Conflict of interest

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Supplementary material

The Supplementary material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fsufs.2025.1502362/full#supplementary-material>

References

- Abakumova, M., Zobel, K., Lepik, A., and Semchenko, M. (2016). Plasticity in plant functional traits is shaped by variability in neighbourhood species composition. *New Phytol.* 211, 455–463. doi: 10.1111/nph.13935
- Brooker, R. W., Karley, A. J., Pakeman, R. J., and Schöb, C. (2015). Newton a.C. Facilitation and sustainable agriculture: a mechanistic approach to reconciling crop production and conservation. *Funct. Ecol.* 30, 98–107. doi: 10.1111/1365-2435.12496
- Chai, Q., Qin, A., Gan, Y., and Yu, A. (2014). Higher yield and lower carbon emission by intercropping maize with rape, pea, and wheat in arid irrigation areas. *Agronomy Sustain* 34, 535–543. doi: 10.1007/s13593-013-0161-x
- Chauhan, Y. S., Thorburn, P., Biggs, J. S., and Wright, G. C. (2015). Agronomic benefits and risks associated with the irrigated peanut–maize production system under a changing climate in northern Australia. *Crop Pasture Sci.* 66, 1167–1179. doi: 10.1071/CP15068
- Chimi, P. M., Mala, W. A., Fobane, J. L., Abdel, K. N., Nkoué, B. B., Nnganmeni, L. F. F., et al. (2024). Factors affecting decision-making to strengthen climate resilience of smallholder farms in the Centre region of Cameroon. *Climate Smart Agricul.* 1:100004. doi: 10.1016/j.csag.2024.100004
- Feng, C., Du, G., Zhang, Y., Feng, L., Zhang, L., Wang, Q., et al. (2024). Maize/Peanut intercropping Affects Legume nodulation in semi-Arid Conditions. *Agronomy* 14:951. doi: 10.3390/agronomy14050951
- Feng, C., Sun, Z., Zhang, L., Feng, L., Zheng, J., Bai, W., et al. (2021). Maize/peanut intercropping increases land productivity: a meta-analysis. *Field Crop Res.* 270:108208. doi: 10.1016/j.fcr.2021.108208
- Feng, L., Sun, Z., Zheng, M., Muchoki, M., Zheng, J., Yang, N., et al. (2016). Productivity enhancement and water use efficiency of peanut-millet intercropping. *Pak. J. Bot.* 48, 1459–1466.
- Franco, J. G., King, S. R., and Volder, A. (2018). Component crop physiology and water use efficiency in response to intercropping. *Eur. J. Agron.* 93, 27–39. doi: 10.1016/j.eja.2017.11.005
- Fu, Z., Chen, P., Zhang, X., Du, Q., Zheng, B., Yang, H., et al. (2023). Maize-legume intercropping achieves yield advantages by improving leaf functions and dry matter partition. *BMC Plant Biol.* 23:438. doi: 10.1186/s12870-023-04408-3
- Gao, X. B., Guo, C., Li, F. M., Li, M., and He, J. (2020). High soybean yield and drought adaptation being associated with canopy architecture, water uptake, and root traits. *Agronomy* 10:608. doi: 10.3390/agronomy10040608
- Guo, M., He, J., Dong, K., Yang, N., Li, Y., Xiao, J., et al. (2023). Factors influencing maize stemflow in western Liaoning, China. *Agronom. J.* 115, 2708–2720. doi: 10.1002/agj2.21234
- Hamd-Alla, W., Shehata, M. A., Leilah, A. A., Darwesh, R. K., and Hefzy, M. (2023). Impact of irrigation regimes on productivity and profitability of maize+ peanut intercropping system in upper Egypt. *Eur. J. Biol. Res.* 13, 218–231. doi: 10.5281/zenodo.10413383
- Lamm, F. R., and Manges, H. L. (2000). Partitioning of the sprinkler irrigation water by a corn canopy. *Transact ASAE* 43, 909–918. doi: 10.13031/2013.2987
- Lou, Y., Wen, X., Hao, W., Mei, X., Feng, L., Sun, Z., et al. (2024). Climate-smart agriculture: insights and challenges. *Climate Smart Agriculture.* 1:100003. doi: 10.1016/j.csag.2024.100003
- Lu, S., and Shi, W. (2024). Modeling the effects of the plastic-mulched cropland over the arid and semi-arid areas of China on the east Asian regional climate. *J. Hydrol.* 634:131123. doi: 10.1016/j.jhydrol.2024.131123
- Ma, L., Li, Y., Wu, P., Zhao, X., Chen, X., and Gao, X. (2019). Effects of varied water regimes on root development and its relations with soil water under wheat/maize intercropping system. *Plant Soil* 439, 113–130. doi: 10.1007/s11104-018-3800-9
- MacArthur, R. (1955). Fluctuations of animal populations, and a measure of community stability. *Ecology* 36, 533–536. doi: 10.2307/1929601
- Mao, L., Zhang, L., Li, W., van der Werf, W., Sun, J., Spiertz, H., et al. (2012). Yield advantage and water saving in maize/pea intercrop. *Field Crop Res.* 138, 11–20. doi: 10.1016/j.fcr.2012.09.019
- Nanko, K., Hudson, S. A., and Levina, D. F. (2016). Differences in throughfall drop size distributions in the presence and absence of foliage. *Hydrol. Sci. J.* 61, 620–627. doi: 10.1080/02626667.2015.1052454
- Nehe, A. S., Foulkes, M. J., Ozturk, I., Rasheed, A., York, L., Kefauver, S. C., et al. (2021). Root and canopy traits and adaptability genes explain drought tolerance responses in winter wheat. *PLoS One* 16:e0242472. doi: 10.1371/journal.pone.0242472
- Nelson, W. C. D., Hoffmann, M. P., Vadez, V., Roetter, R. P., and Whitbread, A. M. (2018). Testing pearl millet and cowpea intercropping systems under high temperatures. *Field Crop Res.* 217, 150–166. doi: 10.1016/j.fcr.2017.12.014
- Nelson, W. C., Hoffmann, M. P., Vadez, V., Rötter, R. P., Koch, M., and Whitbread, A. M. (2022). Can intercropping be an adaptation to drought? A model-based analysis for pearl millet–cowpea. *J. Agron. Crop Sci.* 208, 910–927. doi: 10.1111/jac.12552
- Odum, E. R. (1953). Fundamentals of ecology. Philadelphia: Saunders. doi: 10.1126/science.129.3359.1354.a
- Pelech, E. A., Evers, J. B., Pederson, T. L., Drag, D. W., Fu, P., and Bernacchi, C. J. (2023). Leaf, plant, to canopy: a mechanistic study on aboveground plasticity and plant density within a maize–soybean intercrop system for the Midwest, USA. *Plant Cell Environ.* 46, 405–421. doi: 10.1111/pce.14487
- Ren, Y. Y., Wang, X. L., Zhang, S. Q., Palta, J. A., and Chen, Y. L. (2017). Influence of spatial arrangement in maize-soybean intercropping on root growth and water use efficiency. *Plant Soil* 415, 131–144. doi: 10.1007/s11104-016-3143-3
- Renwick, L. L., Kimaro, A. A., Hafner, J. M., Rosenstock, T. S., and Gaudin, A. C. (2020). Maize-pigeonpea intercropping outperforms monocultures under drought. *Front. Sustain. Food Syst.* 4:562663. doi: 10.3389/fsufs.2020.562663
- Tahir, M., Lv, Y., Gao, L., Hallett, P. D., and Peng, X. (2016). Soil water dynamics and availability for citrus and peanut along a hillslope at the Sunjia red soil critical zone observatory (CZO). *Soil Tillage Res.* 163, 110–118. doi: 10.1016/j.still.2016.05.017
- Wang, J., Liu, Y., Li, B., Li, Z., Zhang, Y., Zhang, S., et al. (2024). The Throughfall, Stemflow, and canopy interception loss in corn and soybean fields in Northeast China. *Water* 16:253. doi: 10.3390/w16020253
- Wang, R., Sun, Z., Bai, W., Wang, E., Wang, Q., Zhang, D., et al. (2021). Canopy heterogeneity with border-row proportion affects light interception and use efficiency in maize/peanut strip intercropping. *Field Crop Res.* 271:108239. doi: 10.1016/j.fcr.2021.108239
- Wang, R., Sun, Z., Zhang, L., Yang, N., Feng, L., Bai, W., et al. (2020). Border-row proportion determines strength of interspecific interactions and crop yields in maize/peanut strip intercropping. *Field Crop Res.* 253:107819. doi: 10.1016/j.fcr.2020.107819
- Wang, Y., Zhao, Z., Li, J., Zhang, M., Zhou, S., Wang, Z., et al. (2017). Does maize hybrid intercropping increase yield due to border effects? *Field Crop Res.* 214, 283–290. doi: 10.1016/j.fcr.2017.09.023
- Xia, H. Y., Zhao, J. H., Sun, J. H., Bao, X. G., Christie, P., Zhang, F. S., et al. (2013). Dynamics of root length and distribution and shoot biomass of maize as affected by intercropping with different companion crops and phosphorus application rates. *Field Crop Res.* 150, 52–62. doi: 10.1016/j.fcr.2013.05.027
- Yang, F., Liao, D., Wu, X., Gao, R., Fan, Y., Raza, M. A., et al. (2017). Effect of aboveground and belowground interactions on the intercrop yields in maize-soybean relay intercropping systems. *Field Crop Res.* 203, 16–23. doi: 10.1016/j.fcr.2016.12.007
- Yang, S., Zhao, Y., Xu, Y., Cui, J., Li, T., Hu, Y., et al. (2024). Yield performance response to field configuration of maize and soybean intercropping in China: a meta-analysis. *Field Crop Res.* 306:109235. doi: 10.1016/j.fcr.2023.109235
- Ye, H., Song, L., Schapaugh, W. T., Ali, M. L., Sinclair, T. R., Riar, M. K., et al. (2020). The importance of slow canopy wilting in drought tolerance in soybean. *J. Exp. Bot.* 71, 642–652. doi: 10.1093/jxb/erz150
- Zhang, C., Gao, J., Liu, L., and Wu, S. (2024a). Compound drought and hot stresses projected to be key constraints on maize production in Northeast China under future climate. *Comput. Electron. Agric.* 218:108688. doi: 10.1016/j.compag.2024.108688

- Zhang, W. P., Liu, G. C., Sun, J. H., Fornara, D., Zhang, L. Z., Zhang, F. F., et al. (2017). Temporal dynamics of nutrient uptake by neighbouring plant species: evidence from intercropping. *Funct. Ecol.* 31, 469–479. doi: 10.1111/1365-2435.12732
- Zhang, D., Sun, Z., Feng, L., Bai, W., Yang, N., Zhang, Z., et al. (2020). Maize plant density affects yield, growth and source-sink relationship of crops in maize/peanut intercropping. *Field Crop Res.* 257:107926. doi: 10.1016/j.fcr.2020.107926
- Zhang, Y., Zhao, F., Feng, C., Bai, W., Zhang, Z., Cai, Q., et al. (2024b). Effects of maize/Peanut intercropping and nitrogen fertilizer application on soil fungal community structure. *Agronomy* 14:1053. doi: 10.3390/agronomy14051053
- Zhang, Y., Zhao, F., Sun, Z., Bai, W., Zhang, Z., Feng, C., et al. (2024c). Effects of maize/Peanut intercropping on yield and nitrogen uptake and utilization under different nitrogen application rates. *Agriculture* 14:893. doi: 10.3390/agriculture14060893
- Zhao, Z., Li, Z., Li, Y., Yu, L., Gu, X., and Cai, H. (2024). Supplementary irrigation and reduced nitrogen application improve the productivity, water and nitrogen use efficiency of maize-soybean intercropping system in the semi-humid drought-prone region of China. *Agricultural water management*, vol. 305, 109126. doi: 10.1016/j.agwat.2024.109126
- Zhu, Z., Zhu, D., and Ge, M. (2021). The spatial variation mechanism of size, velocity, and the landing angle of throughfall droplets under maize canopy. *Water* 13:2083. doi: 10.3390/w13152083
- Zou, X., Xu, J., Xu, H., Gong, L., Zhang, L., Wang, Y., et al. (2024). Ethephon and diethyl Aminoethyl mixture (EDAH) reduces maize lodging and enhances overall productivity in maize/Peanut intercropping. *Agronomy* 15:84. doi: 10.3390/agronomy15010084



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Genotype-specific rhizosphere microbiome assembly and its impact on soybean (*Glycine max* (L.) Merri.) yield traits

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Introduction: The rhizosphere microbiome plays a critical role in plant growth and productivity. However, the genotype-specific dynamics and functional influence of these microbial communities on soybean (*Glycine max* (L.) Merri.) yield traits remain underexplored. This study investigated the composition and functional implications of rhizosphere microbial communities in conventional and genetically modified (GM) soybean varieties under field conditions.

Methods: A comparative analysis was conducted on rhizosphere microbial communities associated with conventional H0269 and transgenic Z1510 and M579 soybean varieties at seedling and flowering stages. High-throughput sequencing of 16S rDNA and ITS regions was used to profile bacterial and fungal communities. Alpha and beta diversity metrics were assessed, and correlation analyses were performed to identify microbial taxa linked to yield traits.

Results: Distinct microbial community structures were observed across soybean genotypes and growth stages. *Proteobacteria*, *Acidobacteriota*, and *Actinobacteria* were dominant bacterial phyla, while *Ascomycota* predominated among fungi. Genotype-specific differences were evident, with M579 exhibiting the highest bacterial alpha diversity. Beta diversity analysis revealed significant shifts in microbial composition between growth stages, particularly for bacterial communities. Correlation analysis identified 15 bacterial and 13 fungal species significantly associated with yield traits such as plant density, grain weight, and theoretical yield.

Discussion: The results highlight genotype-dependent recruitment of rhizosphere microorganisms and their potential impact on soybean productivity. GM soybean varieties selectively enriched beneficial microbes that may enhance nutrient uptake, stress tolerance, and disease resistance. These findings provide valuable insights into plant-microbe interactions, paving the way for developing microbial inoculants and breeding strategies to optimize soybean yield in sustainable agriculture.

KEYWORDS

rhizosphere, soybean, microbiome, 16S rDNA and ITS sequencing, yield trait

1 Introduction

The rhizosphere microorganisms played a crucial role in plant growth, development, and health (Weng et al., 2024; Sharma et al., 2024). These beneficial bacteria, fungi, and archaea formed complex communities around plant roots, creating a dynamic environment. It has been reported that certain *Bacillus* strains have the potential to partially replace chemical fertilizers in rice production (Tripathi et al., 2022). The rhizosphere microorganisms can not only provide phosphorus and nitrogen for promoting plant growth, but also help plant tolerate abiotic stresses such as drought and salinity (Abrahão et al., 2018; Bandara and Kang, 2024). The interactions between plant and rhizosphere microorganisms were bidirectional and led to sustainable agricultural practices, including the use of plant growth-promoting rhizobacteria as biofertilizers and biopesticides (Olanrewaju et al., 2019; Ferreyra-Suarez et al., 2024; Vejan et al., 2016). Recent advances in multi-omics approaches have further revealed how plants actively shape their rhizobiome through root exudate profiles, creating genotype-specific microbial recruitment patterns (Levy et al., 2017; Zhahlnina et al., 2018).

Soybean (*Glycine max* (L.) Merri.), a globally significant food and cash crop, serves as a primary source of high-quality protein and oil for human consumption. While traditional breeding has focused on improving aboveground agronomic traits, there is growing interest in the rhizosphere microbiome's potential to enhance crop productivity and sustainability (Kumar and Dubey, 2020). Soybean and legume microbiomes are shaped by plant genetics, environmental factors, and agricultural practices. Genetically related cowpea cultivars develop similar rhizobacterial communities (de Albuquerque et al., 2022), while soybean genotypes modulate microbial assembly via root exudates and nodulation (Liu et al., 2019; Zhong et al., 2019). Seasonal shifts and soil types alter peanut rhizosphere microbiota (Daraz et al., 2023), and organic farming enhances peanut microbiome diversity compared to conventional methods (Paudel et al., 2023). Soybean nodulation enriches nitrogen-cycling microbes, improving subsequent crop yields (Liu et al., 2024), while intercropping creates unique microbiome configurations (Lanzavecchia et al., 2024). Functional diversity in soybean rhizospheres supports stress resilience and nitrogen fixation (Ajiboye et al., 2022; Mayhood and Mirza, 2021).

With the increasing adoption of genetically modified (GM) soybeans in agricultural fields, field experiments have become crucial in assessing the interactions between GM soybeans and rhizosphere microbiomes. Global research reveals geographically distinct responses. North American studies in the U.S. Midwest show environmental factors outweigh GM traits in shaping bacterial diversity (Liu et al., 2019; Chang et al., 2021), while Argentine trials identify transient *Pseudomonadales* shifts post-glyphosate application mediated by soil organic content (Bento et al., 2019). Nigerian organic GM systems match conventional yields with rainfall-driven microbial shifts (Olowe et al., 2023), whereas Romanian field trials demonstrate microbiome stability patterns aligning with Central European observations (Ichim, 2019; Noack et al., 2024). Despite progress, critical gaps persist in understudied regions like Eastern European chernozems and Africa's Sahel, where unique genotype-environment-microbiome relationships emerge (Sarkar et al., 2022). Crops shape rhizosphere microbiomes via root exudates, selecting bacteria that aid stress resilience and nutrient cycling. While environmental factors and management practices drive community composition, functional

microbial cores underpin plant health under local stressors (Cucio et al., 2016; Debenport et al., 2015). International comparisons further highlight system-specific dynamics. Brazilian glyphosate-resistant soybeans exhibit early *Bradyrhizobium* reductions (Zablotowicz and Reddy, 2004), Canadian systems show seasonal variability overriding genotypic effects, and Australian non-GM cultivars maintain stable variety-specific microbial signatures across soils (Jang et al., 2023). These disparities underscore the need for multinational consortia to disentangle genetic, environmental, and management factors shaping rhizosphere communities.

These findings highlight the need for continued research to fully understand long-term effects of GM soybeans on soil microbial communities in agricultural ecosystems (Ren et al., 2023). Our study addresses this through a comparative analysis of conventional and GM varieties in Inner Mongolia's agriculturally critical yet understudied chernozem (chestnut soil zone), integrating rhizosphere microbiome profiles with soybean phenomic data across growth stages. We reveal genotype-specific microbial recruitment dynamics while contributing foundational datasets from this climate-vulnerable region, elucidating how pedoclimatic conditions interact with soybean genetics to shape yield-linked microbial communities. This work bridges continental research divides, offering insights into how regional pedoclimatic conditions interact with plant genetics to structure rhizosphere communities that influence yield outcomes.

2 Materials and methods

2.1 Plant materials

Three distinct soybean varieties, Zhongliandou (Z1510), Hejiao (H0269), and Maiyu (M579) were used in this study. Z1510 and M579 are both genetically modified soybeans. The Z1510 transformed from ZhongHuang 6,106 with the *gat* and *eps(g2)* gene, conferring glyphosate tolerance. M579 derived from DBN9004, contains *epsps* and *pat* gene, providing glyphosate and glufosinate-ammonium tolerance. In contrast, H0269 is a conventional soybean variety that does not possess these modifications and relies on traditional weed control methods.

2.2 Experimental design and site description

Three distinct soybean varieties cultivated at the experimental base of the Xing'an League Agriculture and Animal Husbandry Science, Institute in Inner Mongolia, a region of significant importance for soybean production in China. The site (45°43'–46°18'N, 121°53'–122°52'E) has a temperate continental climate with chernozem and chestnut soils (pH 8.03, organic matter 34.76 g/kg, total N 3.437 g/kg, total K 2.22%, alkaline N 252.54 mg/kg, available P 20.78 mg/kg, available K 88.75 mg/kg). A randomized complete block design with three replications was employed. Planting utilized a double-row ridge system (60 cm ridge spacing, 0.6 cm plant spacing) at 280,000 plants/ha. Z1510 and M579 received 2,250 mL/ha of 41% glyphosate isopropylamine salt, while H0269 received conventional herbicides. Base fertilizer was applied at >450 kg/ha.

2.3 Rhizosphere soil sampling and microbial community analysis

Samples were collected at seedling and flowering stages using a five-point sampling method. Rhizosphere soil was obtained from roots at 10–30 cm depth, sieved (2 mm), and stored at -80°C . DNA was extracted using HiPure Universal DNA Kit. The V3 and V4 region of 16S rRNA and ITS1 region were amplified and sequenced on a Qsep-400 platform (Persoon et al., 2017). Sequences were processed using QIIME 2 (version 2021.4) and DADA2 to obtain amplicon sequence variants (ASVs; Kesim et al., 2023). Taxonomic annotation used the SILVA 138 database (Bars-Cortina et al., 2023). Alpha diversity was assessed in QIIME 2. Beta diversity was evaluated using principal coordinates analysis (PCoA) based on Bray-Curtis distances. Linear discriminant analysis effect size (LEfSe) identified differentially abundant taxa (LDA > 3.5). Functional classification used FUNGuild (version 1.0; Djemiel et al., 2017).

2.4 Yield trait measurements

At maturity on September 28, yield components were measured following national standards. Plants per m^2 were counted in 2 m^2 areas, while single plant grain weight (g) was calculated by dividing total grain weight by the number of plants in the same 2 m^2 area. The 100-grain weight (g) was determined as an average of 3 replicates, and moisture content (%) was measured using a moisture meter with 3 replicates. Finally, the theoretical yield (kg/ha) was calculated using the formula: $\text{plants}/\text{m}^2 \times 10,000 \times \text{single plant grain weight} \times 10^{-5} \times 0.9$. This comprehensive approach provides a standardized method for estimating crop yields based on key components measured in sample areas, with multiple replicates used for some measurements to enhance accuracy and reliability.

2.5 Statistical analysis

The 16S rRNA gene and ITS amplicon sequencing data were processed using the SILVA 138/16S rRNA database and Unite 8.0 database for taxonomic assignment. Quality control measures were implemented

to ensure data integrity, including the detection and removal of chimeric sequences using the UCHIME (v1.9.1) software. Alpha diversity indices were calculated using the MOTHUR (v1.30.2) software to assess the richness and diversity of microbial communities across samples. To investigate the overall community composition and assess the similarities or dissimilarities between samples, beta diversity analysis was performed using principal coordinate analysis (PCoA) implemented in the QIIME (v1.9.1) software package (Caporaso et al., 2010). The resulting PCoA plots were generated using the R packages “vegan,” “ecodist,” and “ggplot2” in R (v4.1.3), enabling the visual representation and interpretation of beta diversity patterns (Schloss et al., 2009; Cole et al., 2014; Chen and Boutros, 2011). Correlations between microbial community composition (top 20 dominant bacterial taxa) and yield traits were examined using Pearson’s correlation coefficient. Data were subjected to a one-way analysis of variance with factors of treatments and expressed as means \pm SD. Comparisons between any two groups were performed by unpaired Student’s *t*-tests.

3 Results

3.1 Overall analysis of 16S rDNA

The 16S rDNA and ITS sequencing analyses revealed significant microbial diversity in rhizosphere soil samples. Using the 341F-806R primer pair, 404,470 denoised and non-chimeric ASVs were obtained from rhizosphere soil samples, averaging 67,411 ASVs per replicate (Supplementary Table S1). The ITS1F-ITS2R primer pair yielded 807,404 ASVs from surrounding soil samples, with an average of 134,567 ASVs per replicate (Supplementary Table S2). The higher ASV count in rhizosphere soil samples suggested potentially greater microbial diversity.

3.2 Alpha diversity of microbial community in rhizosphere soils

The alpha diversity of rhizosphere microbial communities in M579, Z1510, and H0269 soybean varieties revealed distinct patterns

TABLE 1 Analysis of alpha diversity of three soybean rhizosphere soil microbial communities.

Sample	ACE	Chao1	Shannon
Z1510-Seeding Stage	1144.68 \pm 87.1 ^b	1144.36 \pm 87.02 ^b	8.81 \pm 0.39 ^{ab}
H0269-Seeding Stage	1089.51 \pm 143.97 ^b	1088.74 \pm 143.52 ^b	8.8 \pm 0.34 ^{ab}
M579-Seeding Stage	1395.86 \pm 51.66 ^a	1394.94 \pm 51.27 ^a	8.96 \pm 0.12 ^a
Z1510-Flowering Stage	1202.24 \pm 250.32 ^{ab}	1201.49 \pm 249.98 ^{ab}	8.8 \pm 0.31 ^{ab}
H0269-Flowering Stage	1085.39 \pm 43.8 ^b	1084.45 \pm 43.58 ^b	8.43 \pm 0.09 ^b
M579-Flowering Stage	1313.95 \pm 47.44 ^a	1312.74 \pm 47.39 ^a	8.81 \pm 0.23 ^{ab}
Z1510-Seeding Stage	362.98 \pm 15.49 ^{ab}	362.99 \pm 15.95 ^a	4.88 \pm 0.26 ^a
H0269-Seeding Stage	367.01 \pm 33.57 ^{ab}	366.82 \pm 33.68 ^a	4.77 \pm 0.48 ^a
M579-Seeding Stage	452.89 \pm 57.84 ^a	452.97 \pm 58.79 ^a	5.21 \pm 0.57 ^a
Z1510-Flowering Stage	281.12 \pm 135.3 ^{ab}	280.81 \pm 135.82 ^a	3.86 \pm 2.22 ^a
H0269-Flowering Stage	350.33 \pm 24.99 ^b	350.6 \pm 25.47 ^a	5.26 \pm 0.05 ^a
M579-Flowering Stage	239.29 \pm 20.63 ^{ab}	239.13 \pm 20.62 ^a	3.68 \pm 2.47 ^a

Different letters in the superscripts of the column indicate significant differences ($p < 0.05$).

for bacterial and fungal populations (Table 1). At both seedling and flowering stages, bacterial abundance consistently followed the order M579 > Z1510 > H0269, with M579 exhibiting significantly higher Chao1 and ACE indices compared to H0269. M579 maintained 5.8% higher Shannon diversity than H0269 across growth stages. Notably, bacterial diversity indices remained stable within each soybean variety, suggesting that genetic factors have a stronger impact on bacterial community composition than developmental changes. In contrast, fungal communities showed more conserved traits, with 123 shared ASVs across all samples and no significant diversity differences among varieties or growth stages. However, fungal ASV abundance showed diverged between seedling and flowering stages. M579 and Z1510 decreased significantly, while H0269 remained stable. Shannon indices showed no significant differences among varieties. These findings revealed the complex dynamics of soybean rhizosphere microbiomes, showcasing distinct bacterial and fungal responses to plant genotype and developmental stage.

3.3 Beta diversity of microbial community in rhizosphere soils

Beta diversity analysis using PCoA revealed significant variations in rhizosphere microbial community composition across soybean growth stages and genotypes. The PCoA1 axis accounted for 18.55 and 33.78% of the total variance in bacterial and fungal community composition, respectively. At seedling stage, Z1510 and H0269 showed similar bacterial and fungal communities, distinct from M579. At flowering stage, bacterial communities of Z1510 and M579 converged, while H0269 diverged (Figure 1A). However, Fungal communities at flowering stage showed less distinct clustering among varieties, but M579 displayed high within-group variability (Figure 1B). These findings underscored the dynamic nature of rhizosphere microbiomes, influenced by both plant genotype and developmental stage.

3.4 Alterations in bacterial and fungal community composition

Analysis of soybean microbiomes across growth stages revealed significant variations in bacterial community structure. At the bacterial phylum level, the dominant groups identified were Proteobacteria, Acidobacteriota, and Actinobacteria. During the seedling stage, Proteobacteria exhibited the highest abundance in the H0269 variety, while M579 showed the lowest levels. Conversely, Acidobacteriota was most abundant in M579, with H0269 and Z1510 displaying similar abundances. Notably, the abundance of Actinobacteria remained relatively consistent across all three soybean varieties. The flowering period saw increased Proteobacteria and Acidobacteriota across all varieties, while Actinobacteria declined (Figure 2A). At the genus level, the dominant genera during both seedling and flowering periods were *Sphingomonas*, *Gemmatimonas*, *RB41*, *Vicinamibacteraceae*, and *WD2101_soil_group* (Figure 2B).

Fungal communities were dominated by Ascomycota, Basidiomycota, and Zygomycota phyla. At the seedling stage, Ascomycota was most abundant in H0269, followed by Z1510 and M579, while Basidiomycota peaked in M579. These abundance patterns persisted into the flowering stage, with Ascomycota increased in H0269 and Z1510 but decreased in M579 (Figure 2C). At the genus level, *Fusarium* and *Guehomyces* dominated, with *Guehomyces* showing higher abundance in M579 during the seedling stage. Conversely, *Fusarium* became more prevalent in H0269 during flowering (Figure 2D).

3.5 LEfSe analysis of bacterial and fungal communities

The LEfSe analysis of rhizosphere bacteria across three soybean varieties revealed significant differences in functional bacteria recruitment between seedling and flowering stages. At seedling stage, a total of 89 bacterial species were recruited, with M579 recruiting the highest number

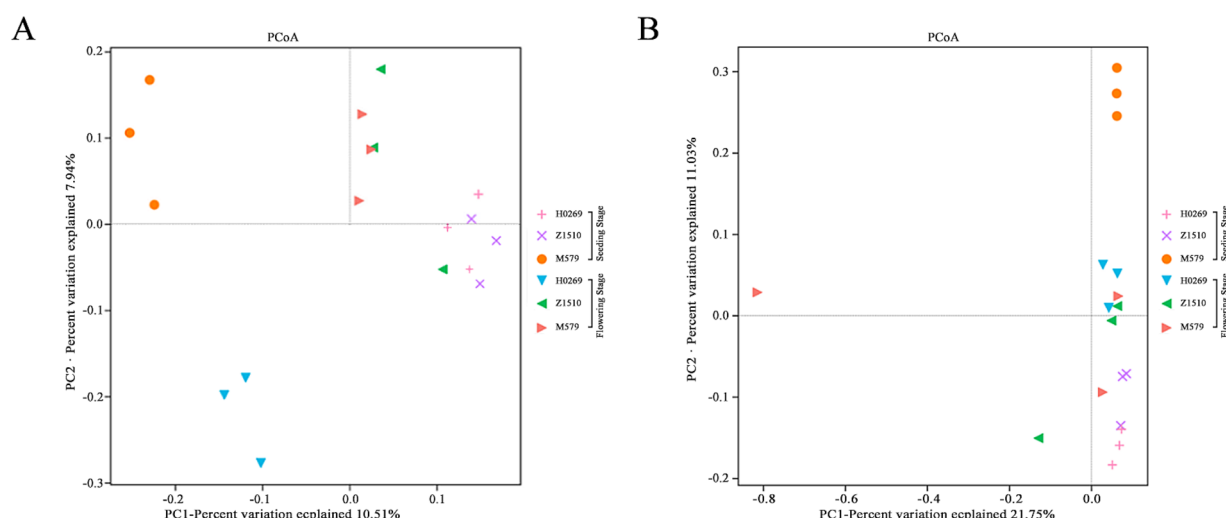


FIGURE 1

Principal component analysis based on the distance matrix calculated using the Bray–Curtis distance matrix for rhizosphere soil. The rhizosphere soil compartments cause the largest source of variance amongst bacterial (A) and fungal (B) communities of conventional soybean variety H0269 and genetically modified soybeans Z1510 and M579 at seedling stage and flowering stage.

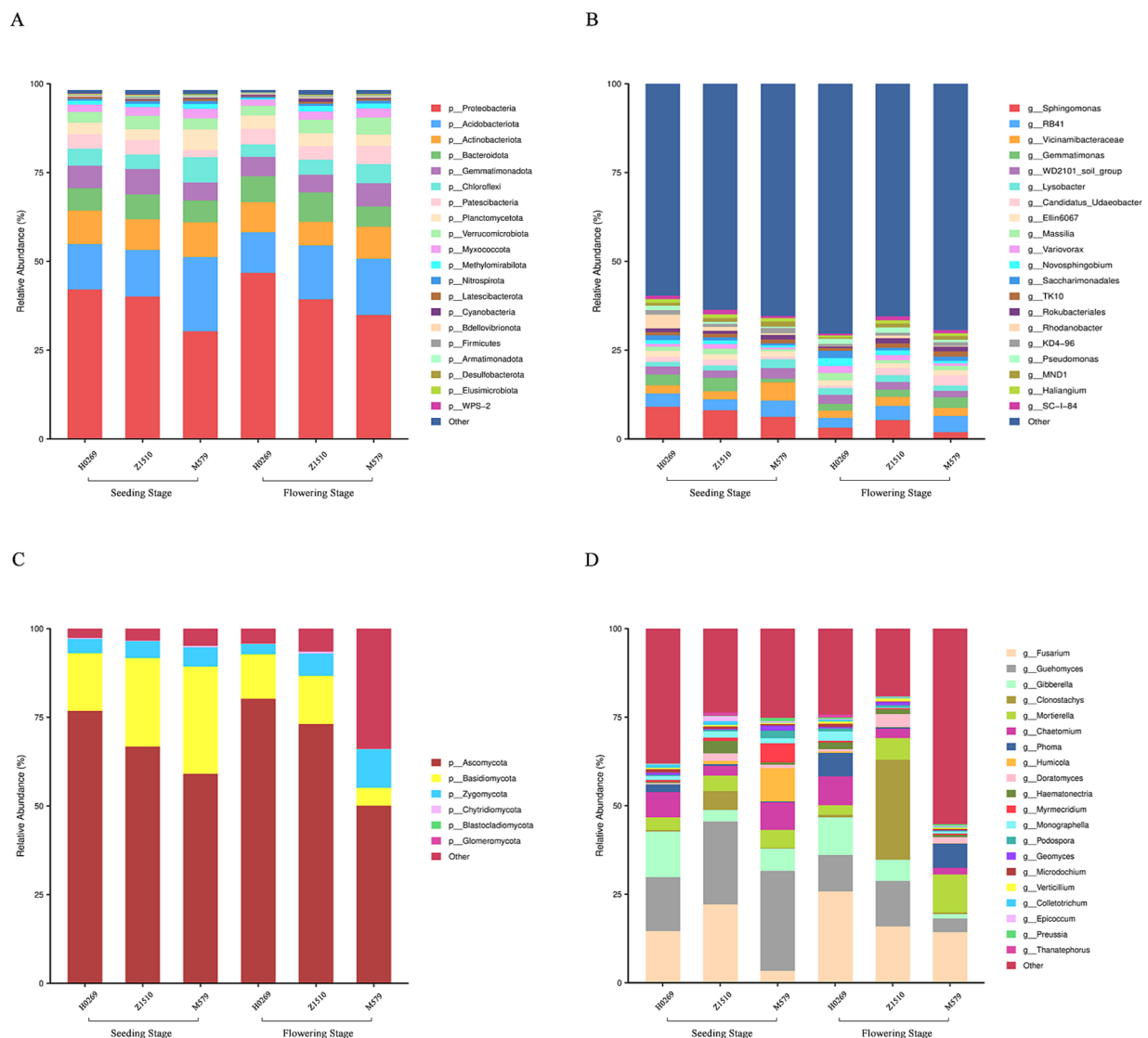


FIGURE 2

Composition and structure of bacterial and fungal communities of conventional soybean variety H0269 and genetically modified soybeans Z1510 and M579 at seeding stage and flowering stage. (A,B) Represent phylum and genus level of bacteria, respectively. (C,D) Represent phylum and genus level of fungi, respectively. The top 20 relative abundances are shown, and the remaining abundances are indicated as 'Others'.

(48 species), followed by Z1510 (21 species), and H0269 (20 species). M579 was enriched with taxa such as *P_Acidobacteriota*, *c_Vicinamibacteriota*, and *P_Chloroflexi*. H0269 had *o-Xanthomonaadales*, *f_Rhodanobacteraceae*, and *d_Rhodanobacter*; and Z1510 had *o-Gemmatimonadales* and related taxa. During flowering stage, the total number of bacterial species decreased to 51, with H0269 recruiting 25 species, and both Z1510 and M579 recruiting 13 species (Figures 3A,B). H0269 showed enrichment in *c_Alphaproteobacteria* and *c_Actinobacteria*. Z1510 in *o_Burkholderiales* and *f_Comamonadaceae*, and M579 in *f_Oxalobacteraceae* and related taxa. From seedling to flowering stage, M579 experienced a substantial decrease of 33 bacterial species, Z1510 decreased by 8, while H0269 increased by 5.

Similarly, LEfSe analysis of rhizosphere fungi indicated significant differences in functional fungi recruitment between growth stages. In the seedling stage, a total of 67 fungal species were recruited: M579 recruited 36 species, Z1510 recruited 18 species, and H0269 recruited

13 species. During the flowering stage, this number dropped to 25 fungal species overall, with H0269 recruiting 12 species, M579 recruiting 8 species, and Z1510 recruiting 5 species. From seedling to flowering stages, M579 saw a decrease of 28 fungal species, Z1510 decreased by 13, and H0269 decreased by 6. Fungal taxa with LDA scores greater than 5 included *f_Nutriaceae* in H0269, *o_Hypocrales* and *s_Clonostachys_rasea_f_catenulata* in Z1510, and *d_Ratobasidium* and *s_Ratobasidium-ramicola* in M579 (Figures 3C,D).

3.6 Comparative analysis of soybean yield traits and rhizosphere microbial communities

Yield trait analysis across three soybean varieties revealed a consistent pattern, with Z1510 > M579 > H0269 for theoretical

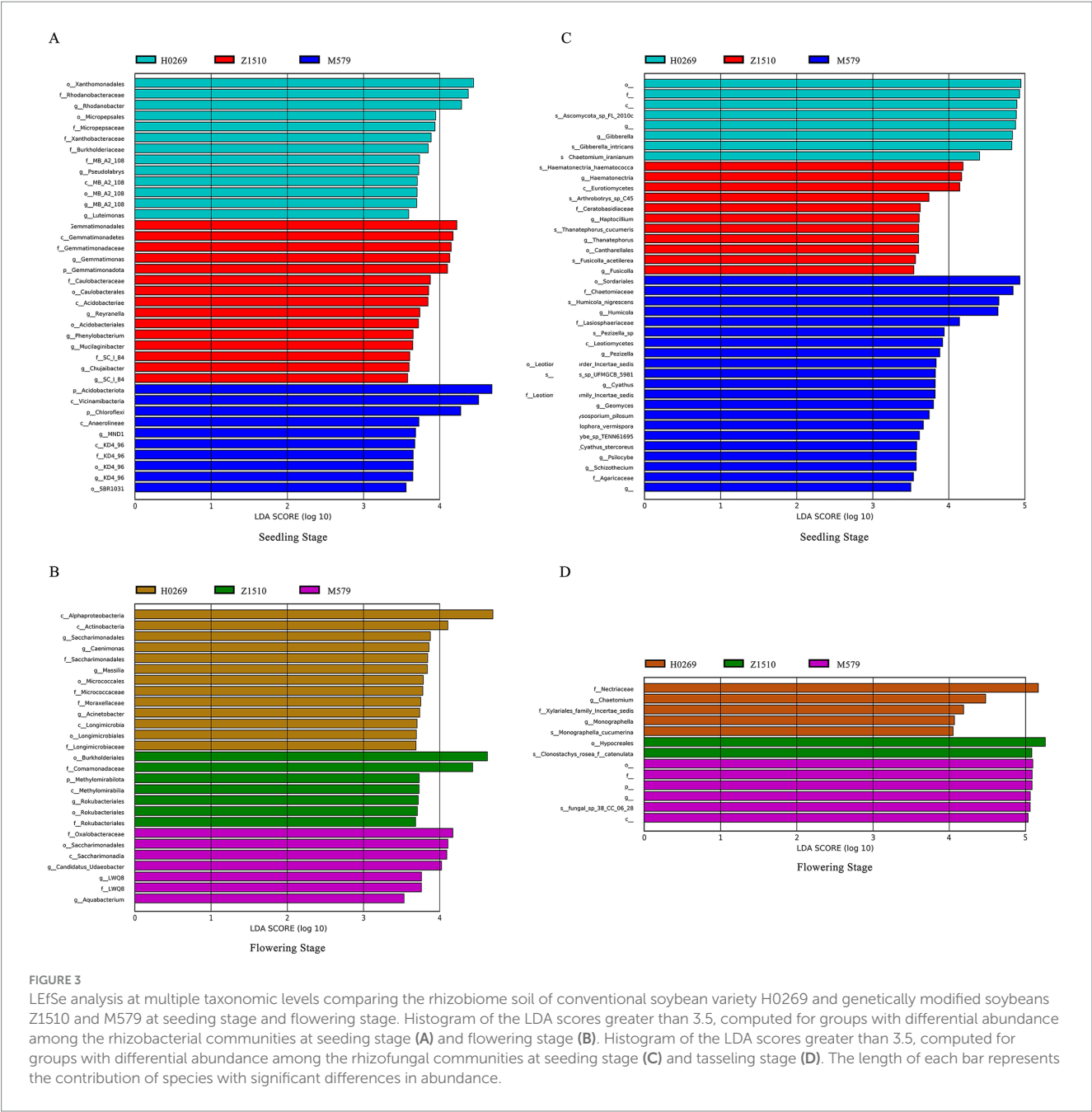


FIGURE 3 LfSe analysis at multiple taxonomic levels comparing the rhizobiome soil of conventional soybean variety H0269 and genetically modified soybeans Z1510 and M579 at seeding stage and flowering stage. Histogram of the LDA scores greater than 3.5, computed for groups with differential abundance among the rhizobacterial communities at seeding stage (**A**) and flowering stage (**B**). Histogram of the LDA scores greater than 3.5, computed for groups with differential abundance among the rhizofungal communities at seeding stage (**C**) and tasseling stage (**D**). The length of each bar represents the contribution of species with significant differences in abundance.

TABLE 2 Production characteristics across three soybean varieties.

Sample	Plants per square meter	Number of grains per plant	Hundred grain weight (g)	Moisture Content (%)	Theoretical yield (kg/hm ²)
Z1510	24.80 ± 0.91	118.33 ± 4.78 ^A	13.38 ± 0.47 ^B	10.42 ± 0.92 ^b	4322.7 ± 83.85 ^A
M579	23.20 ± 2.20	85.95 ± 4.90 ^B	20.19 ± 0.43 ^A	11.56 ± 0.47 ^a	3995.55 ± 117.6 ^B
H0269	23.8 ± 2.49	42.10 ± 5.09 ^C	18.23 ± 2.02 ^A	11.64 ± 0.98 ^a	1800.9 ± 63.75 ^C

A, B, and C denote highly significant differences at the $p = 0.01$ level; a, b, and c indicate significant differences at the $p = 0.05$ level; no label indicates no significant difference.

yield and grain number per plant. Z1510 showed superior yield indicators but lower 100-kernel weight and moisture content compared to M579 and H0269 (Table 2), suggesting a compensatory mechanism of increased grain number offsetting reduced grain weight.

The study examined relationships between rhizosphere microbes and five yield indicators: plant density, grains per plant, 100-grain weight, moisture content, and theoretical yield. The results revealed 15 bacterial and 13 fungal species exhibited significant associations with yield components. Among the bacteria, taxa such as *s_wastewater* metagenome

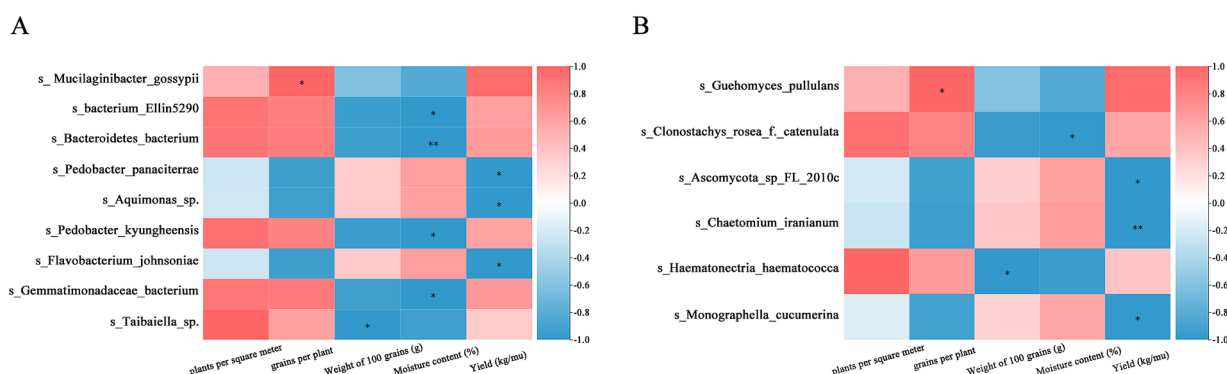


FIGURE 4
Correlation analysis between soybean rhizosphere microbial community and yield traits. (A) The rhizobacterial communities closely related to yield traits. (B) The rhizofungal communities closely related to yield traits.

and *s-Taibaiella* sp. demonstrated positive correlations with plant density but negative associations with grain weight. Conversely, species like *S_Pedobacter panaciterrae* showed positive correlations with theoretical yield, grain weight, and water content (Figure 4A). Fungal species, including *s_Ascomycota* sp. FL 2010c, negatively correlated with grain number and yield per plant while positively associating with water content. Conversely, *S_Guehomyces pullulans* exhibited positive correlations with yield components but negative associations with water content (Figure 4B).

4 Discussion

This study analyzed rhizosphere microbial dynamics in Z1510, M579, and H0269 soybean varieties across growth stages. Bacterial communities were dominated by *Proteobacteria* (40–60%) showing positive correlation with plant development, consistent with global patterns observed in soybean rhizospheres from North American chernozem soils (Wang et al., 2024). The 18–25% reduction in nitrogen-fixing *Sphingomonas* abundance in Z1510 and M579 compared to H0269 aligns with genotype-driven microbiome variations reported in Brazilian GM soybean cultivars, where *Bradyrhizobium* dominance persisted despite genetic modifications (Shen et al., 2025). These findings underscore that genotype effects on microbial recruitment are conserved across continents, though regional soil properties (pH, salinity) may modulate their magnitude, as demonstrated in comparative U.S.–China trials (Wang et al., 2023; Wei et al., 2021).

Fungal communities comprised 50–80% *Ascomycota*, with *Guehomyces* increasing 30–40% during reproductive stages. Z1510 and M579 showed 35% greater microbial fluctuations across growth phases than the H0269 soybean variety. This genotype-driven bacterial diversity patterns (M579 > Z1510 > H0269) contrast with Liu et al.'s identification of stronger genotype-specific recruitment in wild-type cultivars (Liu et al., 2019), but support Yang et al.'s conclusion that environmental factors outweigh GM traits in shaping soybean microbiomes (Yang et al., 2022). However, the impact of GM soybeans on rhizosphere microbiomes appears subtle and context-dependent, influenced by factors such as growth stage and environmental conditions (Wang et al., 2023; Yang et al., 2022). Another study on glyphosate-tolerant soybeans observed transient reductions in

Bradyrhizobium abundance at the seedling stage but no long-term effects on microbial structure (Wei et al., 2021).

Fifteen bacterial and 13 fungal taxa correlated with yield traits, including *Mucilaginibacter gossypii*, *Bacterium Ellin5290*, *Guehomyces pullulans*, and *Doratomyces* sp. NG p07. Results suggest microbes influence yield through nitrogen cycling, water regulation, and plant density optimization. Soybean genetics impacted bacterial diversity twice as strongly as fungal diversity, aligning with Chang et al.'s demonstration of single-gene microbiome alterations, yet revealing broader genotype-level effects here (Chang et al., 2021). Similarly, high-yielding varieties showed rhizosphere microorganisms with higher activity and different carbon source utilization, suggesting superior recruitment and utilization of beneficial microbes, potentially enhancing nutrient absorption and yields (Popescu et al., 2022). Zheng et al. analyzed rhizosphere microbial community structures in three soybean genotypes (high oil, high protein, and high oil and high protein) further confirmed genotype-specific microbial communities and associated root characteristics (Zheng et al., 2019; Song et al., 2020).

While this field experiment provided valuable insights, further research was necessary to refine and expand upon these findings. These include addressing environmental variability, potential unaccounted microbial influences, and expanding the sample size to enhance statistical robustness. The single-site design (chernozem/ chestnut soils, pH 8.03) limited extrapolation to other agroecosystems, as environmental factors like soil type and regional climate influenced microbial recruitment. Future research should prioritize multi-location trials across soil types to assess microbiome stability, complemented by gnotobiotic systems validating causal relationships of key taxa (*Mucilaginibacter gossypii*). While identifying 15 bacterial and 13 fungal yield-associated taxa, taxonomic profiling through 16S/ITS sequencing captured microbial presence but not functional activity. The three-variety comparison with biological triplicates provides foundational insights, but expanded germplasm screening would better resolve subtle plant-microbiome interactions. Integration of metatranscriptomics could bridge taxonomic and functional analyses, while expanded sampling across growth stages would clarify temporal microbial dynamics.

In conclusion, this study illuminated the intricate interplay between soybean genotypes, developmental stages, and rhizosphere microbial communities. The findings advanced our understanding of plant-microbe interactions while revealing potential strategies for

enhancing soybean yield and promoting sustainable agriculture. As this field progresses, it holds promise for significantly improving global food security and agricultural sustainability, paving the way for more efficient and eco-friendly soybean cultivation practices.

Data availability statement

The original contributions presented in the study are included in the article/[Supplementary material](#), further inquiries can be directed to the corresponding authors.

Author contributions

XH: Conceptualization, Investigation, Writing – original draft, Formal analysis, Supervision, Validation. XZ: Investigation, Software, Validation, Visualization, Writing – original draft. MS: Investigation, Validation, Visualization, Writing – original draft. SY: Data curation, Formal Analysis, Investigation, Writing – original draft. SF: Investigation, Visualization, Writing – original draft. TT: Investigation, Writing – original draft, Resources. NC: Investigation, Writing – original draft, Resources. GZ: Conceptualization, Data curation, Project administration, Supervision, Writing – original draft. LH: Project administration, Supervision, Investigation, Writing – original draft. GW: Data curation, Funding acquisition, Resources, Supervision, Writing – review & editing, Investigation, Writing – original draft.

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Supplementary material

The Supplementary material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fsufs.2025.1518597/full#supplementary-material>

References

- Abrahão, A., Ryan, M. H., Laliberté, E., Oliveira, R. S., and Lambers, H. (2018). Phosphorus- and nitrogen-acquisition strategies in two *Bossiaea* species (Fabaceae) along retrogressive soil chronosequences in South-Western Australia. *Physiol. Plant.* 163, 323–343. doi: 10.1111/pp1.12704
- Ajiboye, T. T., Ayangbenro, A. S., and Babalola, O. O. (2022). Functional diversity of microbial communities in the soybean (*Glycine max* L.) rhizosphere from Free State, South Africa. *Int. J. Mol. Sci.* 23:9422. doi: 10.3390/ijms23169422
- Bandara, A. Y., and Kang, S. (2024). Trichoderma application methods differentially affect the tomato growth, rhizomicrobiome, and rhizosphere soil suppressiveness against *Fusarium oxysporum*. *Front. Microbiol.* 15:1366690. doi: 10.3389/fmicb.2024.1366690
- Bars-Cortina, D., Moratalla-Navarro, E., García-Serrano, A., Mach, N., Riobó-Mayo, L., Vea-Barbany, J., et al. (2023). Improving species level-taxonomic assignment from 16S rRNA sequencing technologies. *Curr. Protoc.* 3:e930. doi: 10.1002/cpz1.930
- Bento, C. P. M., van der Hoeven, S., Yang, X., Riksen, M., Mol, H. G. J., Ritsema, C. J., et al. (2019). Dynamics of glyphosate and AMPA in the soil surface layer of glyphosate-resistant crop cultivations in the loess pampas of Argentina. *Environ. Pollut.* 244, 323–331. doi: 10.1016/j.envpol.2018.10.046
- Caporaso, J. G., Kuczynski, J., Stombaugh, J., Bittinger, K., Bushman, F. D., Costello, E. K., et al. (2010). QIIME allows analysis of high-throughput community sequencing data. *Nat. Methods* 7, 335–336. doi: 10.1038/nmeth.f.303
- Chang, H. X., Noel, Z. A., and Chilvers, M. I. (2021). A beta-lactamase gene of *Fusarium oxysporum* alters the rhizosphere microbiota of soybean. *Plant J.* 106, 1588–1604. doi: 10.1111/tpj.15257
- Chen, H., and Boutros, P. C. (2011). VennDiagram: a package for the generation of highly-customizable Venn and Euler diagrams in R. *BMC Bioinform.* 12:35. doi: 10.1186/1471-2105-12-35
- Cole, J. R., Wang, Q., Fish, J. A., Chai, B., McGarrell, D. M., Sun, Y., et al. (2014). Ribosomal database project: data and tools for high throughput rRNA analysis. *Nucleic Acids Res.* 42, D633–D642. doi: 10.1093/nar/gkt1244
- Cucio, C., Engelen, A. H., Costa, R., and Muyzer, G. (2016). Rhizosphere microbiomes of European + seagrasses are selected by the plant, but are not species specific. *Front. Microbiol.* 7:440. doi: 10.3389/fmicb.2016.00440
- Daraz, U., Erhunmwunse, A. S., Dubeux, J. C. B. Jr., Mackowiak, C., Guerra, V. A., Hsu, C. M., et al. (2023). Soil bacterial communities across seven Rhizoma Peanut cultivars (*Arachis glabrata* Benth.) respond to seasonal variation. *Microb. Ecol.* 86, 2703–2715. doi: 10.1007/s00248-023-02277-9
- de Albuquerque, T. M., Mendes, L. W., Rocha, S. M. B., Antunes, J. E. L., Oliveira, L. M. S., Melo, V. M. M., et al. (2022). Genetically related genotypes of cowpea present similar bacterial community in the rhizosphere. *Sci. Rep.* 12:3472. doi: 10.1038/s41598-022-06860-x
- Debenport, S. J., Assigbetse, K., Bayala, R., Chapuis-Lardy, L., Dick, R. P., and McSpadden Gardner, B. B. (2015). Association of shifting populations in the root zone microbiome of millet with enhanced crop productivity in the Sahel region (Africa). *Appl. Environ. Microbiol.* 81, 2841–2851. doi: 10.1128/AEM.04122-14
- Djemiel, C., Grec, S., and Hawkins, S. (2017). Characterization of bacterial and fungal community dynamics by high-throughput sequencing (HTS) Metabarcoding during flax dew-retting. *Front. Microbiol.* 8:2052. doi: 10.3389/fmicb.2017.02052
- Ferreira-Suarez, D., Garcia-Depraet, O., and Castro-Munoz, R. (2024). A review on fungal-based biopesticides and biofertilizers production. *Ecotoxicol. Environ. Saf.* 283:116945. doi: 10.1016/j.ecoenv.2024.116945
- Ichim, M. C. (2019). The Romanian experience and perspective on the commercial cultivation of genetically modified crops in Europe. *Transgenic Res.* 28, 1–7. doi: 10.1007/s11248-018-0095-9

- Jang, S., Choi, S. K., Zhang, H., Zhang, S., Ryu, C. M., and Kloepper, J. W. (2023). History of a model plant growth-promoting rhizobacterium, *Bacillus velezensis* GB03: from isolation to commercialization. *Front. Plant Sci.* 14:1279896. doi: 10.3389/fpls.2023.1279896
- Kesim, B., Ülger, S. T., Aslan, G., Cudal, H., Üstün, Y., and Küçük, M. (2023). Amplicon-based next-generation sequencing for comparative analysis of root canal microbiome of teeth with primary and persistent/secondary endodontic infections. *Clin. Oral Investig.* 27, 995–1004. doi: 10.1007/s00784-023-04882-x
- Kumar, A., and Dubey, A. (2020). Rhizosphere microbiome: engineering bacterial competitiveness for enhancing crop production. *J. Adv. Res.* 24, 337–352. doi: 10.1016/j.jare.2020.04.014
- Lanzavecchia, G., Frascarelli, G., Rocchetti, L., Bellucci, E., Bitocchi, E., Di Vittori, V., et al. (2024). Genotype combinations drive variability in the microbiome configuration of the rhizosphere of maize/bean intercropping system. *Int. J. Mol. Sci.* 25:1288. doi: 10.3390/ijms25021288
- Levy, A., Salas Gonzalez, I., Mittelviefhaus, M., Clingenpeel, S., Herrera Paredes, S., Miao, J., et al. (2017). Genomic features of bacterial adaptation to plants. *Nat. Genet.* 50, 138–150. doi: 10.1038/s41588-017-0012-9
- Liu, Y., Han, Q., Zhang, J., Zhang, X., Chen, Y., Li, M., et al. (2024). Soybean nodulation shapes the rhizosphere microbiome to increase rapeseed yield. *J. Adv. Res.* 34, 1–16. doi: 10.1016/j.jare.2024.11.034
- Liu, F., Hewezi, T., Lebeis, S. L., Pantalone, V., Grewal, P. S., and Staton, M. E. (2019). Soil indigenous microbiome and plant genotypes cooperatively modify soybean rhizosphere microbiome assembly. *BMC Microbiol.* 19:201. doi: 10.1186/s12866-019-1572-x
- Mayhood, P., and Mirza, B. S. (2021). Soybean root nodule and rhizosphere microbiome: distribution of Rhizobial and Nonrhizobial endophytes. *Appl. Environ. Microbiol.* 87, 1–14. doi: 10.1128/AEM.02884-20
- Noack, F., Engist, D., Gantois, J., Gaur, V., Hyjazie, B. F., Larsen, A., et al. (2024). Environmental impacts of genetically modified crops. *Science* 385:9340. doi: 10.1126/science.ado9340
- Olanrewaju, O. S., Ayangbenro, A. S., Glick, B. R., and Babalola, O. O. (2019). Plant health: feedback effect of root exudates-rhizobiome interactions. *Appl. Microbiol. Biotechnol.* 103, 1155–1166. doi: 10.1007/s00253-018-9556-6
- Olowe, V. I. O., Odueme, P. U., Fadeyi, O. J., Tolulope, O., and Somefun. (2023). Agronomic response of soybeans (*Glycine max* (L.) Merrill) to different management practices in the humid tropics. *Technol. Agron.* 18, 263–271. doi: 10.48130/TIA-2023-0018
- Paudel, D., Wang, L., Poudel, R., Acharya, J. P., Victores, S., de Souza, C. H. L., et al. (2023). Elucidating the effects of organic vs. conventional cropping practice and rhizobia inoculation on rhizosphere microbial diversity and yield of peanut. *Environ. Microb.* 18:60. doi: 10.1186/s40793-023-00517-6
- Persoon, I. F., Buijs, M. J., Özok, A. R., Crielaard, W., Krom, B. P., Zaura, E., et al. (2017). The mycobiome of root canal infections is correlated to the bacteriome. *Clin. Oral Investig.* 21, 1871–1881. doi: 10.1007/s00784-016-1980-3
- Popescu, S. C., Tomaso-Peterson, M., Wilkerson, T., Bronzato-Badial, A., Wesser, U., and Popescu, G. V. (2022). Metagenomic analyses of the soybean root Mycobiome and microbiome reveal signatures of the healthy and diseased plants affected by taproot decline. *Microorganisms* 10:856. doi: 10.3390/microorganisms10050856
- Ren, H., Zhang, F., Zhu, X., Lamlo, S. F., Zhao, K., Zhang, B., et al. (2023). Manipulating rhizosphere microorganisms to improve crop yield in saline-alkali soil: a study on soybean growth and development. *Front. Microbiol.* 14:1233351. doi: 10.3389/fmicb.2023.1233351
- Sarkar, S., Kamke, A., Ward, K., Rudick, A. K., Baer, S. G., Ran, Q., et al. (2022). Bacterial but not fungal rhizosphere community composition differ among perennial grass ecotypes under abiotic environmental stress. *Microbiol. Spectr.* 10:e0239121. doi: 10.1128/spectrum.02391-21
- Schloss, P. D., Westcott, S. L., Ryabin, T., Hall, J. R., Hartmann, M., Hollister, E. B., et al. (2009). Introducing mothur: open-source, platform-independent, community-supported software for describing and comparing microbial communities. *Appl. Environ. Microbiol.* 75, 7537–7541. doi: 10.1128/AEM.01541-09
- Sharma, V., Sharma, D. P., and Salwan, R. (2024). Surviving the stress: understanding the molecular basis of plant adaptations and uncovering the role of mycorrhizal association in plant abiotic stresses. *Microb. Pathog.* 193:106772. doi: 10.1016/j.micpath.2024.106772
- Shen, W., Liu, L., Fang, Z., Zhang, L., Ren, Z., Yu, Q., et al. (2025). Cultivation of genetically modified soybeans did not alter the overall structure of rhizosphere soil microbial communities. *Plants (Basel)* 14:457. doi: 10.3390/plants14030457
- Song, Y., Li, X., Yao, S., Yang, X., and Jiang, X. (2020). Correlations between soil metabolomics and bacterial community structures in the pepper rhizosphere under plastic greenhouse cultivation. *Sci. Total Environ.* 728:138439. doi: 10.1016/j.scitotenv.2020.138439
- Tripathi, S., Yadav, S., Sharma, P., Purchase, D., Syed, A., and Chandra, R. (2022). Plant growth promoting strain *Bacillus cereus* (RCS-4 MZ520573.1) enhances phytoremediation potential of *Cynodon dactylon* L. in distillery sludge. *Environ. Res.* 208:112709. doi: 10.1016/j.envres.2022.112709
- Vejan, P., Abdullah, R., Khadiran, T., Ismail, S., and Nasrulhaq, B. A. (2016). Role of plant growth promoting Rhizobacteria in agricultural sustainability-a review. *Molecules* 21:573. doi: 10.3390/molecules21050573
- Wang, M., Ge, A. H., Ma, X., Wang, X., Xie, Q., Wang, L., et al. (2024). Dynamic root microbiome sustains soybean productivity under unbalanced fertilization. *Nat. Commun.* 15:1668. doi: 10.1038/s41467-024-45925-5
- Wang, P., Nie, J., Yang, L., Zhao, J., Wang, X., Zhang, Y., et al. (2023). Plant growth stages covered the legacy effect of rotation systems on microbial community structure and function in wheat rhizosphere. *Environ. Sci. Pollut. Res. Int.* 30, 59632–59644. doi: 10.1007/s11356-023-26703-0
- Wei, B., Zhang, J., Wen, R., Chen, T., Xia, N., Liu, Y., et al. (2021). Corrigendum: genetically modified sugarcane intercropping soybean impact on rhizosphere bacterial communities and co-occurrence patterns. *Front. Microbiol.* 12:835633. doi: 10.3389/fmicb.2021.742341
- Weng, L. Y., Luan, D. D., Zhou, D. P., Guo, Q. G., Wang, G. Z., and Zhang, J. L. (2024). Improving crop health by synthetic microbial communities: Progress and prospects. *Ying Yong Sheng Tai Xue Bao* 35, 847–857. doi: 10.13287/j.1001-9332.202403.028
- Yang, M., Luo, F., Song, Y., Ma, S., Ma, Y., Fazal, A., et al. (2022). The host niches of soybean rather than genetic modification or glyphosate application drive the assembly of root-associated microbial communities. *Microb. Biotechnol.* 15, 2942–2957. doi: 10.1111/1751-7915.14164
- Zablutowicz, R. M., and Reddy, K. N. (2004). Impact of glyphosate on the *Bradyrhizobium japonicum* symbiosis with glyphosate-resistant transgenic soybean: a minireview. *J. Environ. Qual.* 33, 825–831. doi: 10.2134/jeq2004.0825
- Zhalnina, K., Louie, K. B., Hao, Z., Mansoori, N., da Rocha, U. N., Shi, S., et al. (2018). Dynamic root exudate chemistry and microbial substrate preferences drive patterns in rhizosphere microbial community assembly. *Nat. Microbiol.* 3, 470–480. doi: 10.1038/s41564-018-0129-3
- Zheng, T., Liang, C., Xie, H., Zhao, J., Yan, E., Zhou, X., et al. (2019). Rhizosphere effects on soil microbial community structure and enzyme activity in a successional subtropical forest. *FEMS Microbiol. Ecol.* 95:fiz043. doi: 10.1093/femsec/fiz043
- Zhong, Y., Yang, Y., Liu, P., Xu, R., Rensing, C., Fu, X., et al. (2019). Genotype and rhizobium inoculation modulate the assembly of soybean rhizobacterial communities. *Plant Cell Environ.* 42, 2028–2044. doi: 10.1111/pce.13519



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Enhancing ecosystem services in agriculture: the special role of legume intercropping

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Sustainable agriculture confronts significant challenges such as soil degradation, intensification of agricultural production, and the impact of climate change. Legume intercropping is an “underestimated” cultural practice that harnesses the unique ecosystem services of legumes to enhance resilience and productivity of cropping systems. Legumes contribute to biodiversity by supporting beneficial insects, including pollinators, which can enhance crop productivity. Additionally, through nitrogen fixation, legumes reduce synthetic fertilizer inputs, promote efficient nutrient cycling, and improve soil health. The introduction of legumes in intercropping schemes has beneficial effects on soil texture, microbial diversity, water retention, crop growth, and yield. This cultural practice also contributes to reduced emissions of greenhouse gases, carbon sequestration, and lower pesticide inputs. In addition, legume intercropping promotes biodiversity while facilitating natural pest control and weed suppression. Overall, the inclusion of legumes in intercropping schemes and diversified cropping systems can support food security and mitigate environmental risks related to climate change.

KEYWORDS

legumes, ecosystem services, biodiversity, nitrogen fixation, climate adaptation, pollination

1 Introduction

The sustainable use of soil is crucial for human life and ecological stability, as soil supports agriculture, fosters plant development, serves as habitats for wildlife, preserves biodiversity, soil organic carbon storage, and improves the overall quality of the environment (Pereira et al., 2018). These functions are vital for maintaining biodiversity and ecological resilience, especially in an era when the constantly increasing population raises food demands and puts immense pressure on natural resources’ availability (Smith et al., 2016).

Intensive agriculture causes biodiversity loss and extensive land degradation that now affects approximately 30% of global land area and impacts three billion people; each year, an estimated 10 million hectares of arable land are rendered unproductive (Hossain et al., 2020). This intensified land use, along with a heavy reliance on pesticide inputs and fertilizers, gradually diminishes soil fertility and disrupts ecosystem balance (Krasilnikov et al., 2022). Climate change exacerbates these challenges, accelerating resource depletion and posing additional threats to food security and safety (Miraglia et al., 2009; Farooq and Pisante, 2019). Accordingly, the adoption of sustainable agricultural practices is key to strengthening resilience and long-term productivity in agricultural systems. Biodiversity restoration through diversified agroecosystems plays a vital role in maintaining soil fertility and facilitating key ecological processes such as pollination and pest control. Intercropping, as an agronomic practice, is one of the best “fits” in such diversified agroecosystems,

referring to a multiple cropping system where two or more crop species are cultivated together in the same field during overlapping periods of their growing season (Scherr and McNeely, 2008). Intercropping has demonstrated the ability to increase yields across various crop combinations while reducing reliance on chemical inputs and promoting the cultivation of high-quality food (Lulie, 2017). It also improves crop protection and facilitates efficient use of soil resources (Hauggaard-Nielsen et al., 2008). In contrast to crop monocultures, which deplete biodiversity and lead to overreliance on agrochemicals, intercrops reduce soil erosion, increase yield stability, and improve pest-weed management (Figure 1).

All legumes have the potential to fix atmospheric nitrogen (N) due to their symbiotic association with rhizobacteria of the genus *Rhizobium* spp. (Mahieu, 2008; Patel and Shah, 2014). N-fixation contributes about 20–22 million tons of N annually to the globe. Therefore, legume presence can reduce fertilizer inputs and nutrient leaching to groundwater (Büchi et al., 2015). Moreover, legumes can enhance microbial abundance and activity, which contributes to improved soil health (Tang et al., 2014). In addition to these benefits, legumes also support climate change mitigation by reducing greenhouse gas emissions associated with synthetic fertilizer use and enhancing soil carbon sequestration, a function that deserves greater recognition (Hassen et al., 2017). They further contribute to improved nutrient cycling and natural pest regulation, reinforcing their multifunctional role in sustainable agriculture.

Their integration into cropping systems offers a pathway toward reducing input dependence, optimizing ecological performance, and promoting productive, biologically based farming practices that align with long-term sustainability goals.

2 Ecosystem services provided by legumes

Incorporating legumes into existing monoculture and simplified crop rotations is a common strategy for improving agricultural diversity globally (Hufnagel et al., 2020), recognized for its multiple social and ecological advantages. These advantages are referred to as ecosystem services (ES), which are the benefits that people receive from ecosystems crucial for life on Earth, including both biological functions and agricultural aspects (Zhang et al., 2007). Globally, cereal–legume intercropping often pairs major cereals with grain legumes; for example, maize is commonly grown alongside soybean and wheat with field pea (Landschoot et al., 2024). In temperate regions, annual legumes such as pea, vetches, and white lupin have long been intercropped with cereals, representing one of the oldest and most established practices for improving both forage and grain production in diversified systems (Mikić et al., 2015).

2.1 Human-centered ecosystem services provided by legumes

Beyond their environmental and agronomic benefits, legumes also provide significant social advantages, particularly in improving

food security, public health, and economic resilience. In many regions, limited access to nutritious food remains a major issue, affecting over 2 billion people globally, including vulnerable populations in developed nations. Legumes, with their high protein and micronutrient content, offer an affordable and accessible alternative to expensive animal-based proteins, improving dietary diversity and reducing the risk of malnutrition-related health issues (Boye et al., 2010; Marinangeli et al., 2017). However, despite their nutritional and ecological advantages, legumes remain underutilized in both diets and large-scale agricultural production systems (Foyer et al., 2016).

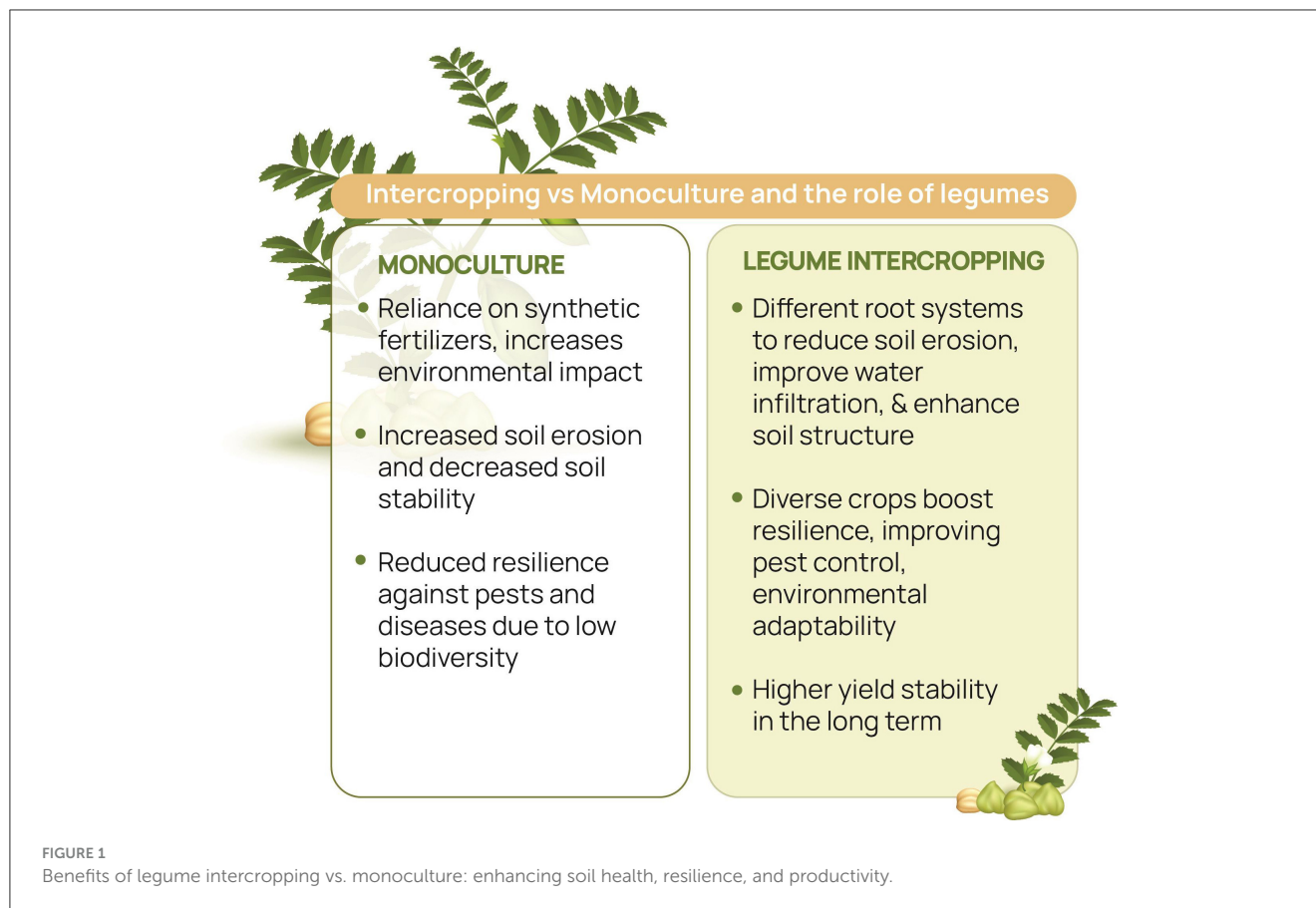
Despite growing awareness of their benefits, legumes have historically been overlooked in global food security policies. However, targeted public procurement initiatives have shown promising results. In Portugal, a national food policy successfully increased institutional legume consumption, demonstrating how policy-driven interventions can promote healthier and more sustainable dietary habits (Graca et al., 2018).

Beyond nutrition and policy, legumes also offer economic and public health benefits. Research in Canada has shown that encouraging legume consumption (100 g cooked legumes/day for 50% of the population) could reduce healthcare costs by \$370 million per year, primarily by lowering the prevalence of cardiovascular disease and type 2 diabetes (Abdullah et al., 2017). Additionally, legumes support local food systems and community-based agriculture, such as home gardens, school meal programs, and cooperative farming projects, making nutritious food more accessible and affordable (Keatinge et al., 2012).

Given their potential to enhance food security, economic resilience, and public health, legumes should be recognized as a cornerstone of sustainable food security strategies. Strengthening policy support, institutional procurement programs, and consumer awareness would help maximize their social benefits, ensuring they contribute more effectively to global food security and sustainable agriculture.

2.2 Enhancing nitrogen fixation through legume intercropping

The use of legumes in intercropping systems is justified by their natural ability to exploit atmospheric nitrogen (N₂), which makes them particularly valuable in cropping systems with nitrogen deficiency (Bedoussac et al., 2015). These legumes enhance nitrogen fixation through facilitative interactions among root systems that improve nutrient availability, including nitrogen and phosphorus, especially under environmental stress (Latati et al., 2016). Their ability to fix nitrogen not only supplies an extra source of nitrogen but also minimizes competition between various crop species and legumes for nitrogen uptake. Research has demonstrated that intercropped legumes significantly benefit adjacent cereal crops, with estimates of nitrogen fixation by legumes ranging from 10 to 38 g N m⁻² a⁻¹ and nitrogen transfer to cereals varying from 0 to 73% (Thilakarathna et al., 2016). Intercropped legumes can store between 40 and 100 kg N/ha in their above ground biomass, which can lead to higher yields for subsequent crops. For instance, a 30% increase in maize yield has been positively correlated with the development of legumes and nitrogen



accumulation in legume tissues (Amossé et al., 2014). Furthermore, the land equivalent ratio (LER) for intercropped systems often exceeds 1, indicating increased productivity compared to sole crops (Mead and Willey, 1980). Legumes exhibit adaptive traits that allow them to optimize nitrogen fixation based on soil nitrogen availability; their nitrogen fixation rate is negatively correlated with the inorganic nitrogen content in the soil, meaning they fix more nitrogen when soil nitrogen is low (Mahieu, 2008). Additionally, research indicates that intercropped cereals absorb 54–64% more soil nitrogen than those grown in monoculture (Rodriguez et al., 2020). Legume intercropping can significantly reduce synthetic fertilizer dependency through several mechanisms. In research conducted by Li et al. (2020), it is shown that intercropping practices can result in 16% to 29% higher grain production per hectare while requiring 19% to 36% less fertilizer per unit of output compared to conventional monocropping systems, this not only enhances profitability for farmers but also reduces environmental impacts, contributing to a more secure food supply.

2.3 Improving legume intercropping for enhanced soil health

Healthy soil is foundational to sustainable agriculture, and legume intercropping contributes to key ecosystem services, such as

soil stability, water retention, and microbial health. Intercropping legumes with cereals enhances soil structure by leveraging complementary root-zone effects, as legumes' deeper root systems break up compacted layers, improve soil aeration, and promote stronger soil aggregates (Garland et al., 2017). Additionally, intercropping a variety of crops helps prevent soil erosion by minimizing the impact of precipitation on the soil surface, thereby reducing the sealing of surface pores, enhancing water infiltration, and decreasing runoff volume (Seran and Brintha, 2010). Specifically, intercropping sorghum with cowpea reduced surface runoff by 20–30% compared to growing sorghum alone and by 45–55% compared to growing cowpea alone. Furthermore, soil loss was cut by 50% when sorghum and cowpea were intercropped rather than cultivated as monocultures (Zougmore et al., 2000). Incorporating legumes into intercropped systems has been found to significantly boost the diversity of soil microbial communities, which is essential for effective nutrient cycling and overall soil health due to the specialized roles played by different microbial species (Lai et al., 2022). Research demonstrates that intercropping cereals with legumes increases microbial biomass and activity (Latati et al., 2014). All this evidence supports the idea that intercropping is vital for promoting soil biodiversity and helps select functional microbial communities that rely on carbon fluxes from plant roots and signaling molecules, which encourage mutualistic relationships (Bartelt-Ryser et al., 2005; Philippot et al., 2013).

2.4 Building climate resilience with legume intercropping

Sustainable agricultural practices are essential for climate change adaptation and mitigation. Legume intercropping has been shown to promote agricultural sustainability, providing both mitigation and adaptation benefits by reducing greenhouse gas emissions (Soussana and Lemaire, 2014) and replacing synthetic nitrogen fertilizers with symbiotic nitrogen fixation (Lüscher et al., 2014). According to Jensen et al. (2012), a study on grass-clover intercropping revealed significantly lower mean annual N₂O emissions (0.54 kg N₂O–N/ha) compared to N-fertilized pasture grass (4.49 kg N₂O–N/ha) and pure legume stands of white clover (0.79 kg N₂O–N/ha), highlighting the potential of legume intercropping to reduce nitrogen-based emissions. Similarly, Senbayram et al. (2015) reported that seasonal N₂O emissions were 35% lower in a wheat-faba bean intercrop compared to N-fertilized wheat in Germany, demonstrating further reductions in fertilizer-derived N₂O emissions through intercropping. Additionally, soil carbon sequestration, which has the technical capacity to mitigate up to 89% of greenhouse gas emissions, is a promising climate change mitigation strategy (Fischlin et al., 2007). Over a 7-year experiment, Cong et al. (2015) found that intercropping improved soil organic carbon by up to 4% in the top 20 cm of soil compared to monoculture systems, underscoring its potential to support long-term carbon storage and climate resilience. Another climate-smart approach involves adopting crop varieties and species adapted to specific environmental conditions. This includes introducing new or heritage crop varieties, which diversify agricultural production and can enhance resilience against climate variability (Chimonyo et al., 2020). Given the ecological diversity across regions, tailored planting strategies and crop selections are necessary to address varying climates and weather conditions effectively.

2.5 Pollination and biodiversity support in legume intercropping

Pollination is a key ecological function that plays a crucial role in preserving biodiversity. Many species within the Fabaceae family rely on animal-mediated pollination, offering floral resources such as nectar and pollen that attract a wide range of insect pollinators (Proctor et al., 1996). This function is especially important as the decline in floral resources within modern agricultural landscapes is recognized as a major factor driving pollinator losses (Rhodes, 2018). Consequently, as a potential solution, legume intercropping may help mitigate pollinator losses and contribute to maintaining essential crop pollination services. Growing legume species alongside non-insect-pollinated crops, such as cereals, has been shown to increase the diversity and abundance of flower-visiting insects compared to monoculture systems (Brandmeier et al., 2021). Additionally, intercropping legumes with cereals improves the overall productivity of neighboring crops by attracting shared pollinators (Galloni et al., 2007). Although legume-cereal intercropping is expected to receive fewer pollinators than legume monoculture due to a lower floral density, the impact on pollination rates may be less significant than anticipated

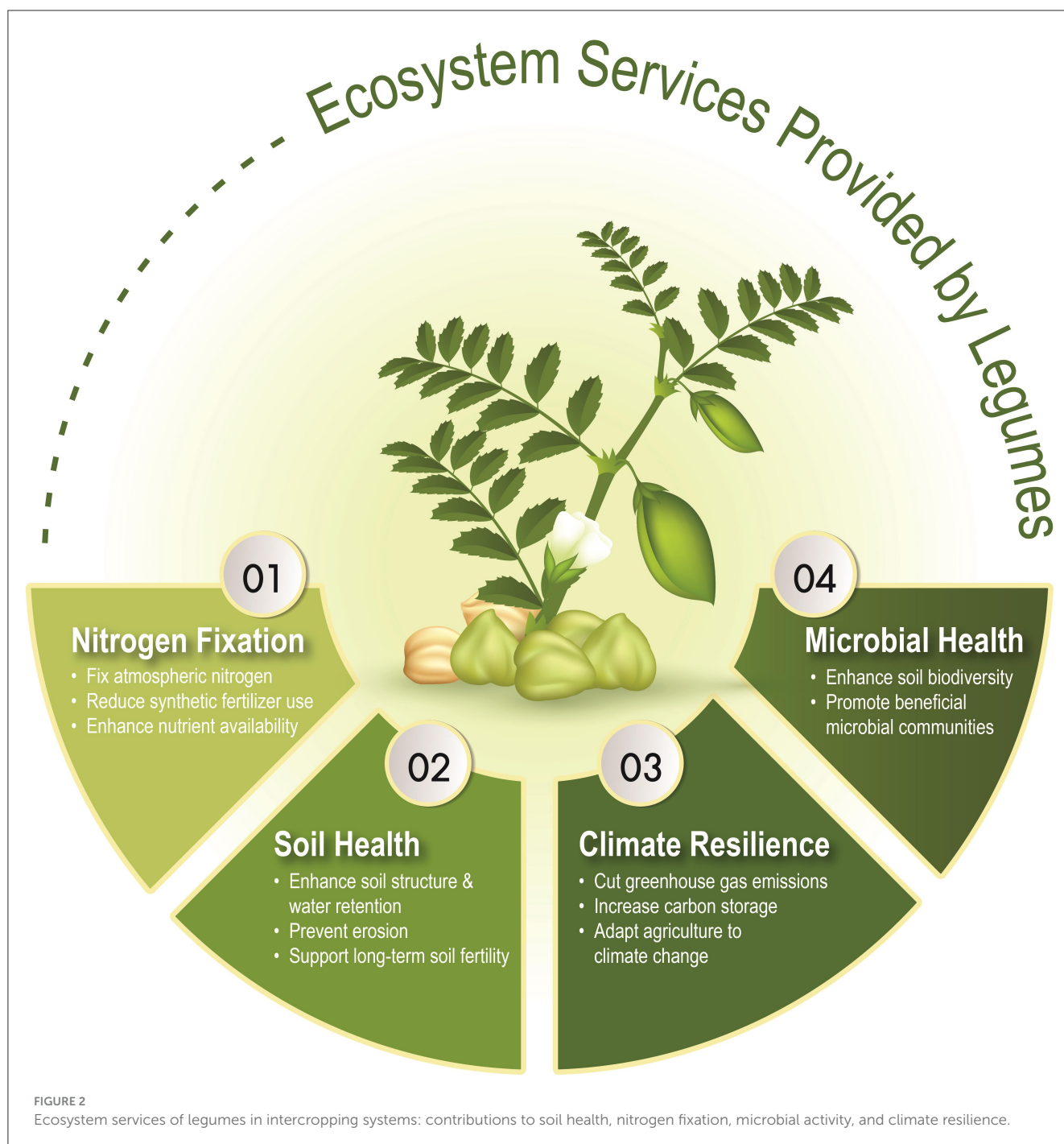
(Beyer et al., 2022). However, in a fava bean (*Vicia faba* L.)—wheat intercropping system, the reduced number of *Vicia faba* inflorescences did not decrease the total number of bee pollinator visits compared to sole fava bean cultivation. This suggests that both cropping systems are equally attractive to foraging insects. Additionally, *Vicia faba* plants in intercropping systems produced 46.7% higher yields compared to monoculture, highlighting how intercropping optimizes resource use, reduces plant competition, and enhances overall growth and productivity (Kirsch et al., 2023). Legume intercropping not only supports pollinator conservation but also improves the sustainability of agricultural systems by means of the provision of various ecosystem services (Figure 2).

3 Discussion

When legumes are included in agricultural systems, farmers are able to take advantage of the natural nitrogen-fixing abilities of these species and, therefore, reduce their reliance on synthetic fertilizers (Crews and Peoples, 2004). This cultural practice mitigates certain nutrient depletion concerns linked to monoculture and also contributes to an increase in the overall productivity of intercropped systems. Some research has shown that intercropping also improves N-use efficiency and further reduce nitrogen leaching, thus lessening the ecological impact of farming (Li et al., 2006). Furthermore, the key ecosystem services provided by legume intercropping contribute to the sustainability of agricultural practices. Synergistic interactions among the root systems of legumes and cereals enhance soil structure and stability, which increases water-holding capacity and reduces the tendency toward soil erosion (Stagnari et al., 2017). Besides, their beneficial effect on soil microbial communities makes nutrient cycling and pest control more efficient, enhancing the resilience of the cropping system (Cardinale et al., 2012).

The use of intercropping reduces the overreliance on chemical fertilizers and significantly lowers greenhouse gas emissions resulting from nitrogen fertilization. Further, this capacity of legumes' carbon sequestration potential in soil makes a quite important role in efforts aimed at mitigating climate change (Yao et al., 2023). The results show that the adoption of sustainable practices enhances not only the efficiency and resilience of agricultural systems but also soil-plant biodiversity, thus making agricultural practices in line with broader environmental goals. Further research is needed to optimize legume intercropping systems to ensure adaptability across diverse agroecosystems, as regional variables such as soil composition, climatic conditions, and water accessibility strongly influence their performance.

Despite these well-documented benefits, several practical challenges continue to hinder the widespread adoption of legume intercropping. Managing intercrops typically involves higher complexity compared to monoculture systems, as it requires precise coordination of planting times, compatible crop selection, and harvest synchronization, thus increasing the demand for specialized knowledge, careful monitoring, and additional labor (Bedoussac et al., 2015). Additionally, poorly designed intercrop combinations or inadequate management can lead to undesirable competition for critical resources such as nutrients, water, and sunlight, which might negatively affect



crop yields and productivity (Yu et al., 2015). Furthermore, economic barriers, including increased initial investment costs, greater labor inputs, and limited market incentives or infrastructure, often discourage wider farmer adoption, especially where supportive policy frameworks are lacking (Mamine and Farès, 2020). Addressing these practical challenges is essential to fully exploit the potential of legume intercropping in diverse agricultural contexts.

While legume intercropping has demonstrated multiple benefits in terms of soil fertility, biodiversity, and yield stability,

research findings are not always consistent across different agroecosystems. Some studies report significant improvements in productivity and nitrogen-use efficiency due to complementary plant interactions (Raseduzzaman and Jensen, 2017), while others highlight cases where intercropping showed minimal or even negative impacts on yield due to interspecific competition and environmental variability (Hauggaard-Nielsen et al., 2009). Similarly, while nitrogen fixation benefits are well-documented, research suggests that phosphorus availability and uptake may not always improve under legume-based intercropping systems,

depending on soil conditions and species selection (Li et al., 2020). These inconsistencies emphasize the importance of region-specific research and tailored management strategies to optimize intercropping performance.

In summary, legume intercropping reinforces its value in sustainable agriculture. Nonetheless, future research should focus on optimizing cropping systems tailored to regional conditions, addressing existing management complexities, and strengthening policy support and market incentives. These steps will ensure broader adoption and enable legume intercropping systems to fully deliver their potential for resilient and sustainable global agriculture.

Author contributions

MK: Conceptualization, Writing – original draft. IG: Writing – review & editing. MD: Data curation, Visualization, Writing – original draft. VK: Data curation, Visualization, Writing – original draft. PK: Data curation, Visualization, Writing – original draft. IT: Conceptualization, Project administration, Writing – review & editing.

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References

- Abdullah, M. M., Marinangeli, C. P., Jones, P. J., and Carlberg, J. G. (2017). Canadian potential healthcare and societal cost savings from consumption of pulses: a cost-of-illness analysis. *Nutrients* 9:793. doi: 10.3390/nu9070793
- Amossé, C., Jeuffroy, M. H., Mary, B., and David, C. (2014). Contribution of relay intercropping with legume cover crops on nitrogen dynamics in organic grain systems. *Nutr. Cycl. Agroecosyst.* 98, 1–14. doi: 10.1007/s10705-013-9591-8
- Bartelt-Ryser, J., Joshi, J., Schmid, B., Brandl, H., and Balser, T. (2005). Soil feedbacks of plant diversity on soil microbial communities and subsequent plant growth. *Perspect. Plant Ecol. Evol. Syst.* 7, 27–49. doi: 10.1016/j.ppees.2004.11.002
- Bedoussac, L., Journet, E. P., Hauggaard-Nielsen, H., Naudin, C., Corre-Hellou, G., Jensen, E. S., et al. (2015). Ecological principles underlying the increase of productivity achieved by cereal-grain legume intercrops in organic farming. A review. *Agron Sustain Dev* 35, 911–935. doi: 10.1007/s13593-014-0277-7
- Beyer, N., Gabriel, D., and Westphal, C. (2022). Landscape composition modifies pollinator densities, foraging behavior and yield formation in faba beans. *Basic Appl. Ecol.* 61, 30–40. doi: 10.1016/j.baae.2022.03.002
- Boye, J., Zare, F., and Pletch, A. (2010). Pulse proteins: processing, characterization, functional properties and applications in food and feed. *Int. Food Res* 43, 414–431. doi: 10.1016/j.foodres.2009.09.003
- Brandmeier, J., Reininghaus, H., Pappagallo, S., Karley, A. J., Kiar, L. P., and Scherber, C. (2021). Intercropping in high input agriculture supports arthropod diversity without risking significant yield losses. *Basic Appl. Ecol.* 53, 26–38. doi: 10.1016/j.baae.2021.02.011
- Büchi, L., Gebhard, C. A., Liebisch, F., Sinaj, S., Ramseier, H., and Charles, R. (2015). Accumulation of biologically fixed nitrogen by legumes cultivated as cover crops in Switzerland. *Plant Soil* 393, 163–175. doi: 10.1007/s11104-015-2476-7
- Cardinale, B. J., Duffy, J. E., Gonzalez, A., Hooper, D. U., Perrings, C., Venail, P., et al. (2012). Biodiversity loss and its impact on humanity. *Nature* 486, 59–67. doi: 10.1038/nature11148
- Chimonyo, V. G. P., Wimalasiri, E. M., Kunz, R., Modi, A. T., and Mabhaudhi, T. (2020). Optimizing traditional cropping systems under climate change: a case of maize landraces and bambara groundnut. *Front. Sustain. Food Syst.* 4:562568. doi: 10.3389/fsufs.2020.562568
- Cong, W. F., Hoffland, E., Li, L., Six, J., Sun, J. H., Bao, X. G., et al. (2015). Intercropping enhances soil carbon and nitrogen. *Glob. Chang. Biol.* 21, 1715–1726. doi: 10.1111/gcb.12738
- Crews, T. E., and Peoples, M. B. (2004). Legume versus fertilizer sources of nitrogen: Ecological tradeoffs and human needs. *Agric. Ecosyst. Environ.* 102, 279–297. doi: 10.1016/j.agee.2003.09.018
- Farooq, M., and Pisante, M. (2019). *Innovations in sustainable agriculture*. New York: Springer International Publishing.
- Fischlin, A., Midgley, G. F., Price, J. T., Leemans, R., Gopal, B., Turley, C., et al. (2007). "Ecosystems, their properties, goods, and services," in *Climate Change 2007: Impacts, Adaptation and Vulnerability*, eds. M. L. Parry, O. F. Canziani, J. P. Palutikof, P. J. van der Linden, and C. E. Hanson (Cambridge: Cambridge University Press), 211–272.
- Foyer, C. H., Lam, H. M., Nguyen, H. T., Siddique, K. H., Varshney, R. K., Colmer, T. D., et al. (2016). Neglecting legumes has compromised human health and sustainable food production. *Nat. Plants* 2, 1–10. doi: 10.1038/nplants.2016.112
- Galloni, M., Podda, L., Vivarelli, D., and Cristofolini, G. (2007). Pollen presentation, pollen-ovule ratios, and other reproductive traits in Mediterranean Legumes (Fam. *Fabaceae* - Subfam. *Faboideae*). *Pl. Syst. Evol.* 266, 147–164. doi: 10.1007/s00606-007-0526-1
- Garland, G., Bünemann, E. K., Oberson, A., Frossard, E., and Six, J. (2017). Plant-mediated rhizospheric interactions in maize-pigeon pea intercropping enhance soil aggregation and organic phosphorus storage. *Plant Soil* 415, 37–55. doi: 10.1007/s11104-016-3145-1

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Conflict of interest

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- Graca, P., Gregorio, M. J., De Sousa, S. M., Bras, S., Penedo, T., Carvalho, T., et al. (2018). A new interministerial strategy for the promotion of healthy eating in Portugal: implementation and initial results. *Health Res. Policy Sys.* 16, 1–16. doi: 10.1186/s12961-018-0380-3
- Hassen, A., Talore, D. G., Tesfamariam, E. H., Friend, M. A., and Mpanza, T. D. E. (2017). Potential use of forage-legume intercropping technologies to adapt to climate-change impacts on mixed crop-livestock systems in Africa: a review. *Reg. Environ. Change* 17, 1713–1724. doi: 10.1007/s10113-017-1131-7
- Hauggaard-Nielsen, H., Gooding, M., Ambus, P., Corre-Hellou, G., Crozat, Y., Dahlmann, C., et al. (2009). Pea–barley intercropping for efficient symbiotic N₂-fixation, soil N acquisition and use of other nutrients in European organic cropping systems. *Field Crops Res.* 113, 64–71. doi: 10.1016/j.fcr.2009.04.009
- Hauggaard-Nielsen, H., Jørgensen, B., Kinane, J., and Jensen, E. S. (2008). Grain legume - Cereal intercropping: The practical application of diversity, competition and facilitation in arable and organic cropping systems. *Renew. Agric. Food Syst.* 23, 3–12. doi: 10.1017/S1742170507002025
- Hossain, A., Krupnik, T. J., Timsina, J., Mahboob, M. G., Chaki, A. K., Farooq, M., et al. (2020). "Agricultural Land Degradation: Processes and Problems Undermining Future Food Security," in *Environment, Climate, Plant and Vegetation Growth*, (New York: Springer International Publishing), 17–61. doi: 10.1007/978-3-030-49732-3_2
- Hufnagel, J., Reckling, M., and Ewert, F. (2020). Diverse approaches to crop diversification in agricultural research. A review. *Agron. Sustain. Dev.* 40. doi: 10.1007/s13593-020-00617-4
- Jensen, E. S., Peoples, M. B., Boddey, R. M., Gresshoff, P. M., Henrik, H. N., Alves, B. J. R., et al. (2012). Legumes for mitigation of climate change and the provision of feedstock for biofuels and biorefineries. A review. *Agron. Sustain. Dev.* 32, 329–364. doi: 10.1007/s13593-011-0056-7
- Keatinge, J. D., Chadha, M. L., Hughes, J. D. A., Easdown, W. J., Holmer, R. J., Tenkouano, A., et al. (2012). Vegetable gardens and their impact on the attainment of the Millennium Development Goals. *Biol. Agric. Hortic.* 28, 71–85. doi: 10.1080/01448765.2012.681344
- Kirsch, F., Hass, A. L., Link, W., and Westphal, C. (2023). Intercrops as foraging habitats for bees: Bees do not prefer sole legume crops over legume-cereal mixtures. *Agric. Ecosyst. Environ.* 343:108268. doi: 10.1016/j.agee.2022.108268
- Krasilnikov, P., Taboada, M. A., and Amanullah (2022). Fertilizer use, soil health and agricultural sustainability. *Agriculture* 12:462. doi: 10.3390/agriculture12040462
- Lai, H., Gao, F., Su, H., Zheng, P., Li, Y., and Yao, H. (2022). Nitrogen distribution and soil microbial community characteristics in a legume–cereal intercropping system: a review. *Agronomy* 12:1900. doi: 10.3390/agronomy12081900
- Landschoot, S., Zustovi, R., Dewitte, K., Randall, N. P., Maenhout, S., and Haesaert, G. (2024). Cereal-legume intercropping: a smart review using topic modelling. *Front. Plant Sci.* 14:1228850. doi: 10.3389/fpls.2023.1228850
- Latati, M., Bargaz, A., Belarbi, B., Lazali, M., Benlahrech, S., Tellah, S., et al. (2016). The intercropping common bean with maize improves the rhizobial efficiency, resource use and grain yield under low phosphorus availability. *Eur. J. Agron.* 72, 80–90. doi: 10.1016/j.eja.2015.09.015
- Latati, M., Blavet, D., Alkama, N., Laoufi, H., Drevon, J. J., Gérard, F., et al. (2014). The intercropping cowpea-maize improves soil phosphorus availability and maize yields in an alkaline soil. *Plant Soil* 385, 181–191. doi: 10.1007/s11104-014-2214-6
- Li, C., Hoffland, E., Kuyper, T. W., Yu, Y., Zhang, C., Li, H., et al. (2020). Syndromes of production in intercropping impact yield gains. *Nature Plants* 6, 653–660. doi: 10.1038/s41477-020-0680-9
- Li, L., Sun, J., Zhang, F., Guo, T., Bao, X., Smith, A. F., et al. (2006). Root distribution and interactions between intercropped species. *Oecologia* 147, 280–290. doi: 10.1007/s00442-005
- Lulie, B. (2017). Intercropping practice as an alternative pathway for sustainable agriculture: a review. *ARJASR* 5, 440–452. doi: 10.14662/ARJASR2017.057
- Lüscher, A., Mueller-Harvey, I., Soussana, J. F., Rees, R. M., and Peyraud, J. L. (2014). Potential of legume-based grassland-livestock systems in Europe: a review. *Grass Forage Sci.* 69, 206–228. doi: 10.1111/gfs.12124
- Mahieu, S. (2008). *Assessment of the Below Ground Contribution of Field Grown Pea (Pisum sativum L.) to the Soil N Pool*. Université d'Angers, 128.
- Mamine, F., and Farès, M. H. (2020). Barriers and levers to developing wheat–pea intercropping in Europe: a review. *Sustainability* 12:6962. doi: 10.3390/su12176962
- Marinangeli, C. P., Curran, J., Barr, S. I., Slavin, J., Puri, S., Swaminathan, S., et al. (2017). Enhancing nutrition with pulses: defining a recommended serving size for adults. *Nutr. Rev.* 75, 990–1006. doi: 10.1093/nutrit/nux058
- Mead, R., and Willey, R. W. (1980). *The concept of a "land equivalent ratio" and advantages in yields from intercropping*. Cambridge: Cambridge University Press.
- Mikić, A., Cupina, B., Rubiales D, Mihailović V., and Šarunaite, L., Fustec J, et al. (2015). Models, developments, and perspectives of mutual legume intercropping. *Adv. Agron.* 130, 337–419. doi: 10.1016/bs.agron.2014.10.004
- Miraglia, M., Marvin, H. J. P., Kleter, G. A., Battilani, P., Brera, C., Coni, E., et al. (2009). Climate change and food safety: an emerging issue with special focus on Europe. *Food. Chem. Toxicol.* 47, 1009–1021. doi: 10.1016/j.fct.2009.02.005
- Patel, S., and Shah, D. B. (2014). Phylogeny in few species of Leguminosae family based on matK sequence. *Comput. Mol. Biol.* 4, 1–5. doi: 10.5376/cmb.2014.04.0006
- Pereira, P., Bogunovic, I., Muñoz-Rojas, M., and Brevik, E. C. (2018). Soil ecosystem services, sustainability, valuation and management. *Curr. Opin. Environ. Sci. Health* 5, 7–13. doi: 10.1016/j.coesh.2017.12.003
- Philippot, L., Raaijmakers, J. M., Lemancau, P., and Van Der Putten, W. H. (2013). Going back to the roots: The microbial ecology of the rhizosphere. *Nat. Rev. Microbiol.* 11, 789–799. doi: 10.1038/nrmicro3109
- Proctor, M., Yeo, P., and Lack, A. (1996). *The natural history of pollination*. London: HarperCollins Publishers, 479 pp.
- Raseduzzaman, M. D., and Jensen, E. S. (2017). Does intercropping enhance yield stability in arable crop production? A meta-analysis. *Eur. J. Agron.* 91, 75–83. doi: 10.1016/j.eja.2017.09.009
- Rhodes, C. J. (2018). Pollinator decline—an ecological calamity in the making? *Sci. Prog.* 101, 121–160. doi: 10.3184/003685018X15202512854527
- Rodriguez, C., Carlsson, G., Englund, J. E., Flöhr, A., Pelzer, E., Jeuffroy, M. H., et al. (2020). Grain legume-cereal intercropping enhances the use of soil-derived and biologically fixed nitrogen in temperate agroecosystems. A meta-analysis. *Eur. J. Agron.* 118:126077. doi: 10.1016/j.eja.2020.126077
- Scherr, S. J., and McNeely, J. A. (2008). Biodiversity conservation and agricultural sustainability: Towards a new paradigm of "ecoagriculture" landscapes. *Phil. Trans. R. Soc. B.* 363, 477–494. doi: 10.1098/rstb.2007.2165
- Senbayram, M., Wenthe, C., Lingner, A., Isselstein, J., Steinmann, H., Kaya, C., et al. (2015). Legume-based mixed intercropping systems may lower agricultural born N₂O emissions. *Energy Sustain. Soc.* 6, 1–9. doi: 10.1186/s13705-015-0067-3
- Seran, T. H., and Brintha, I. (2010). Review on maize based intercropping. *J. Agron.* 9, 135–145. doi: 10.3923/ja.2010.135.145
- Smith, P., House, J. I., Bustamante, M., Sobocká, J., Harper, R., Pan, G., et al. (2016). Global change pressures on soils from land use and management. *Glob. Chang. Biol.* 22, 1008–1028. doi: 10.1111/gcb.13068
- Soussana, J. F., and Lemaire, G. (2014). Coupling carbon and nitrogen cycles for environmentally sustainable intensification of grasslands and crop-livestock systems. *Agric. Ecosyst. Environ.* 190, 9–17. doi: 10.1016/j.agee.2013.10.012
- Stagnari, F., Maggio, A., Galieni, A., and Pisante, M. (2017). Multiple benefits of legumes for agriculture sustainability: an overview. *Chem. Biol. Technol. Agric.* 4, 1–13. doi: 10.1186/s40538-016-0085-1
- Tang, X., Bernard, L., Brauman, A., Daufresne, T., Deleporte, P., Desclaux, D., et al. (2014). Increase in microbial biomass and phosphorus availability in the rhizosphere of intercropped cereal and legumes under field conditions. *Soil Biol. Biochem.* 75, 86–93. doi: 10.1016/j.soilbio.2014.04.001
- Thilakarathna, M. S., McElroy, M. S., Chapagain, T., Papadopoulos, Y. A., and Raizada, M. N. (2016). Belowground nitrogen transfer from legumes to non-legumes under managed herbaceous cropping systems. A review. *Agron. Sustain. Dev.* 36. doi: 10.1007/s13593-016-0396-4
- Yao, F., Wu, Y., Liu, X., Cao, Y., Lv, Y., Wei, W., et al. (2023). Research progress and development trends of greenhouse gas emissions from cereal–legume intercropping systems. *Agronomy* 13:4. doi: 10.3390/agronomy13041085
- Yu, Y., Stomph, T. J., Makowski, D., and van Der Werf, W. (2015). Temporal niche differentiation increases the land equivalent ratio of annual intercrops: a meta-analysis. *Field Crops Res.* 184, 133–144. doi: 10.1016/j.fcr.2015.09.010
- Zhang, W., Ricketts, T. H., Kremen, C., Carney, K., and Swinton, S. M. (2007). Ecosystem services and dis-services to agriculture. *Ecol. Econ* 64, 253–260. doi: 10.1016/j.ecolecon.2007.02.024
- Zoumore, R., Kambou, F. N., Ouattara, K., and Guillobez, S. (2000). Sorghum-cowpea intercropping: an effective technique against runoff and soil erosion in the Sahel (Saria, Burkina Faso). *Arid Soil Res. Rehabil.* 14, 329–342. doi: 10.1080/08903060050136441



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Residual effect of summer legumes incorporation on soil nutrient status and nutrient use efficiency of *kharif* rice

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Sustainable nutrient management in rice-based cropping systems is essential to counteract soil degradation and excessive fertilizer dependence. Legume residue incorporation has been proposed as a strategy to improve soil fertility and nutrient use efficiency (NUE), yet its effectiveness under varying fertilizer regimes remains inadequately explored. A field experiment was conducted with four main treatments, i.e., green gram (*Vigna radiata*), cowpea (*Vigna unguiculata*), dhaincha (*Sesbania aculeata*), and fallow combined with six fertilizer regimes in subplots, i.e., 100% RDF (100 kg N + 30 kg P₂O₅ + 00 K₂O kg/ha), 75% RDF (75 kg N + 22.5 kg P₂O₅ + 00 K₂O kg/ha), 50% RDF (50 kg N + 15 kg P₂O₅ + 00 K₂O kg/ha), 75% RDF + 25% N from FYM, 50% RDF + 50% N from FYM, and No-fertilizer application. This study evaluated the effects of legume residue incorporation on soil nutrient status, total nitrogen (N), phosphorus (P) and potassium (K) uptake, and NUE in *kharif* rice over 2 years and concluded that rice grown in dhaincha-incorporated plots exhibited significantly higher total NPK uptake, improved soil nutrient status, and enhanced NUE, followed by green gram and cowpea. The highest nitrogen and phosphorus recovery was observed in green gram plots under 100% RDF, while fallow plots with no fertilizer application recorded the lowest nutrient uptake and efficiency. Nitrogen use efficiency, agronomic use efficiency was found higher in dhaincha incorporated plots applied with 100% RDF. Preceding summer legumes with residue incorporation could result in nitrogen economy for succeeding *kharif*, as it responded more in 100% RDF + dhaincha incorporation but at par with dhaincha + 75% RDF + 25% N from FYM. Incorporating dhaincha residues reduced synthetic fertilizer requirements by 20–25%, demonstrating its potential to enhance soil fertility while reducing dependency on chemical inputs.

KEYWORDS

nutrient use efficiency, apparent recovery ratio, soil nutrient, nutrient uptake, rice

1 Introduction

Rice is one of the most important food crops contributing to food and nutritional security (Ladha et al., 2022). More than half of the global population cultivating rice making it the third most important crop after sugarcane and maize (Balakrishnan et al., 2024). Asia leads global rice production, accounting for 220 million tonnes (28%) of the total 780 million tonnes (FAO, 2018). The estimates for rice area, production, and productivity are 46.38 Mha, 130.29 MT, and 2.8 t/ha (Agricultural Statistics at a Glance, 2022). Improving fertilizer use efficiency is crucial for enhancing rice productivity and ensuring long-term soil health (Mahajan et al., 2017). Conventionally crops only utilize 30–40% of the nutrients they receive, and various processes like surface runoff, leaching, volatilization, denitrification, soil erosion, and soil fixation lead to the loss of the remaining nutrients. Less than 20 and 50%, respectively, are the average recovery efficiencies for P and N. Reduced organic matter increases nutrient inadequacies; a two-thirds reduction in organic matter indicates a significant reduction in nutrient availability (Stangel, 1991). An over-reliance on chemical fertilizers linked to soil salinization, poor physical and chemical properties, reduced soil microorganisms and declined productivity (Hepperly et al., 2009; Singh, 2000; Bhattacharyya et al., 2015).

To address these, integrated nutrient management system (INM) delivers a balanced nutrient supply by utilizing both organic and chemical sources supporting the sustained fertility (Walia et al., 2024). Organic fertilizers, overlooked for their slow release and limited availability (Geng et al., 2019) now recognized to improve rhizosphere microbes in rice (Ye et al., 2020) partial replacement of inorganic fertilizers (Pan et al., 2022; Puli et al., 2016), elevated micronutrient levels in the soil (Pandey and Verma, 2007). Singh and Kumar found increased production and nutrient usage efficiency in rice with organics. Pulse-based systems demonstrated superior accessible nitrogen (8–29%), phosphorus (3–35%), and sulfur (3–13%) compared to rice-wheat systems (Nath et al., 2023). Two weeks post green manuring using *Macuna pruriens*, soil-accessible nitrogen significantly increased (Maobe et al., 2011). Dhaincha (*Sesbania aculeata*) significantly accumulated readily available nutrients (NPK and Zn) in the soil (Pooniya and Shivay, 2012).

Strategies like residue incorporation can enhance soil health and nutrient use efficiency (Stagnari et al., 2017). Legumes incorporation support the physical soil environment, the restoration of organic matter (Islam et al., 2024), some varieties seem to reduce the amount of nitrate in the soil profile and increase the activity of soil microbes (Rani et al., 2022; Ghosh et al., 2007). Low C:N legumes break down and accelerate the process of N mineralization in the soil, supplying nutrients to subsequent crop (Zhou et al., 2019). By minimizing N loss, dhaincha in a rice cropping system can complement 50–100% artificial N fertilizer (Naher et al., 2019). After picking pods, the entire summer green gram/black gram plant was incorporated into the soil, resulting in the economization of rice in the rice-wheat system (40–60 kg N/ha, 30 kg P₂O₅, and 15 kg K₂O per ha). Similarly, 6–8-week-old dhaincha accumulate about 3.4 t/ha dry matter and 100–120 kg N/ha (Balaji et al., 2023). *In situ* incorporation of green manure increased agricultural output while reducing the need for chemical fertilizer applications mitigating degradation (Lou et al., 2011; Nawaz et al., 2017; Xia et al., 2018; Yang et al., 2019). Incorporating summer legumes enriches soil fertility by enhancing

nitrogen fixation, organic matter decomposition, and microbial activity, leading to improved nutrient availability and higher nutrient use efficiency in *kharif* rice while reducing reliance on synthetic fertilizers (Kaur et al., 2018; Sunil Kumar et al., 2024; Zhao T. et al., 2024). Synergistic application of inorganic fertilizers and organic manures and residue incorporation significantly increased the microbial biomass carbon (MBC), soil organic carbon and soil fertility (Guo et al., 2015; Singh et al., 2008; Baishya et al., 2015; Yadav and Meena, 2014).

To evaluate the residual effect of legumes, a formula-based computation was performed using an apparent recovery approach. Only the use of radioactive tracers or a comparable approach, not regular testing, allows for the assessment of the true recovery of the applied fertilizers. Despite being an advanced technological tool (Russel and Ginn, 2004), only properly equipped research sites can employ tracers. Thus, the so-called “apparent” recovery of nutrients supplied by fertilizers is computed for more realistic scenarios. The apparent recovery ratio is a straightforward method that assesses the apparent recovery efficiency of a nutrient by measuring the difference in nutrient uptake between plots receiving nutrients and those devoid of nutrients. The outcome is a percentage of the nutrient administered at the commencement of that particular time interval (Karklins and Antons Ruza, 2015). The ratio of nutrient uptake in the fertilized treatment is determined by dividing the nutrient absorption in a plot without nitrogen by the nutrient uptake in a plot with fertilization, represented as a percentage. The proportion of nutrients absorbed and obtained from the applied fertilizer remains unverified, so it is referred to as “apparent” recovery of fertilizer nitrogen (Rao et al., 1992). It is sometimes presumed that crops require an identical quantity of nitrogen regardless of the presence of external sources (fertilizers). Low nutrient use efficiency in Indian rice systems may be due to over-reliance on nitrogen fertilizers, poor application methods and water management and degraded soil health and organic matter, NUE can be improved by balanced fertilization and precision tools such as LCC, SSNM, advanced fertilizer technologies such as nano fertilizers and slow release fertilizers, water smart technologies and sustainable soil management such as biofertilizers, organic amendments (Govindasamy et al., 2023; Hu et al., 2023).

The study novelty presents *in situ* incorporation of summer legume residues (green gram, cowpea, dhaincha) into soil under varying fertilizer regimes with objective to assess the impact of incorporating summer legume residues on soil nutrient status and nutrient use efficiency in *kharif* rice. The hypothesis of the study was incorporating summer legume residues will significantly exhibit higher nutrient uptake and NUE compared to rice grown in legume residue incorporation compared to fallow treatments. In this context, this article aims to provide a basic analysis of the role of legume incorporation in succeeding in *kharif* rice in terms residual effect and nutrient use efficiency by traditional approaches.

2 Materials and methods

2.1 Study site description

This study was conducted from 2021 to 2022 at the College Farm of Navsari Agricultural University, Navsari (Gujarat), India. The site is located at 20.9248°N latitude and 72.9079°E longitude at an altitude of 11.98 m (Figure 1). Physiographically, the area lies in the coastal



plains of South Gujarat, characterized by nearly level to gently sloping terrain, with moderate drainage and medium to deep alluvial soils. The region is part of the sub-humid agro-ecological zone, influenced by the Arabian Sea, contributing to high humidity and seasonal monsoonal rainfall (Keniya et al., 2024). The weekly rainfall during the *kharif* season ranged from 0.0 to 248 mm and 0.0 mm to 517 mm in 2021 and 2022, respectively. In both years, the rainfall began in June and concluded in September. The mean annual rainfall and temperature during the research period was 248 mm and 24°C during 2021, 345 mm and 22°C during 2022, as depicted in Figures 2, 3, respectively. The soil taxonomy of the experimental site was classified under soil order “Inceptisols,” and soil series “Jalapor.” The initial soil physico-chemical properties were mentioned in Table 1.

2.2 Field experiment design

The experiment was carried out in two seasons (*viz.*, summer and *kharif* seasons) for 2 years, 2021 and 2022, in split-plot design with three replications. The treatment on the main plot was summer legumes (T) sown in summer season with four legumes *viz.*, T₁: Green gram (*Vigna radiata*), T₂: Cowpea (*Vigna unguiculata*), T₃: Dhaincha, and T₄: Fallow. In sub plots, there were six nutrient management practices (W) *viz.*, W₁: 100% RDF (100 kg N + 30 kg P₂O₅ + 00 K₂O kg/ha), W₂: 75% RDF (75 kg N + 22.5 kg P₂O₅ + 00 K₂O kg/ha), W₃: 50% RDF (50 kg N + 15 kg P₂O₅ + 00 K₂O kg/ha), W₄: 75% RDF + 25% N from FYM, W₅: 50% RDF + 50% N from FYM, and W₆: No-fertilizer application. The main plot treatments, *i.e.*, green gram and cowpea) were incorporated into the soil after the crop harvest, whereas dhaincha was incorporated into the soil at 50 % blooming stage aimed at optimizing nutrient cycling, decomposition rate, and nitrogen use

efficiency (NUE) for the succeeding rice crop and their respective biomass, straw yield and nutrient content were mentioned in Tables 2, 3 (amount of biomass we have incorporated and the respective nutrient we have supplied through the summer legumes). A cropping sequence involving the cultivation of summer legumes green gram (*Vigna radiata*), cowpea (*Vigna unguiculata*), and dhaincha (*Sesbania aculeata*) was grown during the summer season, followed by transplanted rice (*Oryza sativa*) in the *kharif* season, with the land left fallow during the *rabi* season. This sequence was repeated on the same field in the subsequent year. After incorporation of the residues each main plot (summer legumes) was divided into six sub-plots and in each subplot rice crop of variety GNR-3 was grown with different nutrient management practices. Farmyard manure (FYM) was applied 15 days prior to rice transplanting. Inorganic fertilizers (NPK) were administered based on treatment protocols: phosphorus was applied entirely as a basal dose, nitrogen was split across basal, tillering, and at panicle initiation stages, while potassium was applied at basal and panicle initiation. Biomass from summer legumes (green gram, cowpea, and dhaincha) was incorporated into the soil post-harvest, allowing a one-month decomposition period before rice cultivation. Treatments with 100, 75, and 50% of the recommended NPK levels were applied to evaluate whether the added residue could help make up for the reduced fertilizer in the lower NPK treatments. This approach was used to assess the potential of the residue to partially replace chemical fertilizers. Straw incorporation was employed as a strategy to enhance soil fertility by supplementing inorganic nutrient inputs. After harvesting green gram and cowpea, residual biomass was incorporated into the soil through ploughing. In the case of dhaincha, biomass was incorporated at 50% flowering, followed by irrigation to facilitate decomposition. The chemical and other composition details in the experiment is given in Tables 2–5.

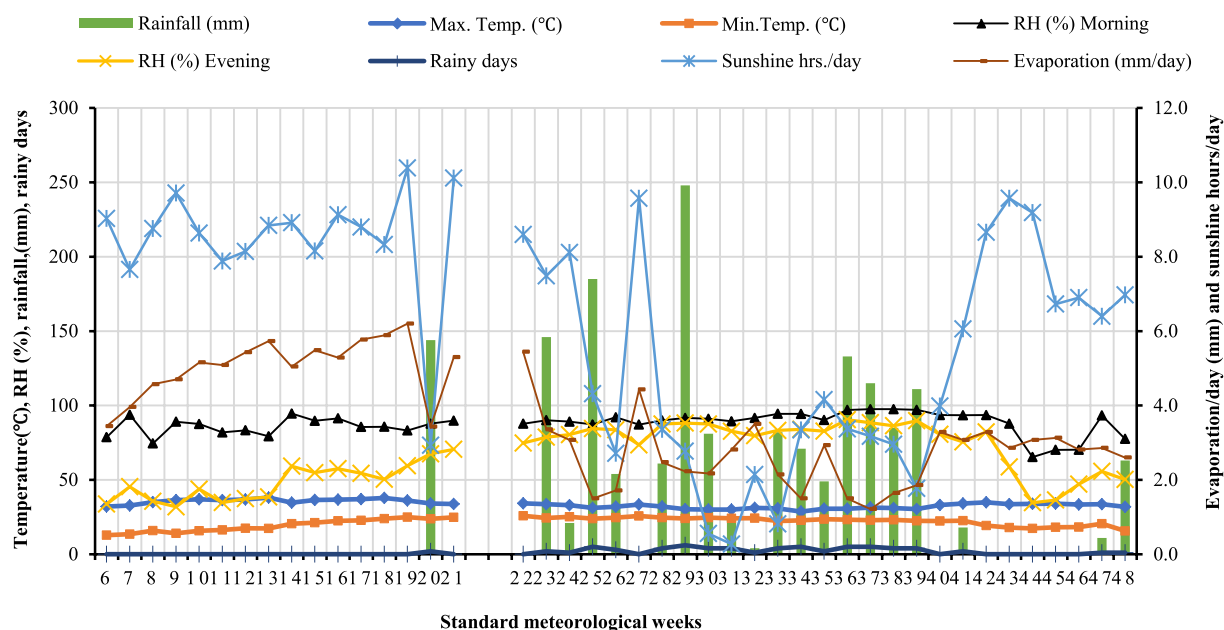


FIGURE 2
Standard week wise meteorological data during the experimental period (2021).

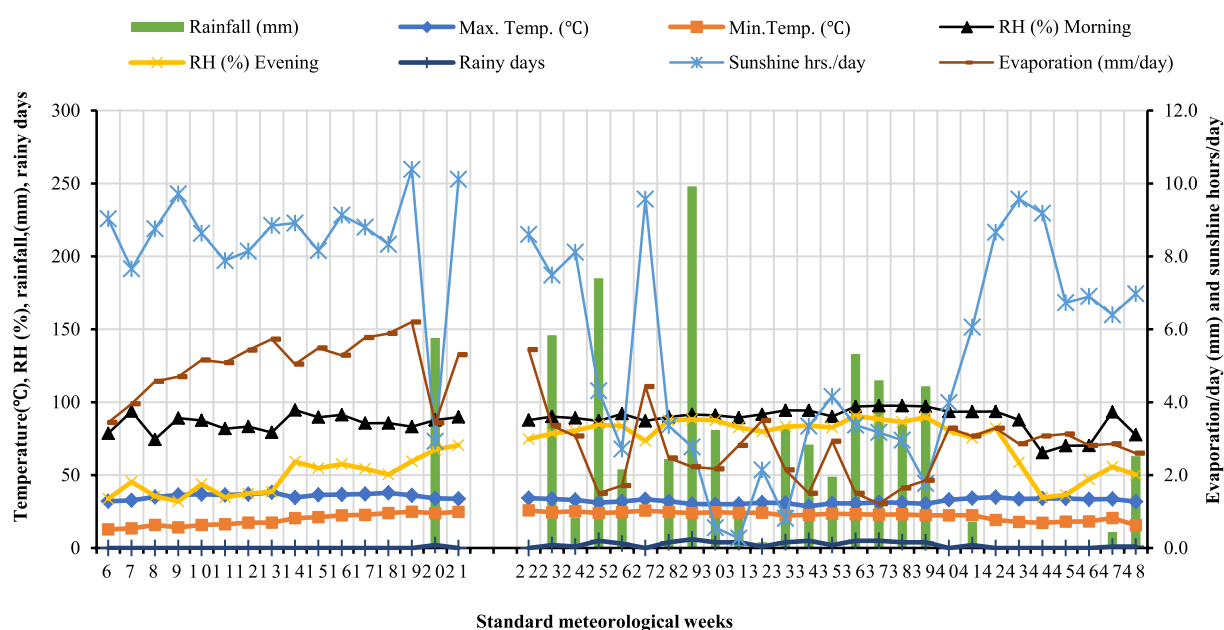


FIGURE 3
Standard week wise meteorological data during the experimental period (2022).

2.3 Methods of soil and plant analysis

Soil samples were collected at the initiation of the experiment, after the soil fertility gradient stabilizing experiment, before and after the test crop experiment, and the verification trial experiment and analyzed for pH and EC (Jackson, 1973), organic carbon (Walkley and Black, 1934), available nitrogen (Subbiah and Asija, 1956), Olsens extractable phosphorus (Bray and Kurtz, 1945), and neutral normal ammonium acetate potassium (Knudsen et al., 1982), respectively.

Nutrient content in grain and straw were obtained by total nitrogen by the modified Micro Kjeldhal method (Bremner, 1996), phosphorus by the vanadomolybdophosphoric yellow method (Morre, 1991), and potassium by the wet digestion method (Chapman and Brown, 1950), respectively. Nutrient absorption by grain and straw was calculated by multiplying grain yield (kg ha^{-1}) by nutrient concentration in the grain (%) and straw yield (kg ha^{-1}) by nutrient concentration in the straw (%), respectively. The total nutrient uptake by the crop is the sum of nutrient absorption in the grain and the straw.

2.4 N, P₂O₅, and K₂O uptake

The nutrient (NPK) uptake (kg/ha) of pods, grain and stover/ straw of summer legumes (green gram, cowpea, dhaincha) and rice was worked out by using Equation 1, according to (Sunil Kumar et al., 2024).

$$\text{Nutrient uptake (kg / ha)} = \frac{\text{Nutrient content (\%)} \times \text{Yield (kg / ha)}}{100} \quad (1)$$

2.5 Nutrient use efficiencies

The agronomic, physiological and apparent recovery efficiencies were estimated by using Equations 2–4 as stated by Congreves et al. (2021) and Sarkar et al. (2021).

$$\text{Agronomic efficiency} \left(\frac{\text{kg}}{\text{ha}} \right) = \frac{Y - Y_0}{\text{Quantity of nutrient applied} \left(\frac{\text{kg}}{\text{ha}} \right)} \times 100 \quad (2)$$

$$\text{Physiological efficiency} \left(\frac{\text{kg}}{\text{kg}} \right) = \frac{Y - Y_0}{U - U_0} \quad (3)$$

$$\text{Apparent recovery efficiency (\%)} = \frac{U - U_0}{\text{Quantity of nutrient applied (kg / ha)}} \times 100 \quad (4)$$

where, Y = Grain yield (kg/ha) with applied nutrient; Y₀ = Grain yield (kg/ha) with no applied nutrient, U = Total nutrient uptake (kg/ha) with applied nutrient; U₀ = total nutrient uptake (kg/ha) with no applied nutrient.

On the other hand, the Partial factor productivity, nutrient efficiency ratio, and nutrient addition through straw, were calculated according to Equations 5–7.

$$\text{Partial factor productivity (kg / kg)} = \frac{\text{Grain yield (kg / ha)}}{\text{Quantity of nutrient applied (kg / ha)}} \quad (5)$$

$$\text{Nutrient efficiency ratio (kg / kg)} = \frac{\text{Biological yield (kg / ha)}}{\text{Nutrient uptake (kg / ha)}} \quad (6)$$

$$\text{Nutrient addition through straw (kg / ha)} = \frac{\text{Nutrient content in straw (\%)} \times \text{straw yield (kg / ha)}}{100} \quad (7)$$

TABLE 1 Initial soil properties of experimental soil.

Particulars	Values
pH (1:2.5 soil: water ratio)	7.70
EC (1:2.5 soil: water ratio) at 25 °C (dS/m)	0.29
Organic carbon (%)	0.72
Available N (kg/ha)	247.70
Available P ₂ O ₅ (kg/ha)	47.82
Available K ₂ O (kg/ha)	377.12

TABLE 2 Fresh biomass, of different summer legumes just before incorporation.

Treatments	Fresh biomass (t/ha)				Straw yield (kg/ha)			
	2021	SD	2022	SD	2021	SD	2022	SD
T ₁ : Green gram	7.23	0.27	7.56	0.17	2,359	168	2,589	186
T ₂ : Cowpea	9.29	0.33	9.71	0.21	2,565	94	2,658	61
T ₃ : Dhaincha	20.32	1.61	21.58	1.09	5,190	317	5,596	509
*T ₄ : Fallow	–	–	–	–	–	–	–	–

TABLE 3 Nutrient content of different summer legumes.

Treatments	Nutrient content in straw (%)								
	Nitrogen			Phosphorus			Potassium		
T ₁ : Green gram	0.98	1.12	1.05	0.193	0.201	0.197	1.15	1.14	1.14
T ₂ : Cowpea	1.01	1.13	1.07	0.190	0.211	0.200	1.12	1.18	1.15
T ₃ : Dhaincha	1.51	1.57	1.54	0.350	0.360	0.360	1.23	1.32	1.27
*T ₄ : Fallow	–	–	–	–	–	–	–	–	–

2.6 Residual effect of summer legumes

The residual effect of summer legumes was approximately calculated based on yield and total uptake data obtained in the field experiments. Apparent recovery ratio was used as a tool to calculate nitrogen and phosphorus accumulation (residual effect). The proportion of nitrogen/phosphorus absorbed and derived from the applied nitrogen/phosphorus cannot be verified; thus, it is referred to as “apparent” nutrient recovery. The residual effect and absolute residual effect were calculated using Equations 8, 9.

TABLE 4 Chemical composition of FYM (dry weight basis).

Sr. no.	Organics	Year	Nutrient content (%)		
			N	P ₂ O ₅	K ₂ O
1	FYM	2021	0.43	0.32	0.41
		2022	0.46	0.36	0.47

$$\text{Residual effect, } R = A - B \quad (8)$$

$$\text{Absolute residual effect, } Ra = A - C \quad (9)$$

where, A = Yield from residue incorporated plot with fertilizer, B = Yield from residue free plot with fertilizer, and C = Yield in residue free plot without fertilizer.

2.7 Statistical analysis and interpretation of data

The statistical procedures outlined by Panse and Sukhatme (1967) were employed to analyze the data on a variety of variables. The 'F' test was implemented to compare the treatment effects on all the characters under investigation. The mean values of the summer legumes were presented, and the subsequent *kharif* rice was analyzed using a Split Plot Design. In the event that the 'F' test revealed significant differences among the interventions, the Critical Difference (CD) at 5% was calculated. Otherwise, the standard error of the mean was computed. Pooled analysis of the summer legumes and succeeding *kharif* rice analysed for two years was worked out as per the method described by Cochran and Cox (1957). Bertlett's test was applied to examine the homogeneity of variance due to error.

2.8 Pooled analysis

The fundamental method of variance analysis may not be suitable for two distinct seasonal conditions, as the error variances between seasons and the treatment \times season interaction could be substantial. Consequently, the method outlined by Cochran and Cox (1957) was employed to conduct an aggregated analysis of the summer legumes and subsequent *kharif* rice over a two-year period. The homogeneity of variance attributable to error was evaluated using Bartlett's test. The presence or absence of a season \times treatment interaction was determined by comparing the variance resulting from the season \times treatment components to the pooled estimate of error variance.

3 Results

3.1 Available soil nutrient status

3.1.1 Organic carbon

Organic carbon status (Table 6) was found highly significant in dhaincha incorporated plots (0.76%), showing a 5.56% increase compared to the fallow treatment (T4, 0.72%). Whereas, cowpea incorporated plots (T2, 0.75%) exhibited a 4.17% increase over fallow,

and were statistically at par with green gram incorporated plots (T3, 0.74%), which showed a 2.78% increase compared to fallow plots. The highest organic carbon content (0.77%) was recorded with application of 50% RDF + 50% N through FYM and 75% RDF + 25% N from FYM, both of which were at par with each other and showed an increase of 10% over unfertilized plots (0.70%). However, the response remained consistent across interactions and years, indicating that the organic carbon status has remained stable.

3.1.2 Available nitrogen

Dhaincha incorporated plots have significantly higher available nitrogen status with 8.96% increase over cowpea incorporated plots and 20.66% increase over fallow, whereas significantly higher available nitrogen was recorded with application of 50% RDF + 50% N through FYM, with 4.95% increase over W4 and 39.44% increase over W6. A two-year study (Table 6) revealed that significantly higher available nitrogen was noted with incorporation of dhaincha (292 kg ha⁻¹). Whereas significantly highest available nitrogen (297 kg ha⁻¹) with application of 50% RDF + 50% N through FYM. The year \times treatment interactions was non-significant, indicating summer legume incorporation and nutrient management practices were consistent across years.

3.1.3 Available phosphorus

A pooled study (Table 6) for 2 years revealed that, highest soil available phosphorus was recorded in dhaincha incorporated plots (58.07 kg/ha) with 28.96 percent increase over fallow. Application of 50% RDF + 50% N through FYM (55.36 kg ha⁻¹) has showed significantly higher soil available phosphorus with 3.73 percent increase over W4 and 15.77% increase over W6. The non-significant interaction between summer legume incorporation and nutrient management practices along with year, suggested a stable phosphorus.

3.1.4 Available potassium

Significantly highly available potassium (Table 6) was noted with incorporation of dhaincha (391 kg ha⁻¹) with 7.71% over T2 and 19.94% over fallow. Whereas significantly highest available potassium (396 kg ha⁻¹) was recorded with application of 50% RDF + 50% N through FYM with 6.74% over W4 and 22.22% over W6. The preceding incorporation of dhaincha has a significant effect on available K₂O content of soil (kg/ha) after the harvest of rice with maximum available K₂O content of soil as 391 kg/ha. Application of 50% RDF + 50% N through FYM has shown significantly higher potassium. Non-significant with year, suggested a stable potassium.

3.2 Total uptake of nutrients

From the pooled analysis, significantly higher total nitrogen uptake was noticed in rice grown in dhaincha incorporated plots (T₃, 80.88 kg ha⁻¹) with 37.43% increase over fallow. Whereas, the application of 100% RDF (W₁) exhibited significantly higher nitrogen uptake (97.09 kg ha⁻¹) with 121.73 percent increase over W6. The interaction effect was found to be significantly with highest total nitrogen uptake recorded in dhaincha incorporated plots along with application (109.29 kg/ha) with over a 113.39 percent increase over absolute control, which it remained consistent for 2 years (Table 7).

TABLE 5 Nutrient status prior to the sowing of *kharif* rice and immediately following the harvest of summer legumes (at the time of incorporation).

Treatment	Nutrient status (kg/ha)											
	OC (%)			Nitrogen			Phosphorus (P ₂ O ₅)			Potassium (K ₂ O)		
	2021	2022	Mean	2021	2022	Mean	2021	2022	Mean	2021	2022	Mean
T ₁	0.72	0.74	0.73	245	249	247	47	50	48.5	348	364	356
T ₂	0.72	0.75	0.73	254	257	256	47	51	49.0	349	371	360
T ₃	0.74	0.77	0.75	262	271	267	53	57	55.0	347	387	367
*T ₄	0.71	0.70	0.70	243	242	243	45	48	46.5	371	376	373
Initial	0.72			248			48			377		

T₁: Green gram; T₂: Cowpea; T₃: Dhaincha (GM); T₄: Fallow.TABLE 6 Nutrient status of the soil after harvest of *kharif* rice as influenced by different treatments.

Treatments	Nutrient status (kg/ha) (pooled)			
	OC (%)	Nitrogen	Phosphorus (P ₂ O ₅)	Potassium (K ₂ O)
Main plots (summer legumes)				
T ₁ : Green gram	0.74	265	52.36	353
T ₂ : Cowpea	0.75	268	53.41	363
T ₃ : Dhaincha (GM)	0.76	292	58.07	391
T ₄ : Fallow	0.72	242	45.04	326
SEm±	0.01	4.58	1.14	5.74
CD ($p \leq 0.05$)	0.02	14	3.46	18
CV (%)	5.70	10.07	12.89	9.60
Sub plots (<i>kharif</i> rice)				
W ₁ : 100% RDF	0.76	276	52.94	361
W ₂ : 75% RDF	0.73	270	52.67	352
W ₃ : 50% RDF	0.72	262	51.02	347
W ₄ : 75% RDF + 25% N from FYM	0.77	283	53.37	371
W ₅ : 50% RDF + 50% N from FYM	0.77	297	55.36	396
W ₆ : No fertilizer application	0.70	213	47.82	324
SEm±	0.01	4.43	1.01	5.73
CD ($p \leq 0.05$)	0.02	13	2.84	16
Interaction (T × W)				
SEm±	0.02	12.52	2.85	18.04
CD ($p \leq 0.05$)	NS	NS	NS	NS
Significant interactions with Y	NS	NS	NS	NS
CV (%)	3.90	8.12	9.46	7.83

RDF: 100–30–00 NPK kg/ha; GM: Green manure.

Rice sown after incorporation of dhaincha recorded significantly higher total phosphorus uptake (16.01 kg ha⁻¹) with 44.08 increases over fallow treatment. Application of 100% RDF has shown significantly higher total phosphorus uptake (21.12 kg/ha) with 233.65 percent over W₆. Interaction effect i.e., dhaincha incorporation along with 100%RDF as 24.03 kg ha⁻¹, and the interaction effect with year was found to be non-significant (Table 8).

Pooled analysis results revealed that incorporation of dhaincha recorded significantly higher potassium uptake (100.04 kg ha⁻¹) with 39.06 percent increase over fallow. Among the nutrient levels applied to rice crops, significantly the highest total potassium uptake by rice

(111.61 kg/ha) was found with 100% RDF with 95.72 percent increase over control. Interaction effect of dhaincha incorporation along with 100%RDF was found significant (129.38 kg ha⁻¹) with 166.01 percent increase over absolute control, but interaction with year was consistent over 2 years (Table 9).

3.3 Agronomic use efficiency

Pooled analysis revealed that significantly highest agronomic use efficiency (kg grain/kg N applied through fertilizer + FYM) of rice

TABLE 7 Total uptake of nitrogen in *kharif* rice influenced by treatments during pooled study.

Treatments	Total uptake of nitrogen (kg/ha)						
	W ₁	W ₂	W ₃	W ₄	W ₅	W ₆	Mean
T ₁	100.43	68.44	53.98	91.19	74.22	44.08	72.06
T ₂	96.43	64.26	52.77	88.36	73.76	43.34	69.82
T ₃	109.29	77.29	61.74	99.33	86.43	51.22	80.88
T ₄	82.20	51.69	45.87	72.53	64.22	36.55	58.84
Mean	97.09	65.42	53.59	87.85	74.66	43.80	70.40
SEm±	1.346						
CD ($p \leq 0.05$)	3.787						
CV	4.68						

crop was noted with dhaincha incorporation. In sub plots, the agronomic use efficiency of rice crops was significantly highest in 100%RDF. The interaction effect was found to be non-significant with highest obtained in treatment dhaincha + 100% RDF, which was found to be efficient in using nitrogen with agronomic use efficiency of 25.20 kg grain/kg N applied as depicted in Figure 4 and it remained consistent throughout 2 years. Nutrient applied through fertilizer and FYM was mentioned in Table 10.

3.4 Nitrogen use efficiency (fertilizer + FYM + residue)

The nitrogen use efficiency of rice in the study was expressed in terms of grain yield, i.e., (kg grain/kg N applied through fertilizer + FYM + residue) presented in Table 11. Among the different summer legumes, the highest nitrogen use efficiency (11.68 kg grain⁻¹ kg⁻¹ N applied through fertilizer + FYM + residue) of rice crop was registered with green gram incorporation and it is statistically at par with cowpea, dhaincha and summer fallow.

Nitrogen use efficiency of rice crops was significantly highest (16.41 kg grain/kg N applied through fertilizer + FYM + residue) in the treatment that received 100% RDF (W₁) and percent increase over W₆ was 269.59 percent. However, during the experimentation, the treatment of 75% RDF + 25% N from FYM (W₄) was at par with 50% RDF + 50% N from FYM (W₅) in the pooled study.

3.5 Nitrogen and phosphorus apparent recovery ratio (ARR)

Rice grown in green gram-incorporated plots recorded significantly higher ARR-N (Figure 5) as depicted in 4,688 kg/ha 34.60%, Whereas ARR-P was not significant, but higher ARR-P was found with incorporation of green gram. Significantly higher ARR-N (%) in rice was noticed in 100% RDF (45.72%, pooled basis) as denoted in Figure 5. The treatment 100% RDF (W₁) recorded a 42.67% apparent recovery ratio of phosphorus during pooled studies (Figure 6). From the pooled analysis, it can be revealed that the interaction effect of summer legume incorporation along with nutrient application was found to be non-significant for ARR-N and noted as significant for ARR-P, respectively.

TABLE 8 Total uptake of phosphorous in *kharif* rice influenced by treatments during pooled study.

Treatments	Total uptake of phosphorous (kg/ha)						
	W ₁	W ₂	W ₃	W ₄	W ₅	W ₆	Mean
T ₁	21.99	12.94	8.21	19.12	15.32	6.27	13.98
T ₂	20.86	11.62	7.93	18.34	14.83	6.05	13.27
T ₃	24.03	15.15	10.00	21.24	17.84	7.81	16.01
T ₄	17.58	9.49	6.19	15.81	12.39	5.18	11.11
Mean	21.12	12.30	8.08	18.63	15.10	6.33	13.59
SEm±	0.232						
CD ($p \leq 0.05$)	0.654						
CV	4.19						

3.6 Physiological efficiency

Summer legume-incorporated plots have no significant influence on physiological efficiency of rice (Figure 7). However, higher physiological efficiency was found in rice grown in dhaincha plots (34.83 kg kg⁻¹). Higher physiological efficiency was found with the application of 50% RDF (W₃, 38.24 kg kg⁻¹), but it was statistically at par with W₂, W₅, W₄, and W₆, which remained consistent for 2 years.

4 Discussion

4.1 Soil available nutrient status

Significant variations in post-harvest soil N, P₂O₅, and K₂O levels were observed following summer legume incorporation and nutrient applications in *kharif* rice. Dhaincha, with its high nutrient content and rapid growth, outperformed other legumes, contributing significantly where N, P₂O₅, and K₂O become more available, underlining the critical role of legume incorporation in enhancing soil health, fertility, and overall ecosystem sustainability (Zhao N. et al., 2024). The plots that received 50% RDF + 50% N from FYM or 75% RDF + 25% N from FYM maintained soil fertility as effectively as 100% NPK treatments over 2 years and pooled data. The increase in soil nitrogen was linked to legume nitrogen fixation, residue incorporation, and fertilizer use.

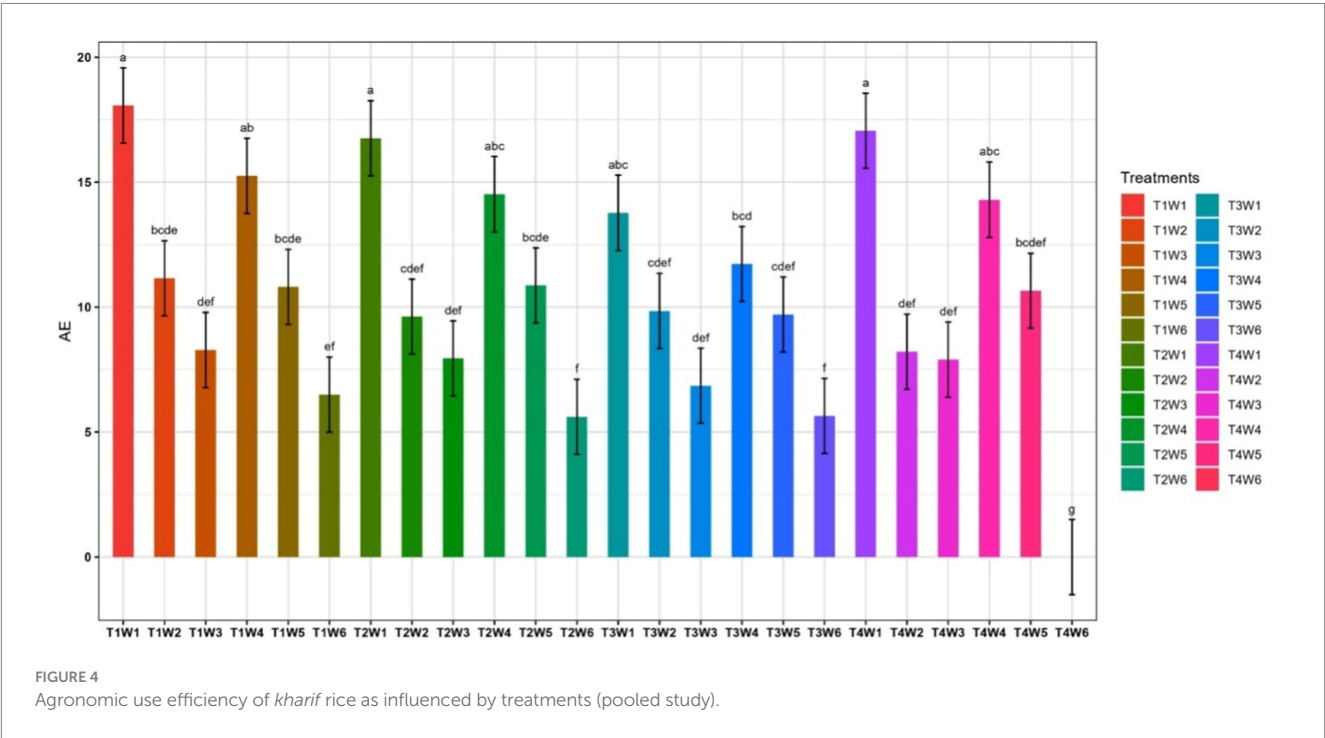
TABLE 9 Total uptake of potassium in *kharif* rice influenced by treatments during pooled study.

Treatments	Total uptake of potassium (kg/ha)						
	W ₁	W ₂	W ₃	W ₄	W ₅	W ₆	Mean
T ₁	116.94	84.04	70.78	105.68	90.90	57.01	87.56
T ₂	105.66	78.12	68.27	100.47	88.75	54.97	82.71
T ₃	129.38	99.28	81.48	116.38	106.28	67.47	100.04
T ₄	94.44	65.71	59.90	85.94	76.99	48.66	71.94
Mean	111.61	81.79	70.11	102.12	90.73	57.03	85.56
SEm±	2.12						
CD (<i>p</i> ≤ 0.05)	5.94						
CV	6.74						

TABLE 10 Nitrogen and phosphorus contribute through different sources.

Treatments	From crop residue (kg/ha)				Mineral fertilization (kg/ha)			
	N		P		Fertilizer + FYM			
	2021	2022	2021	2022	Sub plots	N	P 2021	P 2022
Green gram	23.11	29.01	4.56	5.26	W ₁ : 100% RDF	100	30	30
Cowpea	25.82	30.03	4.87	8.15	W ₂ : 75% RDF	75	22.5	22.5
Dhaincha	78.55	87.68	18.51	20.33	W ₃ : 50% RDF	50	15	15
Fallow	0	0	0	0	W ₄ : 75% RDF + 25% N from FYM	100	41.10	41.98
Nutrient from residue is calculated by nutrient content in straw multiplied with straw yield and divided by 100.					W ₅ : 50% RDF + 50% N from FYM	100	52.18	54.10
					W ₆ : No fertilizer application	0	0	0

FYM nutrient content (NPK) is presented in Table 4.



Phosphorus and potassium levels improved due to the breakdown of crop residues and organic matter, aided by inorganic fertilizers. The integration of FYM and inorganic fertilizers and green manure likely created favorable conditions for nutrient mineralization for increased accessible nitrogen and organic carbon enhancement (Sharma and Ghosh, 2000). Applying NPK along with organic manures (vermicompost, FYM, or green manure) significantly raised available phosphorus compared to NPK fertilizers alone, potentially due to the

TABLE 11 Nitrogen uses efficiency of *kharif* rice.

Treatments	Nitrogen use efficiency (kg grain/kg N applied)
	Pooled
Main plots (summer legumes)	
T ₁ : Green gram	11.68
T ₂ : Cowpea	10.89
T ₃ : Dhaincha (GM)	9.59
T ₄ : Fallow	9.69
SEm±	0.55
CD ($p \leq 0.05$)	NS
CV (%)	16.3
Sub plots (<i>kharif</i> rice)	
W ₁ : 100% RDF	16.41
W ₂ : 75% RDF	9.71
W ₃ : 50% RDF	7.74
W ₄ : 75% RDF + 25% N from FYM	13.95
W ₅ : 50% RDF + 50% N from FYM	10.51
W ₆ : No fertilizer application (control)	4.44
SEm±	0.51
CD ($p \leq 0.05$)	1.43
Interaction (T × W)	
SEm±	1.46
CD ($p \leq 0.05$)	NS
Significant interactions with Y	NS
CV (%)	14.5
	T ₄ = Control, W ₆ = Control; T ₄ W ₆ – Absolute Control

RDF: 100–30–00 NPK kg/ha; GM: Green manure.

ability of organic inputs to complex cations that contribute to phosphorus fixation (Kamla et al., 2005; Bajpai et al., 2006). Organic acids released during green manure decomposition may have further boosted phosphorus availability (Alagappan and Venkitaswamy, 2016). Additionally, green manuring improved potassium availability through the release of exchangeable K during residue decomposition (Maiti et al., 2006; Upadhyay et al., 2011).

4.2 Plant nutrient uptake

Incorporating summer legumes significantly increased N, P, and K uptake in rice, with dhaincha showing the highest uptake due to its incorporation at 50% flowering, unlike green gram and cowpea, which were incorporated post-harvest. The decomposition of green manures improved soil conditions, enhancing root growth and nutrient absorption (Talathi et al., 2009; Saraswat et al., 2010; Islam et al., 2014, 2019). Rice uptake of N, P, and K was significantly higher when inorganic fertilizers were combined with organic manures compared to when no fertilizer was used (W₆). The highest N uptake was observed with 100% RDF, followed by 75% RDF + 25% N from FYM and 50% RDF + 50% N from FYM, may be due to optimal nutrient balance and immediate nutrient availability and similar trend

observed for P and K uptake across both years and in pooled analysis. This correlation aligns with dry matter accumulation and yield per hectare across treatments and improved nutrient availability (Sunitha et al., 2010; Kumar et al., 2012, and Kumari et al., 2013).

Fertilizer contribution (Figure 8) was more in total uptake of NP, followed by others. It is because of the readily available nature of fertilizers. But in the long run, due to the decomposition of crop residues, the nutrient availability may increase after complete decomposition. Tarafdar et al. (2016) reported that FYM applied to the crop will be available by about 30% in the first year of application and the rest will be available in subsequent years. A considerable amount of N in FYM is lost during its preparation and storage, mainly as NH₃ volatilization and leaching. Hence, in this study, the treatments with FYM were efficient only after 100% RDF chemical fertilizer application.

4.2.1 Nitrogen use efficiency (fertilizer + FYM + residue)

Results stated that increased nutrients through crop residue are found to decrease the nutrient use efficiency as they are not readily available to the crop. Hence, there was non-significant behavior in summer legumes, though higher biomass was applied through dhaincha, but NUE was higher in green gram. But in fertilizer treatments, 100% RDF was found significant. Therefore, we can predict that fertilizer use efficiency is higher than residues and FYM, as it was readily available to crops. Because of this condition, more yields were found in 100% RDF (W₁) when compared to other treatments. These results align with the findings of Kouelo et al. (2013). The elevated nitrogen usage efficiency in the green gram-incorporated plot may result from green manure sequestering nitrogen in the soil during the early decomposition phase, minimizing nitrogen losses, and guaranteeing sufficient nutrient availability in the subsequent reproductive phases (Zhu et al., 2014). Furthermore, the low carbon-to-nitrogen ratio, which facilitates substantial atmospheric nitrogen fixation and enhances nitrogen availability, ultimately increases nitrogen use efficiency. As a leguminous green manure crop, it augments nitrogen supply through fixation, and the majority of green manure nitrogen residues in soils consist of organic nitrogen, which is not readily volatilized or leached (Meng et al., 2019). Comparable results were also documented by Song et al. (2022), Mangaraj et al. (2023), and Singh et al. (2024).

4.3 Agronomic use efficiency

The dhaincha crop has a higher biomass nutrient concentration when compared to other legumes whose incorporation has shown better nutrient availability, which enhanced the growth and yield of rice in treatments involving dhaincha incorporation, ultimately improving the agronomic use efficiency (Irin et al., 2019). Enhanced agronomic use efficiency due to dhaincha crop incorporation was also reported by Chen et al. (2018), Islam et al. (2019), Walia et al. (2024), and Thulasi et al. (2024).

4.4 Nitrogen and phosphorus apparent recovery ratio (ARR)

The apparent recovery ratio (%) of nitrogen varied from 17.67 to 50.69% during the pooled study. Among the summer legumes tested for incorporation, significantly higher ARR of nitrogen (50.69%) was

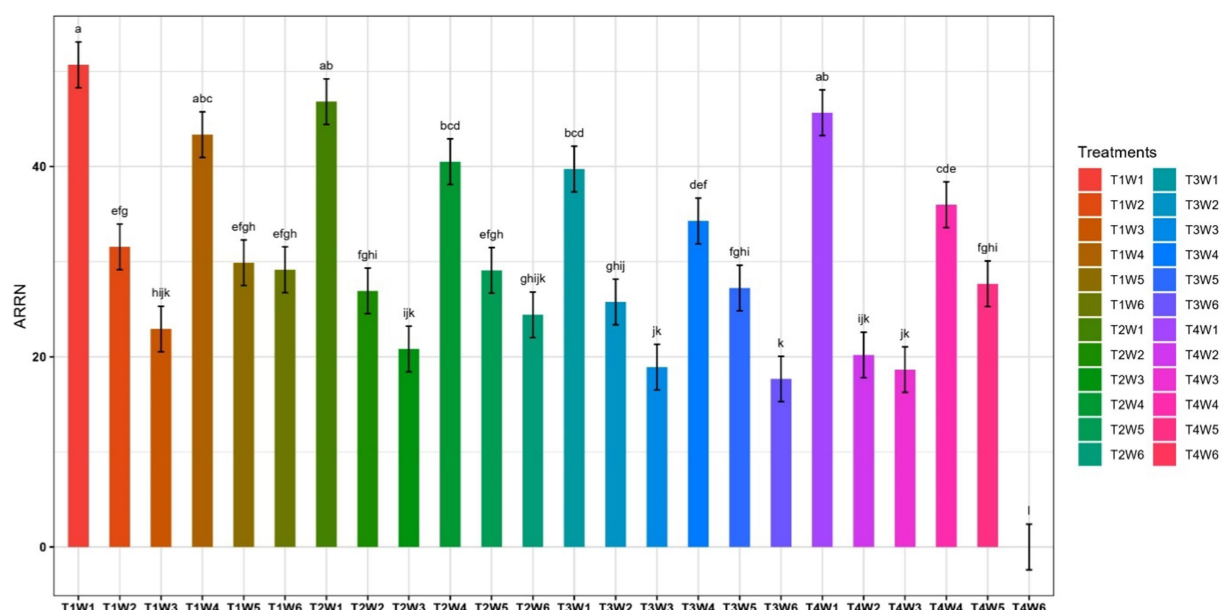


FIGURE 5
Apparent recovery ratio of nitrogen in *kharif* rice as influenced by treatments (pooled study).

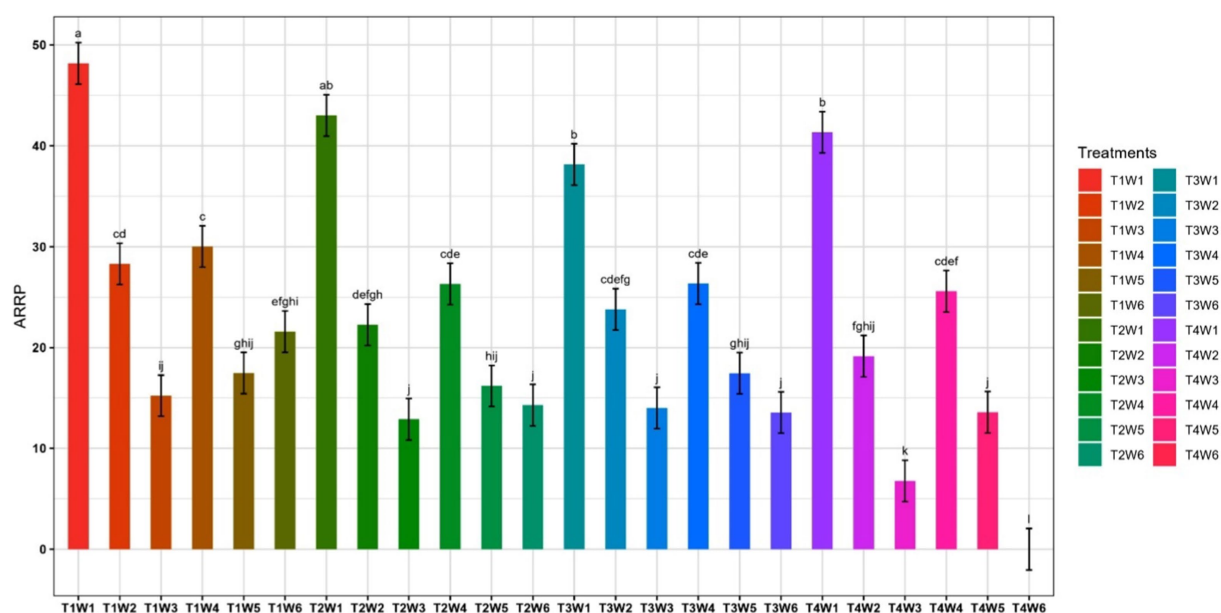


FIGURE 6
Apparent recovery ratio of phosphorous in *kharif* rice as influenced by treatments (pooled study).

found in green gram—100% RDF (T1W1) and it was followed by T2W1 (cowpea-100% RDF), and the lowest was found in T3W6 (17.67%) and T4W6 (0) in the pooled study (Figure 5). The data of ARR of phosphorus (Figure 6) showed that significantly higher ARR-P was found in the treatment when rice was grown in green gram incorporated plots with 100% application of fertilizer (T1W1) with ARR-P of 48.17% during the pooled study, and the lowest was observed in T4W3 (Fallow-50% RDF, 6.77), besides absolute control (0%, T4W6). The apparent recovery ratio of phosphorus varied from 6.77 to

48.17% in pooled. The higher ARR-N was found in green gram-incorporated plots with 100% RDF when compared to dhaincha-incorporated plots with 100% RDF. Even though dhaincha supplied a larger amount of biomass, green gram biomass decomposed and released nutrients in such a way that it correlated with the uptake requirement of the *kharif* rice crop, which might be the cause for better apparent recovery efficiency of nitrogen and phosphorus, respectively (Peoples et al., 2017). Similar findings were supported by Rani et al. (2022), Govindasamy et al. (2023), and Vaziritabar et al. (2024).

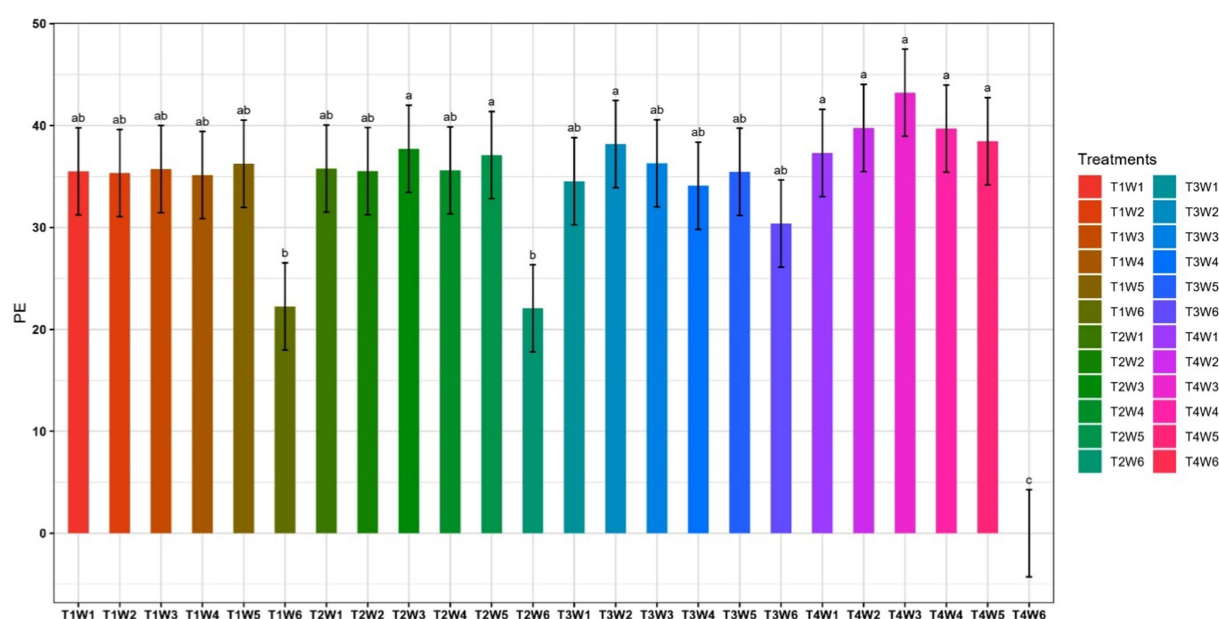


FIGURE 7
Physiological efficiency of *kharif* rice as influenced by treatments in *kharif* rice (pooled study).

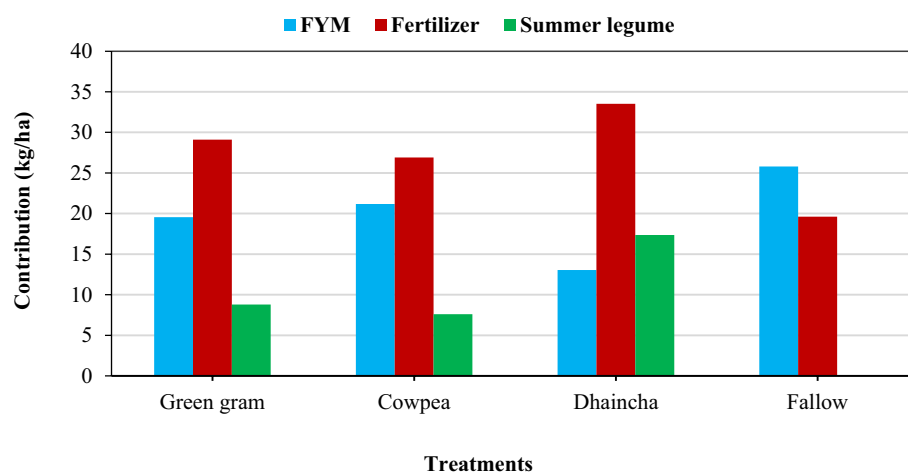


FIGURE 8
Contribution of sub plot treatments and different summer legumes toward total uptake as influenced by different treatments in *kharif* rice.

4.5 Physiological efficiency

Physiological efficiency (PE) indicates the effectiveness of nutrient accumulation and conversion from source to sink. In a pooled study, rice grown in dhaincha-incorporated plots achieved the highest PE (34.83 kg/kg), attributed to enhanced soil organic matter, nitrogen content, and microbial activity. Conversely, the lowest PE (33.08 kg/kg) was recorded in fallow plots, highlighting the role of green manuring in improving soil fertility (Figure 7). Among fertilizer treatments, the highest PE (38.24 kg/kg) was observed with 50% RDF (W3), although this was statistically comparable to other nutrient regimes (W2, W5, W4, W1). The absence of fertilizers (W6) resulted in the lowest PE

(18.68 kg/kg), underlining the necessity of nutrient supplementation for optimal rice performance. The interaction of summer legumes and nutrient doses revealed that fallow plots with fertilizers yielded higher PEN, whereas legume-incorporated plots without fertilizers showed reduced efficiency (22.25–30.38 kg/kg). This suggests that while legume incorporation enhances soil fertility through nitrogen fixation and organic matter addition, it cannot entirely replace inorganic fertilizers. Instead, integrating legumes with moderate fertilizer application is more effective for optimizing PE. Overall, treatments involving summer legumes significantly outperformed the control (W6), reinforcing the synergistic benefits of green manuring and nutrient management for improved physiological efficiency in rice.

5 Residual effect of summer legumes on *kharif* rice

Data presented in Tables 13, 14 and Figures 9, 10 reveal Rice crop grown in dhaincha-incorporated plots have a better yield ($4,688 \text{ kg ha}^{-1}$). The rice grown in fallow plots with 100% RDF has a yield of $3,873 \text{ kg ha}^{-1}$. This reveals that the extra yield of 815 kg/ha ($4,688 - 3,873 = 815 \text{ kg/ha}$) recorded in rice grown in dhaincha-incorporated plots was due to the residual effect of residue incorporation of dhaincha before rice sowing as depicted in Figures 9, 10 and Tables 12–14. Similarly, it was noticed in green gram ($4,310 - 3,873 = 571 \text{ kg/ha}$) and cowpea ($4,310 - 3,873 = 437 \text{ kg/ha}$) incorporated plots. Nearly dhaincha incorporation has provided

68 kg/ha nitrogen and 16.8 kg/ha phosphorus extra to the succeeding rice crop, whereas for green gram and cowpea it was 35.96 and 30.30 kg/ha nitrogen and 12.39 and 9.15 kg/ha phosphorus to the succeeding *kharif* rice, respectively. This causes the yield to increase in incorporation treatments when compared to fallow treatments. The data also reveals that total uptake of phosphorus and nitrogen was also recorded in dhaincha-incorporated plots fed by green gram and cowpea because of the residual effect of incorporation. Hence, dhaincha, because of its higher residual effect, rice grown in dhaincha-incorporated plots recorded higher yield, uptake of NPK, and soil nutrient status. Incorporation of dhaincha with 75% RDF to rice yielded almost the same as of 100% RDF + fallow [$(3,873 \times 75)/100 = 2,904 \text{ kg ha}^{-1}$]. In a similar way, dhaincha without

TABLE 12 Nutrient applied to *kharif* rice (pooled).

Treatment	Effect	Yield (kg/ha)	Nitrogen applied (kg/ha)	Phosphorus applied (kg/ha)
Dhaincha + 100% RDF	Main effect	3,873	100	30
	Residual effect	815	68	16.8
	Cumulative effect	4,688	168	46.8
Green gram + 100% RDF	Main effect	3,873	100	30
	Residual effect	571	35.96	12.39
	Cumulative effect	4,444	135.96	42.39
Cowpea + 100% RDF	Main effect	3,873	100	30
	Residual effect	437	30.30	9.15
	Cumulative effect	4,310	130.30	39.15
Fallow + 100% RDF	Main effect	3,873	82.17	17.58
	Residual effect	–	–	–
	Cumulative effect	3,873	82.17	17.58

TABLE 13 Residual effect of summer legumes on yield of *kharif* rice as influenced by treatments (pooled basis).

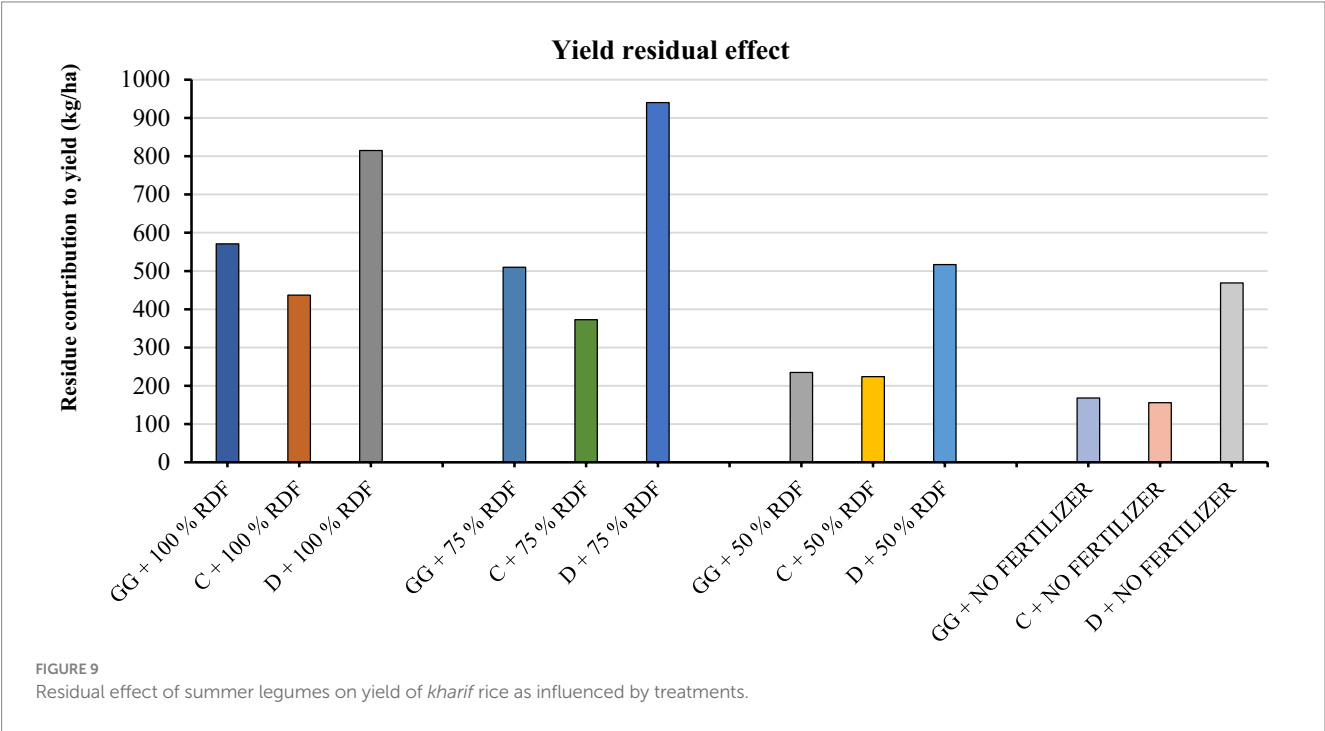
Treatments	Main effect (Yield)	Soil (A)	Fertilizer + summer legume effect	Summer legume residual effect (C)	Cumulative effect (D) = A + B + C
F + 100% RDF	3,873	2,167	1,706 (B)	100% chemical	3,873
GG + 100% RDF	4,444	2,167	2,277	571	4,444
C + 100% RDF	4,310	2,167	2,143	437	4,310
D + 100% RDF	4,688	2,167	2,521	815	4,688
F + 75% RDF	2,784	2,167	617 (B)	75% chemical	2,784
GG + 75% RDF	3,294	2,167	1,127	510	3,294
C + 75% RDF	3,157	2,167	990	373	3,157
D + 75% RDF	3,724	2,167	1,557	940	3,724
F + 50% RDF	2,562	2,167	395 (B)	50% chemical	2,562
GG + 50% RDF	2,797	2,167	630	235	2,797
C + 50% RDF	2,786	2,167	619	224	2,786
D + 50% RDF	3,079	2,167	912	517	3,079
GG + NO FERTILIZER	2,335	2,167	–	168	2,335
C + NO FERTILIZER	2,323	2,167	–	156	2,323
D + NO FERTILIZER	2,636	2,167	–	469	2,636
F + NO FERTILIZER (ONLY SOIL EFFECT)	2,167	2,167	–	–	2,167

GG = Green gram; C = Cowpea; D = Dhaincha; F = Fallow. Bold value indicates fallow and no fertilizer.

TABLE 14 Residual effect of summer legumes on yield of *kharif* rice as influenced by treatments (pooled).

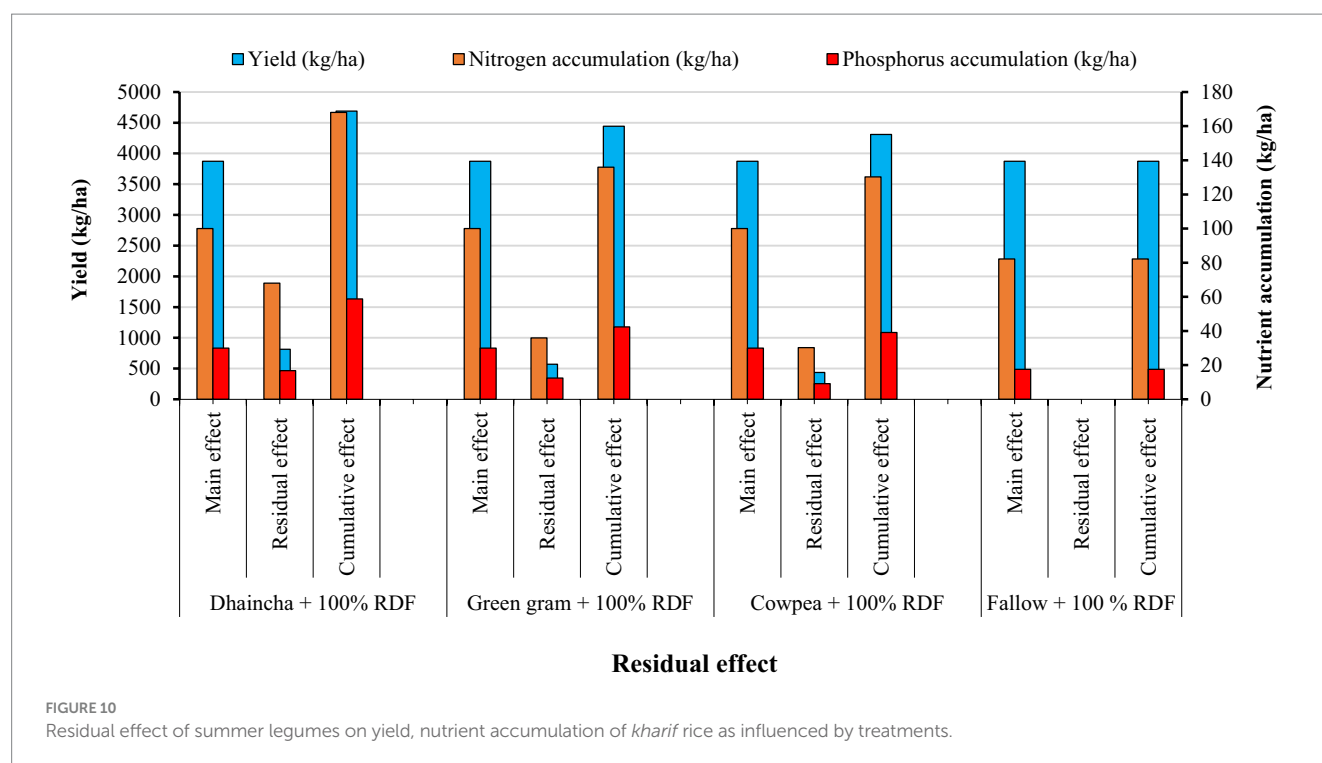
Treatments	Main effect (Yield)	Soil (A)	Fertilizer + summer legume effect	Summer legume Residual effect (C)	Cumulative effect (D) = A + B + C
F + 100% RDF	3,873	2,167	1,706 (B)	100% chemical	3,873
GG + 100% RDF	4,444	2,167	2,277	571	4,444
C + 100% RDF	4,310	2,167	2,143	437	4,310
D + 100% RDF	4,688	2,167	2,521	815	4,688
F + 75% RDF	2,784	2,167	617 (B)	75% chemical	2,784
GG + 75% RDF	3,294	2,167	1,127	510	3,294
C + 75% RDF	3,157	2,167	990	373	3,157
D + 75% RDF	3,724	2,167	1,557	940	3,724
F + 50% RDF	2,562	2,167	395 (B)	50% chemical	2,562
GG + 50% RDF	2,797	2,167	630	235	2,797
C + 50% RDF	2,786	2,167	619	224	2,786
D + 50% RDF	3,079	2,167	912	517	3,079
GG + NO FERTILIZER	2,335	2,167	–	168	2,335
C + NO FERTILIZER	2,323	2,167	–	156	2,323
D + NO FERTILIZER	2,636	2,167	–	469	2,636
F + NO FERTILIZER (ONLY SOIL EFFECT)	2,167	2,167	–	–	2,167

GG = Green gram; C = Cowpea; D = Dhaincha; F = Fallow.



fertilizer had given a yield of 2,636 kg/ha, and fallow + 100% RDF resulted in a yield of 3,873 kg ha⁻¹, whereas dhaincha + 75% RDF yielded 3,724 kg ha⁻¹, which was almost similar to the yield of 100% RDF. Hence, we can understand that dhaincha incorporation added nutrients and compensated for the chemical fertilizer, resulting in saving 20–25% of nitrogen and phosphorus (approximately).

Incorporation of legume residues releases beneficial nitrogen for the subsequent crop through decomposition and mineralization while minimizing negative environmental impacts, thereby showing residual effect on the subsequent crop (Muschietti-Piana et al., 2020; Regassa et al., 2023). Incorporation of summer legumes might have deposited residues of nitrogen for steady release to the standing crop,



which enhanced the economic as well as biological yield (Ammaji and Rao, 2020). Residual effects of summer legumes were also reported by Pathak et al. (2018) and Bharadwaj et al. (2023).

6 Conclusion, recommendations and future study

Incorporation of summer legumes had no impact on organic carbon (%). Enhanced available N, P_2O_5 and K_2O content of the soil after harvesting of the crop as compare to initial soil values. However, more increase in available N, P_2O_5 and K_2O content was recorded under dhaincha incorporated plot. Nitrogen use efficiency, agronomic use efficiency was found higher in dhaincha incorporated plots applied with 100% RDF. Total uptake of NPK in rice plants was higher in dhaincha-100% RDF. Preceding summer legumes with residue incorporation could result in nitrogen economy for succeeding *kharif*, as it responded more in 100% RDF + dhaincha incorporation but at par with dhaincha + 75% RDF + 25% N from FYM. Exact quantification of nitrogen economy was not studied but the increment in yield and total nutrient uptake by rice when incorporated with dhaincha residues compared to fallow treatments gives an idea of residual effect of summer legumes and it may save an amount of 20–25% fertilizer approximately.

From this study, Dhaincha (*Sesbania aculeata*) incorporation in conjunction with 100% recommended dose of fertilizers (RDF) or 75% RDF + 25% N from FYM can be suggested to farmers to reduce synthetic fertilizer usage and achieving economic benefits.

Future study: To draw more robust and comprehensive conclusions, future research should focus on long-term studies that incorporate detailed carbon profiling, nutrient recycling, microbial assessments, and climate resilience to evaluate the broader ecological impacts. Additionally,

precise quantification of nitrogen savings and an analysis of the economic implications would provide actionable insights for farmers.

Data availability statement

The original contributions presented in the study are included in the article/supplementary material, further inquiries can be directed to the corresponding authors.

Author contributions

TS: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Resources, Software, Validation, Writing – original draft, Writing – review & editing. HV: Conceptualization, Methodology, Project administration, Supervision, Validation, Writing – review & editing. KP: Conceptualization, Methodology, Writing – review & editing. MC: Formal analysis, Writing – original draft. MS: Data curation, Writing – review & editing. SM: Formal analysis, Funding acquisition, Writing – review & editing. AE: Writing – review & editing. AS: Formal analysis, Funding acquisition, Writing – review & editing. AEE: Data curation, Writing – review & editing. DE-S: Data curation, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

References

- Agricultural Statistics at a Glance (2022). Economics & Statistics division, Department of Agriculture & farmers welfare. Government of India: Ministry of Agriculture & Farmers Welfare.
- Alagappan, S., and Venkataswamy, R. (2016). Performance of different sources of organic manures in comparison with RDF and INM on nutrient uptake, nutrient balance, and soil properties in rice-green gram cropping sequence. *Int. J. Agril. Sci.* 12, 326–334. doi: 10.15740/HAS/IJAS/12.2/326-334
- Ammaji, P., and Rao, P. C. (2020). Effect of kharif legume crop residue incorporation in combination with nitrogen levels on growth and yield of succeeding maize during Rabi. *Andhra Agric. J.* 67, 7–11.
- Baishya, L. K., Rathore, S. S., Singh, D., Sarkar, D., and Deka, B. C. (2015). Effect of integrated nutrient management on rice productivity, profitability and soil fertility. *Ann. Plant Soil Res.* 17, 86–90.
- Bajpai, R. K., Chitale, S., Upadhyay, S. K., and Urkurkar, J. S. (2006). Long-term studies on soil physico-chemical properties and productivity of rice-wheat system as influenced by integrated nutrient management in Inceptisol of Chhattisgarh. *J. Indian Soc. Soil Sci.* 54, 24–29.
- Balaji, A., Nilima, K., Kamlesh, P., Nitin, G., Ritesh, P., Ajay, N., et al. (2023). Study on dhaincha (*Sesbania bispinosa*) genotypes for N fixing capability and rate of mineralization under field and laboratory condition. *Org. Agr.* 13, 119–132. doi: 10.1007/s13165-022-00420-3
- Balakrishnan, D., Bateman, N., and Kariyat, R. R. (2024). Rice physical defenses and their role against insect herbivores. *Planta* 259:110. doi: 10.1007/s00425-024-04381-7
- Bharadwaj, A. K., Mailk, K., Rani, M., Mandal, U. K., Basak, N., Singh, A., et al. (2023). Residue recycling options and their implications for sustainable nitrogen management in rice–wheat agroecosystems. *Ecol. Process* 12:53. doi: 10.1186/s13717-023-00464-7
- Bhattacharyya, R., Ghosh, B. N., Mishra, P. K., Mandal, B. P., Srinivasa Rao, C., Sarkar, D., et al. (2015). Soil degradation in India: challenges and potential solutions. *Sustain. For.* 7, 3528–3570. doi: 10.3390/su7043528
- Bray, R. H., and Kurtz, L. T. (1945). Determination of total organic and available forms of phosphorus in soils. *Soil Sci.* 59, 39–46. doi: 10.1097/00010694-194501000-00006
- Bremner, J. M. (1996). “Nitrogen Total” in Methods of soil analysis part 3: chemical methods, SSSA book series 5. ed. D. L. Sparks (Madison, Wisconsin: Soil Science Society of America), 1085–1122.
- Chapman, H. D., and Brown, S. M. (1950). Analysis of organics leaves for diagnosing nutrient status with reference to potassium. *Hilgardia*, 19, 501–540.
- Chen, S., Shaowen, L., Zheng, X., Yina, M., Chua, G., Xua, C., et al. (2018). Effect of various crop rotations on rice yield and nitrogen use efficiency in paddy–upland systems in southeastern China. *Crop J.* 6, 576–588. doi: 10.1016/j.cj.2018.07.007
- Cochran, W. G., and Cox, G. M. (1957). Experimental design. 2nd Edn. London: John Wiley and Sons.
- Congreves, K. A., Olivia, O., Daphnée, F., Soudeh, F., Shanay, W., and Melissa, M. A. (2021). Nitrogen use efficiency definitions of today and tomorrow. *Front. Plant Sci.* 12:637108. doi: 10.3389/fpls.2021.637108
- FAO (2018). Rice market monitor, vol. XXI. Rome, Italy: Food and Agriculture Organization.
- Geng, Y., Cao, G., Wang, L., and Wang, S. (2019). Effects of equal chemical fertilizer substitutions with organic manure on yield, dry matter, and nitrogen uptake of spring maize and soil nitrogen distribution. *PLoS One* 14:e0219512. doi: 10.1371/journal.pone.0219512
- Ghosh, P. K., Bandyopadhyay, K. K., Wanjari, R. H., Manna, M. C., Misra, A. K., Mohanty, M., et al. (2007). Legume effect for enhancing productivity and nutrient use efficiency in major cropping systems—an Indian perspective: a review. *J. Sustain. Agric.* 30, 59–86. doi: 10.1300/J064v30n01_07
- Govindasamy, P., Muthusamy, S. K., Bagavathiannan, M., Mowrer, J., Jagannadham, P. T. K., Maity, A., et al. (2023). Nitrogen use efficiency—a key to enhance crop productivity under a changing climate. *Front. Plant Sci.* 14, 1–19. doi: 10.3389/fpls.2023.1121073
- Guo, L. J., Zhang, Z. S., Wang, D. D., Li, C. F., and Cao, C. G. (2015). Effects of short-term conservation management practices on soil organic carbon fractions and microbial community composition under a rice–wheat rotation system. *Biol. Fertil. Soils* 50, 65–75.
- Hepperly, P., Lotter, D., Ulsh Christine, Z., Seidel, R., and Reider, C. (2009). Compost, manure and synthetic fertilizer influences crop yields, soil properties, nitrate leaching and crop nutrient content. *Compost Sci. Util.* 17, 117–126. doi: 10.1080/1065657X.2009.10702410
- Hu, B., Wang, W., Chen, J., Liu, Y., and Chu, C. (2023). Genetic improvement toward nitrogen use efficiency in rice: lessons and perspectives. *Mol. Plant* 16, 64–74. doi: 10.1016/j.molp.2022.11.007
- Irin, I. J., Biswas, P. K., Ullah, M. J., Roy, T. S., and Khan, M. A. (2019). Influence of green manuring crops on dry matter production and soil health improvement. *Bangladesh Agron. J.* 22, 39–45.
- Islam, M. R., Hossain, M. B., Siddique, A. B., Rahman, M. T., and Malika, M. (2014). Contribution of green manure incorporation in combination with nitrogen fertilizer in rice production. *SAARC J. Agric.* 12, 134–142. doi: 10.3329/sja.v12i2.21925
- Islam, M. A., Sarkar, D., Alam, M. R., Jahangir, M. M. R., Ali, M. A., Sarker, D., et al. (2024). Legumes in conservation agriculture: a sustainable approach in rice-based ecology of the eastern Indo-Gangetic plain of South Asia – an overview. *Technol. Agron.* 3, 1–17. doi: 10.48130/TIA-2023-0003
- Islam, M., Tahmina, A., Sohel, R., Saiful, A., and Moynul, H. M. (2019). Green manuring effects on crop morpho-physiological characters, rice yield and soil properties. *Physiol. Mol. Biol. Plants* 25, 303–312. doi: 10.1007/s12298-018-0624-2
- Jackson, M. L. (1973). Soil and chemical analysis. New Delhi: Prentice Hall of India Private Limited.
- Kamla, K., Gupta, C. S., and Paliyal, S. S. (2005). Effect of chemical fertilizers Vis-a-Vis organic manures (vermicompost, FYM) on wheat yield and soil health. *Himachal J. Agril. Res.* 31, 48–51.
- Karklins, A., and Antons Ruza, A. (2015). Nitrogen apparent recovery can be used as the indicator of soil nitrogen supply. *Zemdirbyste-Agriculture* 102, 133–140. doi: 10.13080/z-a.2015.102.017
- Kaur, R., Shivay, Y. S., Singh, G., Virk, H. K., Sen, S., and Rajni. (2018). Increasing area under pulses and soil quality enhancement in pulse-based cropping systems-retrospect and prospects. *Indian J. Agric.* 88, 10–21.
- Keniya, B. J., Zinzala, V. J., and Sisodiya, R. R. (2024). Assessment of soil physico-chemical properties in sugarcane cultivation areas of Navsari District, Gujarat, India. *Asian J. Soil Sci. Plant Nutr.* 10, 13–20. doi: 10.9734/ajsspn/2024/v10i4377
- Knudsen, D., Paterson, G. A., and Pratt, P. F. (1982). Lithium, sodium and potassium. In: A. L. Page (ed.) *Methods of Soil Analysis. Part 2*, 2nd edn. Agronomy No. 9. (Madison, WI: American Society of Agronomy), pp. 225–246.
- Kouelo, F. A., Pascal, H., and Dercon, G. (2013). Contribution of seven legumes residues incorporated into soil and NP fertilizer to maize yield, nitrogen use efficiency and harvest index in degraded soil in the center of Benin. *Int. J. Biol. Chem. Sci.* 7, 2468–2489.

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- Kumar, V., Tripathi, H. C., and Mishra, S. K. (2012). Influence of integrated nutrient management on yield, economics, and nutrient uptake of hybrid rice (*Oryza sativa* L.). *New Agriculturist* 23, 117–121.
- Kumari, N., Pal, S. K., and Barla, S. (2013). Effect of organic nutrient management on productivity and economics of scented rice. *Oryza* 50, 249–252.
- Ladha, J. K., Peoples, M. B., Reddy, P. M., Biswas, J. C., Bennett, A., Jat, M. L., et al. (2022). Biological nitrogen fixation and prospects for ecological intensification in cereal-based cropping systems. *Field Crop Res.* 283:108541. doi: 10.1016/j.fcr.2022.108541
- Lou, Y., Xu, M., Wang, W., Sun, X., and Zhao, K. (2011). Return rate of straw residue affects soil organic C sequestration by chemical fertilization. *Soil Tillage Res.* 113, 70–73. doi: 10.1016/j.still.2011.01.007
- Mahajan, G., Kumar, V., and Chauhan, B. S. (2017). "Rice production in India" in Rice production worldwide. Springer publications, 53–91.
- Maiti, S., Saha, M., Banerjee, H., and Pal, S. (2006). Integrated nutrient management under hybrid rice (*Oryza sativa*) - hybrid rice cropping sequence. *Indian J. Agron.* 51, 157–159.
- Mangaraj, S., Paikaray, R. K., Garnayak, L. M., Behera, S. D., Patra, B., Sethi, D., et al. (2023). Crop and soil productivity of a rice-green gram system under integrative nutrient management. *Agron. J.* 115, 2631–2645. doi: 10.1002/agj.2.21401
- Maobe, S. N., Akundabweni, L. S. M., Mburu, M. W. K., Ndafa, J. K., Mureithi, J. G., Gachene, C. K. K., et al. (2011). Effect of Mucuna green manure application rate on decomposition and soil available nitrogen under field conditions: I. During season of incorporation. *World J. Agric. Sci.* 7, 430–438.
- Meng, X., Li, Y., Zhang, Y., and Yao, H. (2019). Green manure application improves rice growth and urea nitrogen use efficiency assessed using ¹⁵N labeling. *Soil Sci. Plant Nutr.* 65, 511–518. doi: 10.1080/00380768.2019.1635872
- Morre, K. P. (1991). Determination of phosphorus in plant tissue by colorimetry. In: *Plant Analysis Reference Procedures for the Southern Region of the United States*, C. O. Plank (ed). Southern Cooperative Bull, 368, (Athens, GA: University of Georgia). pp. 29–32.
- Muschietti-Piana, P., McBeath, T. M., McNeill, A. M., Cipriotti, P. A., and Gupta, V. V. S. R. (2020). Combined nitrogen input from legume residues and fertilizer improves early nitrogen supply and uptake by wheat. *J. Plant Nutr. Soil Sci.* 183, 355–366. doi: 10.1002/pln.202000002
- Naher, U. A., Choudhury, T. M. A., Biswas, J. C., Qurban, A. P., and Ivan, R. K. (2019). Prospects of using leguminous green manuring crop *Sesbania rostrata* for supplementing fertilizer nitrogen in rice production and control of environmental pollution. *J. Plant Nutr.* 43, 1532–4087. doi: 10.1080/01904167.2019.1672734
- Nath, C. P., Kumar, N., Dutta, A., Hazra, K. K., Praharaj, C. S., Singh, S. S., et al. (2023). Pulse crop and organic amendments in cropping system improve soil quality in rice ecology: evidence from a long-term experiment of 16 years. *Geoderma* 430:116334. doi: 10.1016/j.geoderma.2023.116334
- Nawaz, A., Farooq, M., Lal, R., Rehman, A., Hussain, T., and Nadeem, A. (2017). Influence of sesbania brown manuring and rice residue mulch on soil health, weeds and system productivity of conservation rice-wheat systems. *Land Degrad. Dev.* 28, 1078–1090. doi: 10.1002/ldr.2578
- Pan, Y., Guo, J., Fan, L., Ji, Y., Liu, Z., Wang, F., et al. (2022). The source-sink balance during the grain filling period facilitates rice production under organic fertilizer substitution. *Eur. J. Agron.* 134:126468. doi: 10.1016/j.eja.2022.126468
- Pandey, N., and Verma, A. K. (2007). Integrated nutrient management in transplanted hybrid rice (*Oryza sativa*). *Indian J. Agron.* 52, 40–42. Anurag and Tripathi, R. S.
- Panse, V. G., and Sukhatme, P. V. (1967). Statistical methods for agricultural workers. New Delhi: Indian Council of Agricultural Research, 145–152.
- Pathak, H., Nayak, A. K., Jena, M., Singh, O. N., Samala, P., and Sharma, S. G. (2018). Rice research for enhancing productivity, profitability and climate resilience. Cuttack, Odisha, India: ICAR-National Rice Research Institute, 542.
- Peoples, M., Swan, A., Goward, L., Kirkegaard, J., Hunt, J., Li, G., et al. (2017). Soil mineral nitrogen benefits derived from legumes and comparisons of the apparent recovery of legume or fertilizer nitrogen by wheat. *Soil Res.* 55:600. doi: 10.1071/SR16330
- Pooniya, V., and Shivay, Y. S. (2012). Effect of green manuring and zinc fertilization on productivity and nutrient uptake in basmati rice (*Oryza sativa* L.)-wheat (*Triticum aestivum*) cropping system. *Indian J. Agron.* 56, 28–34. doi: 10.59797/ija.v56i1.4665
- Puli, M. R., Prasad, P. R. K., Ravindra, P. B., Jayalakshmi, M., and Burla, S. R. (2016). Effect of organic and inorganic sources of nutrients on rice crop. *Oryza* 53, 151–159.
- Rani, Y. S., Jamuna, P., Triveni, U., Patro, T. S. S. K., and Anuradha, N. (2022). Effect of in situ incorporation of legume green manure crops on nutrient bioavailability, productivity and uptake of maize. *J. Plant Nutr.* 45, 1004–1016. doi: 10.1080/01904167.2021.2005802
- Rao, A. C. S., Smith, J. L., Parr, J. F., and Papendick, R. I. (1992). Considerations in estimating nitrogen recovery efficiency by the difference and isotopic dilution methods. *Fertilizer Res.* 33, 209–217. doi: 10.1007/BF01050876
- Regassa, H., Elias, E., Tekalign, M., and Legese, G. (2023). The nitrogen fertilizer replacement values of incorporated legumes residue to wheat on vertisols of the Ethiopian highlands. *Heliyon* 9:e22119. doi: 10.1016/j.heliyon.2023.e22119
- Russel, B. J., and Ginn, J. S. (2004). Practical handbook of soil, vadose zone and ground water contamination: assessment, prevention and remediation. 2nd Edn Lewis publishers, 691.
- Saraswat, P. K., Kumar, K., Tiwari, R. C., and Singh, V. K. (2010). Influence of different summer green manures on rice-wheat yield, nutrient uptake, and soil characteristics. *J. Hill Agric.* 1, 23–29.
- Sarkar, D., Sankar, S., Siva, D. O., Sonam, S., Shikha, Manoj, P., et al. (2021). Optimizing nutrient use efficiency, productivity, energetics, and economics of red cabbage following mineral fertilization and biopriming with compatible rhizosphere microbes. *Sci. Rep.* 11:15680. doi: 10.1038/s41598-021-95092-6
- Sharma, A. R., and Ghosh, A. (2000). Effect of green manuring with *Sesbania aculeate* and nitrogen fertilization on the performance of direct-seeded flood-prone lowland rice. *Nutr. Cycle Agroecosyst.* 57, 141–153. doi: 10.1023/A:1009863100224
- Singh, R. B. (2000). Environmental consequences of agricultural development: a case study from the green revolution state of Haryana, India. *Agric. Ecosyst. Environ.* 82, 97–103. doi: 10.1016/S0167-8809(00)00219-X
- Singh, F., Ravindra, K., and Samir, P. (2008). Integrated nutrient management in rice-wheat cropping system for sustainable productivity. *J. Indian Soc. Soil Sci.* 56, 205–208.
- Singh, B., Sidhu, G. S., and Singh, V. (2024). Effect of moong bean as green manuring and residue incorporation on growth, productivity of basmati rice. *Int. J. Res. Agron.* 7, 323–326. doi: 10.33545/2618060X.2024.v7.i2e.323
- Song, S., Lin, L., Yin, Q., and Nie, L. (2022). Effect of in situ incorporation of three types of green manure on soil quality, grain yield and 2-acetyl-1-pyrrolidine content in tropical region. *Crop Environ.* 1, 189–197. doi: 10.1016/j.crope.2022.08.005
- Stagnari, F., Maggio, A., Galieni, A., and Pinate, M. (2017). Multiple benefits of legumes for agriculture sustainability. *Chem. Biol. Technol. Agric.* 4, 3–13. doi: 10.1186/s40538-016-0085-1
- Stangel, P. J. (1991). Presentation in the international workshop on evaluation for sustainable land management in the developing world, Chiangrai, Thailand. Bangkok, TH: International Board for Soil Research and Management.
- Subbiah, B. V., and Asija, G. L. (1956). A rapid procedure for the determination of available nitrogen in soil. *Curr. Sci.* 25, 259–260.
- Sunil Kumar, T., Virdia, H. M., Patel, K. G., Ragi, S., Chowdhury, M., Kumar, P., et al. (2024). Effect of summer legume residue incorporation and fertilizer regimes on rice growth, yield, and nutrient uptake. *Front. Sustain. Food Syst.* 8:1467201. doi: 10.3389/fsufs.2024.1467201
- Sunitha, B. P., Prakasha, H. C., and Gurumurthy, K. T. (2010). Effect of INM approach on soil physical properties, available nutrient status, concentration, and their uptake by rice crop in Bhadra Command, Karnataka. *Mysore J. Agric. Sci.* 44, 905–910.
- Talathi, M. S., Pinjari, S. S., Ranshur, N. J., Bhondave, T. S., and Suryawanshi, J. S. (2009). Response of hybrid rice (*Oryza sativa* L.) to green leaf manure, FYM and chemical fertilizers. *Int. J. Agric. Sci.* 5, 501–506.
- Tarafdar, J. C., Nandy, P., and Das, S. K. (2016). Effect of integrated nutrient management and foliar spray of zinc in nanoform on rice crop nutrition, productivity and soil chemical and biological properties in inceptisols. *J. Soil Sci. Plant Nutr.* 23, 540–555.
- Thulasi, V., Moosa, P. P., Santosh, P. P., Drishya, D. S., Nisha, N. S., and Raji, P. (2024). Green manuring – a cost effective and farmer friendly alternative for farm. *Yard Manure J. Krishi Vigyan* 12, 285–291. doi: 10.5958/2349-4433.2024.00081.0
- Upadhyay, V. B., Jain, V., Vishwakarma, S. K., and Kumar, A. K. (2011). Production potential, soil health, water productivity and economics of rice (*Oryza sativa*) – based cropping systems under different nutrient sources. *Indian J. Agron.* 56, 311–316.
- Vaziritarbar, Y., Frei, M., Yan, F., Vaziritarbar, Y., and Honermeier, B. (2024). Enhancing nitrogen use efficiency and plant productivity in long-term precrop/crop rotation and fertilization management. *Field Crop Res.* 306:109210. doi: 10.1016/j.fcr.2023.109210
- Walia, S. S., Dhaliwal, S. S., Gill, R. S., Kaur, T., Kaur, K., Randhawa-Obrocnik, O., et al. (2024). Improvement of soil health and nutrient transformations under balanced fertilization with integrated nutrient management in a rice-wheat system in Indo-Gangetic Plains – a 34-year research outcomes. *Heliyon* 10:e25113. doi: 10.1016/j.heliyon.2024.e25113
- Walkley, A., and Black, I. A. (1934). An examination of the Degtjareff method for determining soil, organic matter and proposed modification of the chromic acid titration method. *Soil Sci.* 34, 29–38.
- Xia, L., Lam, S. K., Wolf, B., Kiese, R., Chen, D., and Butterbach-Bahl, K. (2018). Trade-offs between soil carbon sequestration and reactive nitrogen losses under straw return in global agroecosystems. *Glob. Chang. Biol.* 24, 5919–5932. doi: 10.1111/gcb.14466
- Yadav, L., and Meena, N. (2014). Performance of aromatic rice (*Oryza sativa*) genotype as influenced by integrated nitrogen management. *Indian J. Agron.* 59, 51–255.
- Yang, L., Zhou, X., Liao, Y., Lu, Y., Nie, J., and Cao, W. (2019). Co-incorporation of rice straw and green manure benefits rice yield and nutrient uptake. *Crop Sci.* 59, 749–759. doi: 10.2135/cropsci2018.07.0427
- Ye, L., Zhao, X., Bao, E., Li, J., Zou, Z., and Cao, K. (2020). Bio-organic fertilizer with reduced rates of chemical fertilization improves soil fertility and enhances tomato yield and quality. *Sci. Rep.* 10, 1–11. doi: 10.1038/s41598-019-56954-2

Zhao, N., Bai, L., Han, D., Yao, Z., Liu, X., Hao, Y., et al. (2024). Combined application of leguminous green manure and straw determined grain yield and nutrient use efficiency in wheat–maize–sunflower rotations system in Northwest China. *Plan. Theory* 13:1358. doi: 10.3390/plants13101358

Zhao, T., He, A., Khan, M. N., Yin, Q., Song, S., and Nie, L. (2024). Coupling of reduced inorganic fertilizer with plant-based organic fertilizer as a promising fertilizer management strategy for colored rice in tropical regions. *J. Integr. Agric.* 23, 93–107. doi: 10.1016/j.jia.2023.04.035

Zhou, G., Cao, W., Bai, J., Xu, C., Zeng, N., Gao, S., et al. (2019). Non-additive responses of soil C and N to rice straw and hairy vetch (*Vicia villosa* Roth L.) mixtures in a paddy soil. *Plant Soil* 436, 229–244. doi: 10.1007/s11104-018-03926-6

Zhu, B., Yi, L. X., Hu, Y. G., Zeng, Z. H., Lin, C. W., Tang, H. M., et al. (2014). Nitrogen release from incorporated ¹⁵N-labelled Chinese mil vetch (*Astragalus sinicus* L.) residue and its dynamics in a double rice cropping system. *Plant Soil* 374, 331–344. doi: 10.1007/s11104-013-1808-8



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Greening rice-fallow areas: integrating pulses and oilseeds for sustainable cropping in eastern India

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Rice-fallow areas, widespread in rainfed rice-growing regions of South Asia, remain uncultivated during the post-rainy (winter) season due to multiple challenges, including inadequate irrigation infrastructure, cultivation of long-duration rice varieties, and soil moisture imbalances. South Asia has approximately 22.3 million hectares of rice-fallow land, with India contributing the largest share (88.3%). Eastern Indian states, which account for 82% of India's rice-fallow area, presents significant opportunities for cropping intensification. However, several constraints—such as biotic (pest and disease), abiotic stresses (temperature extremes, drought, etc.), rapid soil moisture depletion, and disturbances from free-grazing livestock-hinder efforts to cultivate a second crop, perpetuating poverty among the small and marginal farmers. Introducing stress-tolerant rabi crops, particularly pulses (chickpea, lentil, lathyrus, field pea) and oilseeds (mustard, toria, safflower, linseed), offers a promising solution to enhance system productivity and improve the farmers' livelihoods. Policymakers have recently increased the public investment in rice-fallows intensification, yet fragmented and ad-hoc initiatives often fail to deliver sustainable outcomes due to complex and

multidimensional challenges involved. This study critically examines the key issues affecting rice-fallow lands and provides strategic recommendations to convert these underutilized areas into the productive cropping systems during winter and spring. Additionally, it reviews Central and State Government programs related to rice-fallow management, emphasizing the need for research to align with ongoing policy initiatives for maximum impact. The findings of this study offers a valuable insights for the policymakers, planners, and stakeholders, highlighting the potential of pulses and oilseeds to enhance the food security, reduce poverty, and promote sustainable, climate-resilient agricultural production systems in the region.

KEYWORDS

crop diversification, cropping intensification, integrated crop management, oilseeds, pulses, rice-fallow

Highlights

- Crop diversification in rice-fallow lands can boost smallholder farmers' income and soil health.
- Integrating pulses and oilseeds into rice-fallow periods enhances the land use efficiency and overall system yield
- Short-duration, low-water-demanding crops thrive well in rice-fallow systems with supplemental life saving irrigation.
- Expanding pulse and oilseed cultivation by 4.0 million hectares can significantly boost the crop productivity.
- Sustainable rice-fallow intensification supports poverty reduction and aligns with sustainable development goals (SDGs).

1 Introduction

Rice-fallow areas are rainfed rice-growing regions where land remains uncultivated during post-rainy (winter) season. This practice persists due to the several challenges, including inadequate irrigation infrastructure, cultivation of the long-duration rice varieties that are harvested late (such as MTU 7029, BPT 5204, and traditional local varieties), and soil moisture imbalances at the time of crop establishment. Additionally, rapid soil moisture depletion caused by early withdrawal of monsoon coupled with disturbances from free-grazing livestock and blue bulls, further discourages winter cropping (Ali and Kumar, 2009).

In South Asia, approximately 22.3 million hectares of rice-fallow land are present, with India accounting for the largest share (88.3%), followed by Bangladesh (8.7%), Nepal (1.4%), Sri Lanka (1.1%), Pakistan (0.5%), and Bhutan (0.02%) (Kumar et al., 2020). In India, around 11.7 million hectares of rice-fallow land are primarily concentrated in the eastern region (82%), spanning the seven states—Bihar, Chhattisgarh, Odisha, Assam, eastern Uttar Pradesh, Jharkhand, and West Bengal (Kumar et al., 2018a,b). With growing demand for food due to population expansion, intensifying agricultural production in these areas is imperative (Kumar et al., 2016). These regions offer significant opportunities for expanding cultivated areas through targeted research and intervention (Kumar et al., 2020). However, cultivating a second crop in winter presents the multiple challenges, including biotic and abiotic stresses (NAAS, 2013). Addressing these constraints is essential for scientists, policymakers, and other stakeholders to fully utilize the untapped potential of rice-fallow lands in eastern India and similar regions globally.

In rainfed, rice-based monocropping systems, small and marginal farmers often struggle with limited resources, trapping them in a cycle of poverty. Integrating a second crop after rice harvesting in eastern

India's rice-fallow lands offers a viable solution to enhance agricultural productivity (NAAS, 2013). The selection of suitable rabi (winter) crops depends largely on their ability to withstand biotic and abiotic stresses (NAAS, 2013). Oilseeds such as safflower, mustard, toria, groundnut, sesame, and linseed, along with pulses like lathyrus, chickpea, and lentil, have been identified as promising options for improving system productivity of rice-fallow lands (Bandyopadhyay et al., 2016; Kumar et al., 2021).

Recently, issue of rice-fallow lands has gained significant attention from the policymakers, leading to increased public investment. However, ad-hoc investments (temporary solutions without a long-term strategy) in intensification efforts often fail to yield sustainable outcomes due to complex, multidimensional challenges, including biotic and abiotic stresses, policy constraints, and socio-economic limitations. This article analyzes the challenges of rice-fallow lands and offers strategic recommendations to transform these underutilized areas into highly productive systems during winter and spring.

Additionally, this paper reviews the ongoing Central and State Government programmes related to rice-fallow management, emphasizing the need for research initiatives to align with these efforts for greater impact. The study's findings will provide a valuable insights for policymakers and planners, for shaping the policies, designing effective programmes, and identifying priority areas for investment. Ultimately, this research aims to promote the sustainable and environmentally friendly agricultural management practices, contributing to the poverty reduction and ensuring the food and nutritional security in the region.

2 SWOT analysis of rice fallow

The SWOT analysis of rice-fallow areas in India highlights the significant strengths such as vast land availability and potential for high yields in pulses and oilseeds. However, challenges like poor seed accessibility, lack of irrigation, and abiotic stress persist. Opportunities include innovative farmers and rising demand for pulses and oilseeds, while threats like production uncertainty and market volatility pose risks. The detail is given in Figure 1.

3 Climatic variabilities

Eastern India experiences a hot and dry, sub-humid climate, characterized by scorching summers and relatively cooler winters. The annual average temperature ranges between 24–26°C, with summer



FIGURE 1
Strength, weakness, opportunity and threat of rice-fallow (modified from Singh et al., 2016).

temperatures (April to June) fluctuating between 29–32°C and peaking at 37–42°C in April and May. In winter (December to February), temperatures average around 16–18°C, with low reaching 8–10°C. The region receives annual rainfall between 1,200 and 1,500 mm, increasing up to 1,600 mm in eastern parts. The rainy season is marked by high humidity, excess water accumulation of 200–300 mm, and potential evapotranspiration (PET) between 1,400 and 1,700 mm (Bandyopadhyay et al., 2015). Crop cultivation typically begins with the onset of monsoon and lasts between 180–210 days, extending beyond 240 days in West Bengal. Soils in this region are generally shallow, poorly drained, and predominantly clayey to clay loam in texture.

4 Distribution of rice-fallow areas

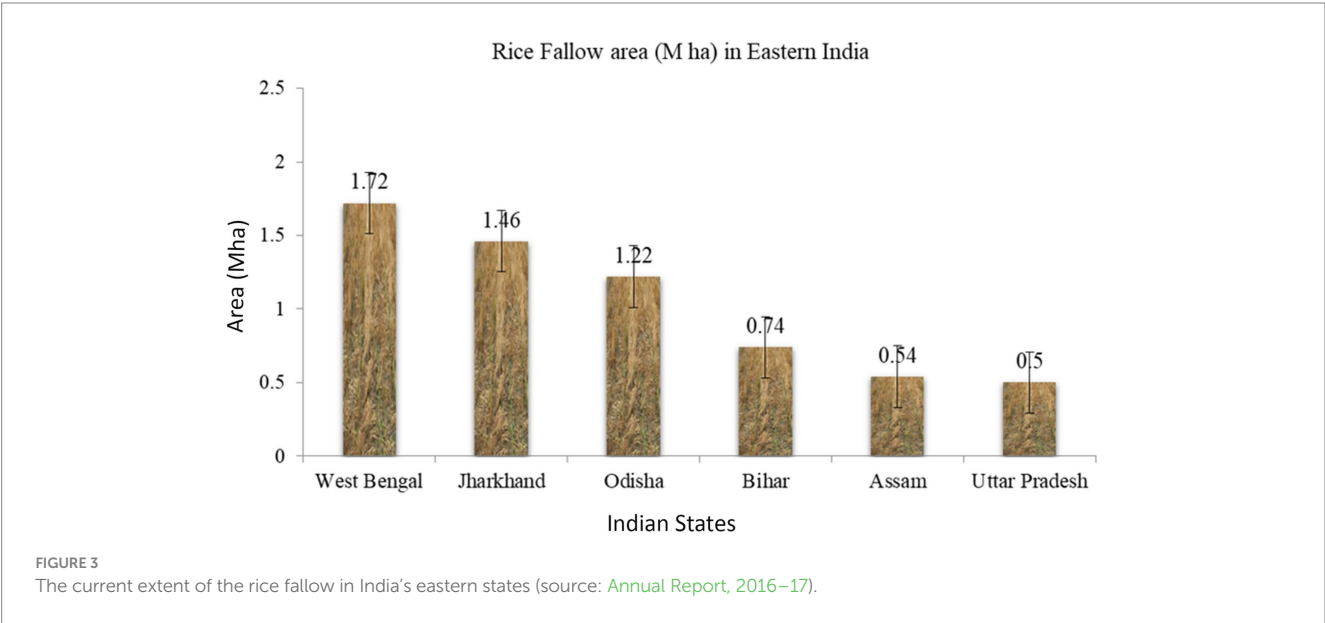
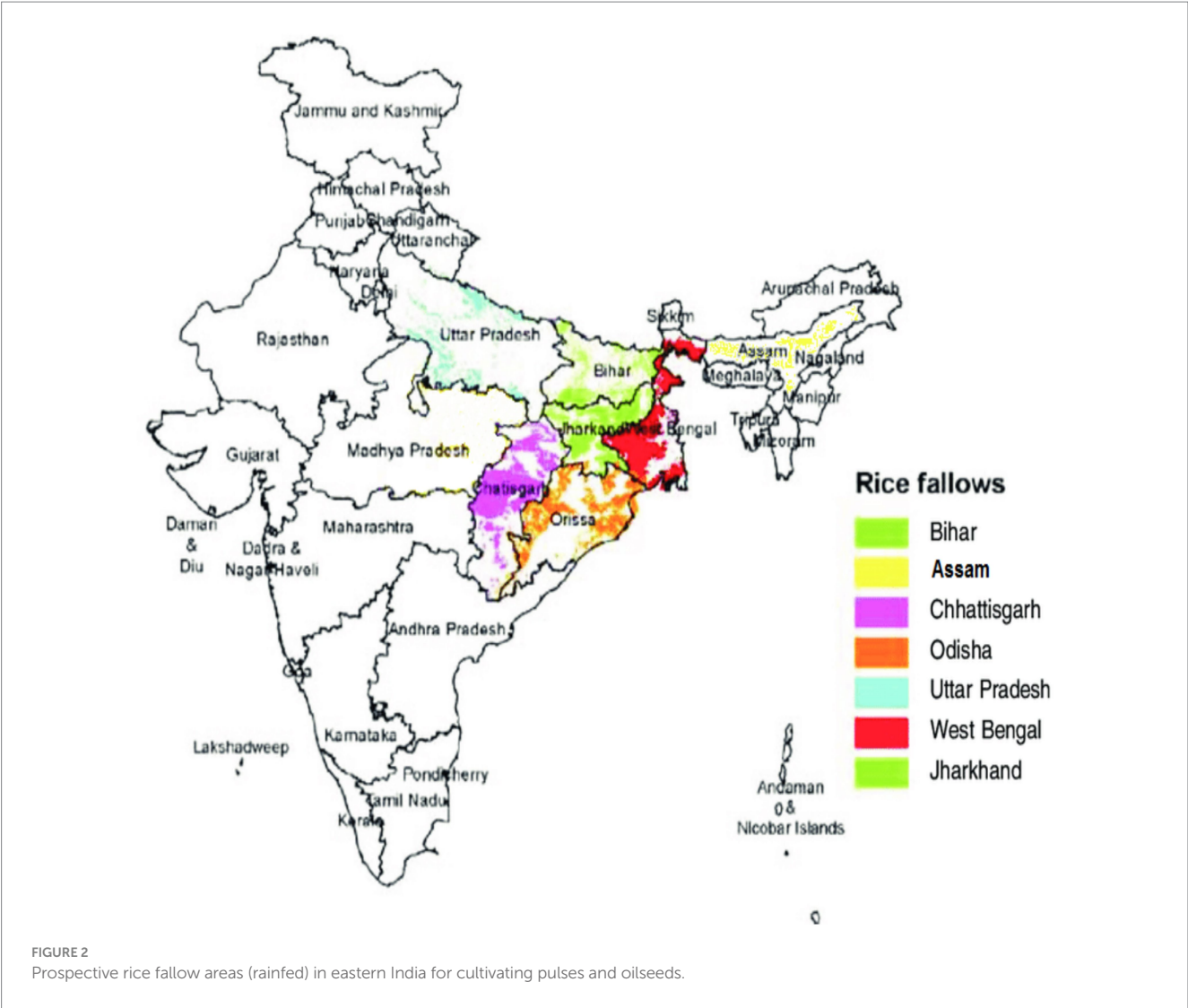
The fallow lands offer an immense potential for cropping intensification through inclusion of short to medium-duration rice varieties, improved soil moisture conservation, and introduction of short-duration pulses and oilseeds, ultimately enhancing soil health and productivity (Kumar et al., 2019a).

Low water-requiring, short-duration pulses like chickpea, lentil, lathyrus, and black gram, along with oilseeds such as mustard, toria, linseed, groundnut, sesame, and safflower, present viable options for increasing smallholder farmers' incomes while improving soil health. Rice-fallow areas are predominantly found in rainfed agro-ecosystems, characterized by deep alluvial soils with neutral to acidic pH (Figure 2).

In states such as Bihar, West Bengal, and Chhattisgarh, crops like chickpea, lentil, and lathyrus are typically grown as utera crops, sown in the standing rice fields 10–12 days before crop harvesting to utilize the residual soil moisture (Gupta and Bhowmick, 2005; Rautaray, 2008; Mondal and Ghosh, 2005). Several districts in eastern India follow rice–fallow cropping systems (Figure 3).

- *Assam*: Karbi Anglong, Dibrugarh, Golaghat, Jorhat, Lakhimpur, Morigaon, Nagaon, and Sibsagar
- *Bihar*: Aurangabad, Banka, Bhagalpur, Gaya, Jamui, Katihar, Kishanganj, Nawada, and Sheikhpura
- *Jharkhand*: Deoghar, Dhanbad, Dumka, East Singhbhum, Gumla, Hazaribagh, Palamu, Ranchi, Sahibganj, and West Singhbhum
- *Chhattisgarh*: Bastar, Surguja, Jashpur, Raigarh, and Durg
- *Odisha*: Bhadrak, Cuttack, Dhenkanal, Kalahandi, Koraput, Mayurbhanj, Puri, Sambalpur, and Sundergarh
- *West Bengal*: Bankura, Bardhaman, Birbhum, Cooch Behar, Malda, Medinipur, Murshidabad, North Dinajpur, Purulia, and South 24 Parganas
- *Eastern Uttar Pradesh*: Bahraich, Balrampur, Bhadohi, Pilibhit, Chandauli, Etawah, Ghazipur, Gonda, Lakhimpur Kheri, Maharajganj, Mirzapur, Siddharthnagar, and Sonbhadra (NAAS, 2013; Annual Report, 2016–17).

According to the Expert Group on Pulses, approximately 2.46 million hectares of rice–fallow land in these eastern states have a high potential for pulses cultivation (Figures 4, 5).



5 Categorization of rice fallows

India cultivates rice on about 43.4 million hectares, producing 104.3 million tonnes, with an average yield of 2,404 kg per hectare (Anonymous, 2015). However, lower crop yields are often attributed to the water scarcity during the peak growth stages and challenges related to biotic and abiotic stress management. While rice yields are generally satisfactory under puddled conditions, around 30% of cultivated area remains fallow during subsequent winter due to various agronomic and socio-economic constraints. Rice-fallow areas can be classified into four sub-groups based on the soil type and agro-climatic conditions:

5.1 Northeast region

This region experiences a warm, dry, and humid climate with cool winters and hot summers. Annual rainfall ranges from 1,200 to 1,500 mm, with higher precipitation in the eastern states like Bihar, Jharkhand, Odisha, and West Bengal. Crop growth is often limited by deep alluvial soils deficient in organic carbon, phosphorus, and zinc. Lowland regions frequently face excessive moisture or waterlogging during winter (October–November). Additionally, stray cattle pose a significant challenge to subsequent crops. The growing season lasts between 180 to 210 days in the northern areas and up to 240 days in the eastern regions. Lentil, chickpea, and lathyrus are commonly grown as relay or paira crops after rice. However, in Odisha, higher humidity favors black gram and horse gram, while mung bean thrives in mild winter conditions. States such as Chhattisgarh, Jharkhand, Bihar, and West Bengal favor small-seeded varieties of lentil, mung bean, urd bean, lathyrus, and peas under utera cropping system. The region holds a great potential for pulse and oilseed cultivation on fallow lands.

5.2 Central region

This region has a hot and dry sub-humid to moist-humid climate, with dry-summers and cool winters. Annual rainfall ranges from 1,000 to 1,200 mm, particularly in Maharashtra, Madhya Pradesh, and Chhattisgarh. The clayey soils in this region are nutrient-deficient, hard, and prone to deep cracking when dry. During winter cropping season, early rainfall and soil moisture stress are the common challenges. Typically, primed lathyrus and lentil seeds are broadcasted in standing rice fields using utera production system.

5.3 Coastal peninsula

This region, encompassing the coastal areas of Andhra Pradesh, Karnataka, and Tamil Nadu, features a dry sub-humid climate with hot summers and mild winters. Average annual rainfall ranges between 1,000 to 1,200 mm, and soils are predominantly deep clay. Mild winters and excessive soil moisture create favorable conditions for urd and mung bean production. The region is also benefited from bi-modal rainfall patterns.

5.4 Northeastern hills (NEH region)

The NEH region has a humid climate with cool winters and hot summers. Central Brahmaputra Valley, including Assam, receives an average annual rainfall of between 1,600 and 2000 mm. However, pulses productivity faces challenges due to decreasing availability of arable land, increasing population pressure, rising food demand, and deteriorating soil health. Pulses cultivation remains low due to several constraints, including soil acidity, poor fertility, aluminum toxicity, and an undulating topography that creates an unfavorable microclimate. High rainfall leads to excessive leaching, further

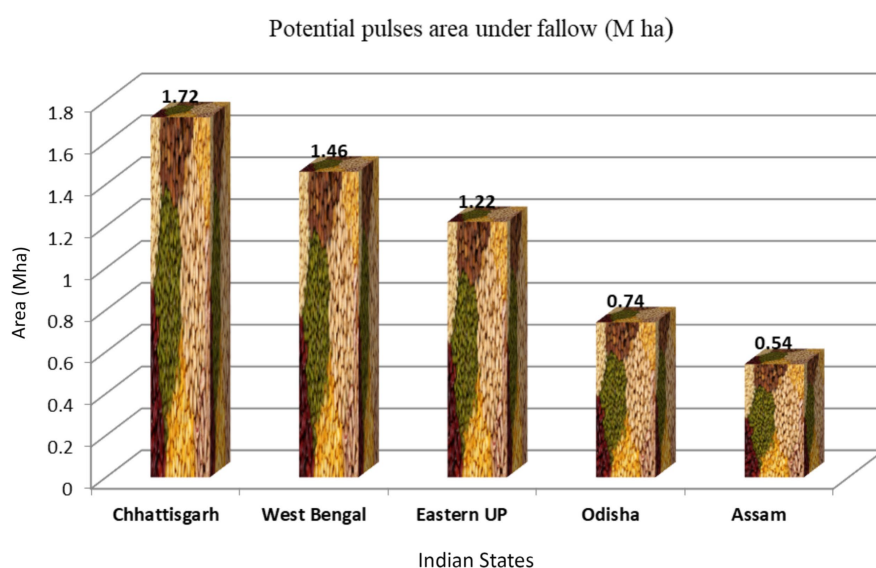
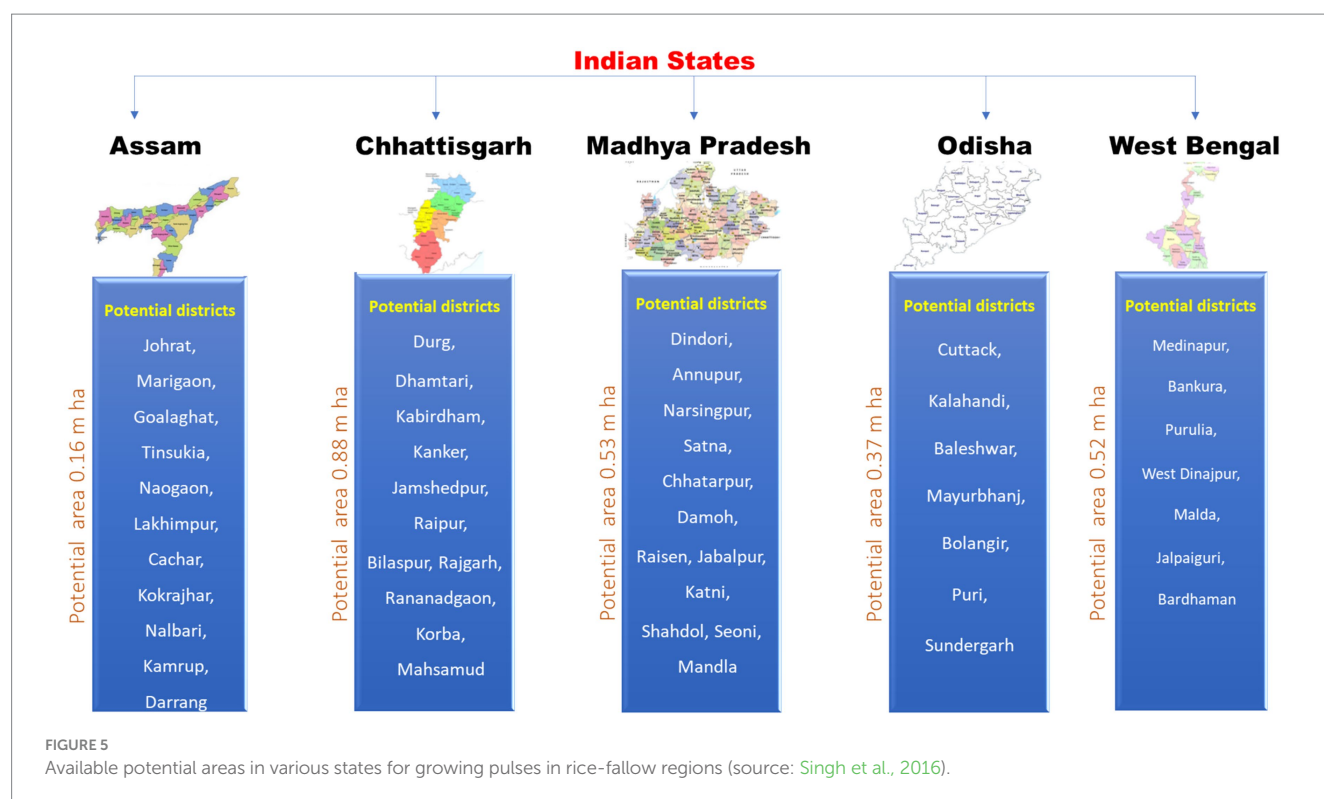


FIGURE 4

Possible areas for growing pulses in India's rice-fallow regions (source: Annual Report, 2016–17).



degrading the soil health. Small-seeded lentil and urd bean varieties are commonly grown in this region.

6 Challenges of rice-fallow cultivation

According to Bandyopadhyay et al. (2015), eastern region of India spans 73.7 million hectares, accounting for 22% of the nation's total land area. The net cultivated area in this region is 33.6 million hectares, which constitutes approximately 45% of India's total farmland. The region contributes 34.6% of country's total food production. In eastern India, productivity of food crops is ranked as follows: West Bengal > Eastern Uttar Pradesh > Bihar > Assam > Odisha > Jharkhand > Chhattisgarh. Cropping intensity varies significantly across these states, ranging from 115% in Chhattisgarh to 177% in West Bengal. Despite housing 38% of India's population, agricultural development in this region remains below its full potential.

The cultivation of pulses and oilseeds in rice-fallow areas faces the several challenges, including soil degradation and poor management practices (Pande et al., 2012). One of the major yield-limiting factors is soil moisture deficit, particularly during the later crop growth stages. Reliance on residual soil moisture from rice harvesting often results in inadequate moisture availability, leading to decline in water tables and mid-to-terminal droughts during flowering and pod-filling stages. These conditions significantly affect crop productivity of pulses and oilseeds in rice-fallow systems. Additionally, terminal drought and heat stress can cause premature maturation, reducing crop yields by 50% in tropical regions, particularly when rainfall is scarce (Ali et al., 2014).

Rice-fallow systems also suffer from poor soil structure, reduced aeration, and mechanical resistance in the seeding zones, negatively affecting seed germination, seedling emergence, and crop

establishment (Kumar et al., 2020). Soil hardening, a major constraint in puddled rice fields, deteriorates the soil's hydraulic properties, disrupting moisture distribution and thus, limiting the growth of deep-rooted pulses and oilseeds (Ali et al., 2014). These conditions weaken microbial activity, reduce the nutrient availability, and confine root growth to the top-soil, thus restricting the water and nutrient uptake. Additionally, combination of compact soil coupled with low levels of organic matter, which is common in tropical and sub-tropical areas, further depletes the soil fertility, rendering it unsuitable for profitable crop cultivation.

Physical deterioration of the puddled transplanted rice soils affects moisture retention, plant root penetration, and microbial life, leading to inefficient nutrient absorption in the subsequent crops. Two major approaches in rice-fallow production systems are-relay cropping and crop rotations, which have potential but face implementation challenges (Kumar et al., 2019b; Kumar et al., 2020). Pulses are particularly suitable for these systems due to their short duration, low input requirements, and adaptability to the surface broadcasting in standing rice fields. In coastal regions, urd and mung bean are commonly cultivated (Kumar et al., 2019b). However, relay cropping is often constrained by poor plant populations, inadequate seed-to-soil contact, seed rot, and patchy soil dryness, all of which reduce the seed germination, plant density, and crop yield potential.

Weed management in standing rice fields remains a major issue, even after harvest, due to inadequate land preparation. Problematic weeds such as *Cuscuta* can severely impact pulse crops (Mishra et al., 2016). In contrast, crop rotations require ploughing immediately after rice harvesting to remove stubbles, delay sowing of winter pulses. This leads to formation of large soil clods that hinders the seed germination and accelerate moisture evaporation from the top soil, causing water stress during critical growth stages of pulses such as chickpea, lentil, and black gram.

Soil acidity in Eastern India and Northeastern Hill (NEH) region, along with alkalinity or salinity in the lower and middle Indo-Gangetic Plains, further diminishes soil productivity (Kumar et al., 2019b). The anaerobic conditions created by puddled rice fields are detrimental to beneficial soil microbes like *Rhizobia*, impairing biological nitrogen fixation (BNF) in leguminous crops. Additionally, pulses and oilseeds in rice-fallow systems are vulnerable to high incidences of insect pests due to unstable soil-plant-atmosphere interactions. Chickpea crops in states such as Chhattisgarh, Jharkhand, and Madhya Pradesh are particularly susceptible to pod borer (*Helicoverpa* spp.), while root-knot nematodes (*Meloidogyne* spp.) are also prevalent. Urd and mung bean often suffer from powdery mildew during winter, while lentil are affected by rust and *Fusarium* wilt.

Limited employment opportunities in agriculture contribute to widespread poverty and malnutrition in these regions. The per capita availability of cultivated land in our country is just 0.15 ha (Kumar et al., 2016). Farming in these areas is dominated by the small and marginal landholding, which complicates the adoption of mechanized farming techniques.

Although this region receives 1,100 to 1,200 mm of annual rainfall—which is sufficient to meet the crop water demands but high variability in spatial and temporal rainfall distribution causes farming instability. By the end of winter, these soils dry and crack, making it difficult to sustain a second crop. Additionally, post-harvest plowing results in large, hard clods, further restricting seed germination and root penetration, ultimately reducing yields (Kumar et al., 2020).

Resource-poor farmers face additional challenges due to the high costs of irrigation and fertilizers needed for growing winter crops, further discouraging the second cropping. Pulses and oilseeds can effectively utilize the residual soil moisture, but optimal moisture management strategies and research-driven solutions are essential for maximizing their productivity.

Rice, the primary crop, is typically cultivated through transplantation during rainy season. To facilitate its growth, farmers practice puddling, a method that disrupts the soil macro-pores and aggregates, increasing bulk density. After the rainy season, these puddled soils dry and crack, restricting the moisture availability for winter crops. Furthermore, ploughing after rice harvesting creates large, hard soil clods, impeding the root growth and leading to reduced yields in subsequent crops. Resource-limited farmers often struggle with high cost of irrigation and fertilizers required for winter cropping, further constraining their ability to sustain agricultural production throughout year.

Pulses and oilseeds can effectively utilize the residual soil moisture left after rice harvesting, making efficient moisture management critical for establishing a second crop. By implementing well-researched strategies, fallow lands can be converted into productive agricultural areas. In states like West Bengal, Odisha, Chhattisgarh, and Jharkhand, conventional rice-pulse cropping systems are commonly practiced. However, challenges such as poor crop establishment of pulses like chickpea and oilseeds like mustard, toria, and safflower significantly reduce the region's yield potential. Kumar et al. (2016) identified key limitations affecting plant populations in rice-fallow systems, including inadequate seed-soil contact, low soil moisture, and severe weed infestations.

In lowland rice areas with higher soil moisture levels, lentil and lathyrus are better suited for cultivation than chickpea, mustard, and linseed (Mishra et al., 2016; Mishra and Kumar, 2018). The productivity of pulses and oilseeds in rice-fallow lands is further

affected by site-specific nutrient deficiencies, particularly phosphorus, zinc, sulfur, boron, and molybdenum, as well as soil acidity and low organic carbon levels. Addressing these constraints is essential for achieving the optimal yields in rice-fallow cropping system.

Farmers in rice-fallow areas also face challenges due to the dominance of long-duration rice varieties, which take 155 to 160 days to mature (e.g., MTU 7029, BPT 5204, and local traditional cultivars). The extended growing period delays the sowing of subsequent crops, such as pulses and oilseeds, resulting in reduced crop yields due to soil moisture deficits during flowering and maturation stages. Additionally, lack of high-quality seeds and superior crop varieties exacerbates these challenges. Weed infestations pose another major issue, particularly in utera/paira cropping systems, where rapid surface soil moisture loss complicates manual weeding, further affecting crop establishment and productivity. Utera cropping (also known as paira cropping) is a traditional relay cropping system in which next crop is sown in standing rice crop before its harvest, utilizing the residual soil moisture for germination and early growth. This practice is commonly used in rainfed, lowland rice-growing areas to optimize the land use, reduce fallow periods, and enhance productivity without additional irrigation. Common utera crops include lentil, chickpea, linseed, lathyrus, and mustard, which are well-suited to the residual soil moisture conditions in rice fields.

7 Interventions for intensification of rice-fallow areas

7.1 Cultivation of short-duration rice varieties

Farmers should adopt short-duration rice varieties with quicker maturity periods to enable the timely sowing of subsequent crops. This approach reduces the risk of terminal drought and enhances overall crop productivity.

7.2 Improvement in farm mechanization

Encouraging the adoption of the modern farm machinery and equipment can significantly boost productivity in rice-fallow farming. Mechanization accelerates essential agricultural tasks such as land preparation, planting, and harvesting, reducing labor requirements and improving the overall farm efficiency.

7.3 Adoption of soil conservation measures

Implementing soil conservation practices such as contour plowing, terracing, and bunding can effectively reduce soil erosion and enhance soil health. These techniques help retain moisture, mitigate the effects of drought, and ultimately improve crop performance.

7.4 Creation of water harvesting structures

Constructing water harvesting systems such as ponds and check dams helps capture and store the rainwater. This stored water can

be utilized for irrigation during dry-periods, ensuring a steady water supply even when rainfall is insufficient.

7.5 Development of irrigation facilities

Investing in irrigation infrastructure, including canals, tube wells, and drip irrigation systems, can provide a reliable water source for rice-fallow areas. These facilities help overcome the constraints of variable rainfall and sustain optimal moisture levels for crop growth.

7.6 Supply of quality seeds and inputs

Ensuring access to high-quality seeds and essential agricultural inputs such as fertilizers and pesticides is crucial for enhancing crop yields. Farmers should be provided with certified seeds and recommended inputs to maximize their production potential.

7.7 Use of drought-tolerant, climate-resilient crops and varieties

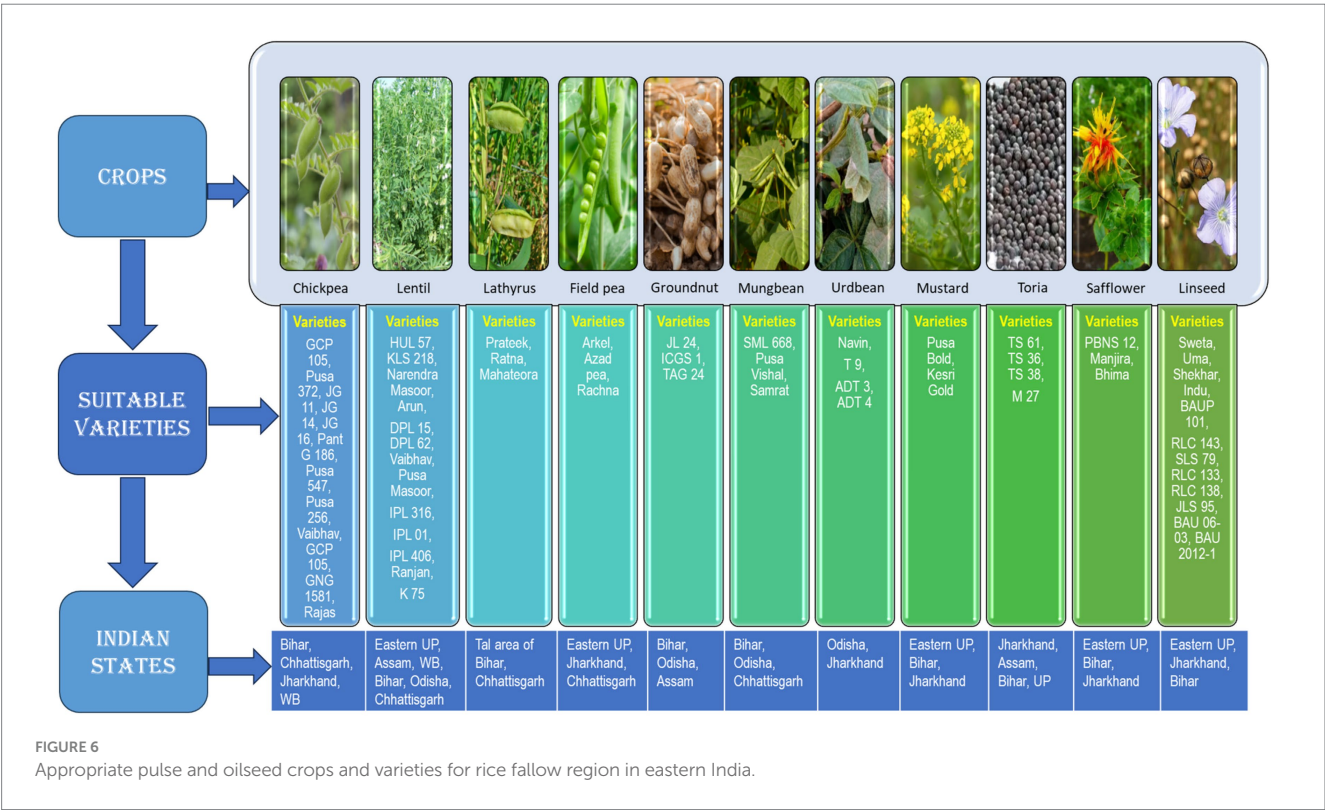
Encouraging the cultivation of drought-tolerant, climate-resilient crops can help in mitigate the challenges posed by water scarcity during fallow period. Farmers should consider alternative crops that require less water and can withstand the dry conditions, fostering a more sustainable and productive farming systems.

8 Potential for cultivating oilseeds and pulses in rice-fallow areas

Rainfed regions in India plays a vital role in food production and rural economy but are often fragile and prone to distress. Approximately 11.65 million hectares of land remain uncultivated after rice harvesting, with 82% of this area located in eastern India, while remaining portion is distributed across Tamil Nadu, Karnataka, and Andhra Pradesh. These regions offer significant opportunities for growing upland pulses such as lentil, chickpea, lathyrus, mung and urd bean, which require minimal inputs and water (Figure 6). However, depleted soil moisture post-harvest can delay sowing and reduce crop yields. Limited moisture further affects plant growth, making supplementary irrigation essential during critical growth stages.

Conservation agriculture practices including crop residue retention, zero tillage (ZT), and appropriate crop rotation show great potential for improving pulse yields in rice-fallow areas. Both crop rotation and relay/paira cropping of pulses in standing rice fields could become widely adopted solutions. However, a thorough understanding of local ecology and constraints is necessary to address the challenges effectively. Techniques such as using suitable pulse varieties, zero tillage, retaining crop residues, seed priming, foliar nutrition, and mulching can significantly enhance pulse productivity.

Pulses and oilseeds have several advantages, including short growth cycles, climate resilience, and low input requirements, making efficient use of residual soil moisture. Despite India producing around 17–18 million tonnes of pulses annually on an area of 24–26 million hectares, demand still exceeds supply, necessitating imports. Integrating pulses into rice-fallow systems can help bridge this gap, enhance sustainability, and improve farmers' incomes by expanding cultivation areas and boosting crop productivity.



The development and implementation of the research and development (R&D) programs, supported by government schemes and interventions, have significantly advanced the utilization of rice-fallow lands for pulse and oilseed cultivation. In India, nearly one-third of agricultural land remains fallow after paddy harvesting, representing a substantial opportunity for conversion into productive farmland. With appropriate policy measures, an additional 3.0 million hectares could be brought under the pulse cultivation and 1.0 million hectares under oilseed production. The promotion of crops such as lentil, lathyrus, and chickpea in rice-fallow areas, supported by initiatives like the National Food Security Mission (NFSM) has shown the positive results.

However, the impact of such programs on pulses and oilseeds cultivation has been limited due to restricted implementation areas and frequent changes in beneficiaries.

To overcome these challenges, more innovative and targeted strategies are required to enhance the effectiveness of rice-based cropping systems. This involves focusing on region-specific characteristics to optimize the utilization of fallow lands and benefit resource-poor farmers. Despite the potential of short-duration pulse and oilseed crops, efforts to expand their cultivation have been insufficient. All India Coordinated Research Project on mung bean, Lathyrus, Lentil, Rajmash, and Pea (AICRP-MuLLaRP) has not effectively promoted high-yielding varieties in the region. However, projects funded by the Department of Science and Technology (DST) and National Fund for Basic, Strategic, and Frontier Application Research in Agriculture (NFBSRA) have made progress in mitigating abiotic stress and improving resource efficiency in pulse production.

Consortium Research Platform on Conservation Agriculture (CRP on CA), established by Indian Council of Agricultural Research (ICAR), has identified soil and water management as critical factors limiting crop production in fallow areas. A comprehensive approach to soil and crop management is an essential to unlock the potential of rice-fallow lands for short-duration crops.

As highlighted by Mohapatra et al. (2022), efficient natural resource management and integrated crop management (ICM) practices are crucial for sustainable cropping intensification in rice-fallow systems. Addressing the multifaceted challenges of rice-fallow management requires coordinated efforts across research, policy development, infrastructure improvement, and community engagement. Programs like “Targeting Rice-Fallow Areas in Eastern India for the Promotion and Production of Pulses & Oilseeds” under Rashtriya Krishi Vikas Yojana (RKVY), along with advocacy by Commission for Agricultural Costs and Prices (CACP), are steps in the right direction. However, tackling the complexities of fallow land intensification requires the precise assessments, identification of the constraints, and development of tailored crop plans to enhance the farm incomes, reduce poverty, and ensure the food security.

9 Strategies for converting mono-cropped areas into double-cropped systems in rice-fallow production

To enhance pulses and oilseeds cultivation in rice-fallow areas, several key interventions are necessary. A cluster-based approach for demonstrating improved production technologies, along with increasing the availability of quality seeds, is a crucial. Seed priming, along with

Rhizobium or fungicide treatments, can enhance seed performance. Effective agronomic measures such as micronutrient application, pest management, and supplemental irrigation further improve productivity. Resource conservation technologies (RCTs) help conserve soil moisture and increase farm efficiency. Additionally, increasing cropping intensity can alleviate winter fodder shortages. Simple interventions such as seed priming and applying urea/DAP and micronutrients at critical growth stages have significantly improved crop yields for resource-poor farmers (Kumar et al., 2018a,b). Implementing these strategies can foster the sustainable and profitable pulse and oilseed farming while addressing the agronomic challenges. The following integrated strategies can significantly boost the system productivity of rice-fallow areas in India.

9.1 Water harvesting and storage

Moisture scarcity during winter remains a significant constraint for second-season cropping in rice-fallow areas, despite ample monsoon rainfall. Studies suggest that rainwater harvesting and small-scale irrigation infrastructure can enhance water availability during dry months (Das et al., 2014). The construction of ponds and reservoirs, supported by government initiatives, has proven effective in several regions for ensuring life-saving irrigation (Richards et al., 2021). Research indicates that harvesting excess rainwater—often lost as runoff—can supplement winter water supplies, reducing the dependency on erratic rainfall patterns (Velasco-Muñoz et al., 2019). Field trials in high-rainfall regions demonstrate that integrating water conservation measures with improved agronomic practices mitigates abiotic stresses, such as waterlogging in valleys and rapid soil moisture depletion in uplands (Manik et al., 2019). These strategies collectively enhance agricultural resilience, promoting sustainable intensification of rice-fallow areas.

9.2 Utilization of RCT

Zero-tillage (ZT) and residue retention significantly enhance soil moisture conservation and crop productivity in rice-fallow systems. Reduced tillage (RT) techniques have been shown to increase pulses yield by 33–44% as compared to conventional tillage (CT), particularly for chickpea, lentil, and black gram (Kar and Kumar, 2009). Retaining 30% of rice residue and using ZT-practices, such as those involving Happy Seeder, have resulted in substantial yield improvements for lentil, chickpea, and safflower (Ghosh et al., 2016). Utera cropping system, a specific form of ZT, allows for early sowing and optimal moisture utilization, benefiting crops like lathyrus, linseed, and lentil (Mishra et al., 2016).

9.3 Systematic crop production approach

Replacing the long-duration rice varieties with short-to medium-duration alternatives facilitates early harvesting and timely sowing of subsequent crops. For relay cropping (paira/utera), proper field leveling ensures the uniform soil moisture and improved seed germination. Mechanized or line transplanting of rice enhances yield potential in fallow-based cropping systems (Mishra and Kumar, 2018). The challenge of limited quality seed availability for late-season

sowing can be addressed through community-based seed multiplication programs and enhanced distribution channels supported by the National/State Seed Corporations (NSC).

9.4 Ensuring access to high-quality seeds

Community-based seed multiplication programs and improved storage and distribution systems are essential for sustaining the productivity in rice-fallow systems. National and State Seed Corporations (NSC) should ensure the timely availability of certified seeds. Short-duration pulse and oilseed crop varieties with terminal drought resistance, such as Pusa Masoor 5 (lentil), C 235 (chickpea), Uma (linseed), and Ratan (grasspea), have demonstrated high yield potential (Kumar et al., 2021). Seed priming that involves soaking seeds in water or nutrient solutions before sowing-enhances the germination and early seedling growth, and improving overall yield potential (Ali et al., 2005).

9.5 Weed management

Integrated weed management (IWM) strategies, including residue mulching, ZT sowing, and post-emergence herbicides like quizalofop (50 g/ha) applied 15–20 days after sowing (DAS), effectively control weeds (Kumar et al., 2016). In legumes such as groundnut and mung bean, application of Imazethapyr (100 g/ha) has been successful in controlling the narrow-leaved weeds.

9.6 Timely plant protection

Seed treatments with fungicides such as carbendazim and biological agents like *Trichoderma viride* (8–10 g/kg seed) have been widely recommended to prevent seed rot and early seedling diseases, enhancing crop establishment and yield (Nazir et al., 2022). Studies have demonstrated that integrating these treatments with proper agronomic practices reduces disease incidence and improves seedling vigor, particularly in pulse crops grown under the moisture-limited conditions (Kumar et al., 2021).

9.7 Soil moisture conservation

Conservation agriculture (CA) practices, including raised bed planting, play a crucial role in soil moisture management and thereby enhancing productivity in rice-fallow systems (Kumar et al., 2022a). Raised bed planting effectively conserves moisture, increases the soil organic carbon (SOC), and improves soil properties. This method has been shown to increase the pulses yield-such as lathyrus, lentil, and chickpea by 33–44% as compared to the conventional tillage (CT), outperforming no-till (NT) and relay cropping systems in moisture conservation (Kar et al., 2004; Gangwar et al., 2006). Zero tillage (ZT) also contributes to reducing the moisture loss and allows for earlier planting of post-rainy season crops by 7–10 days (Mishra et al., 2016). To optimize residual soil moisture, pulses and oilseeds should be sown immediately after rice harvesting. Multi-location trials conducted in Kanpur, Kalyani, and Raipur have demonstrated that practices such as

rice stubble retention, mulching, and no-till sowing significantly enhance productivity by conserving soil moisture in rice-fallow areas (Ali et al., 2005). These conservation practices are vital for mitigating the moisture stress and terminal drought, ultimately improving crop yield sustainability in rice-fallow systems (Kumar et al., 2022b).

9.8 Crop establishment options

Research by Mishra et al. (2016) demonstrated that zero tillage (ZT) combined with mulching significantly boosts crop yield of winter pulses such as chickpea (JG-14), lathyrus (Ratna), and lentil (HUL-57). Similarly, Kumar et al. (2018a,b) observed that ZT consistently improved crop productivity of subsequent winter crops. Increasing stubble height in conventional tillage (CT) production systems enhances the soil moisture conservation, benefiting winter crop yields in rice-fallow areas. Kar and Kumar (2009) reported that raised bed planting (RT) following rice harvest resulted in higher pulses yield. Retaining crop residue enhances soil quality by reducing erosion, evaporation, and weed growth while improving the nutrient availability and resource management. In no-till (NT) production systems, residue retention prevents the soil sealing and crust formation. Small-scale farmers in the developing regions often prioritize crop residues for biofuel or livestock feed. However, maintaining a portion of residues improves the long-term soil quality. Retaining crop residues and employing techniques such as utera cropping help mitigate terminal drought by preserving the soil moistures and reducing evaporation, making these practices highly effective for cultivating pulses and oilseeds.

9.9 Ensuring timely availability of essential inputs

In rice-fallow areas, post-rainy season crops predominantly rely on residual soil moisture, often facing nutrient deficiencies due to the limited application of fertilizers, biofertilizers, and agrochemicals. Studies have shown that optimizing agronomic practices, including timely sowing, appropriate plant spacing, and moisture conservation techniques, significantly improves the crop establishment and yields in such moisture-limited conditions (Kumar et al., 2020). Ensuring the timely availability of quality seeds, fertilizers, and plant protection chemicals is critical for enhancing productivity. Research indicates that use of improved seed varieties with better drought tolerance and early maturity can substantially increase crop yields in rice-fallow systems (Kumar et al., 2014). Additionally, integrating biofertilizers such as Rhizobium and phosphate solubilizing bacteria has been found to enhance nutrient uptake and soil fertility, leading to better crop performance (Shome et al., 2022). These evidence-based interventions collectively contribute to the sustainable intensification of rice-fallow systems.

9.10 Credit facilities and marketing infrastructure

Economically poor farmers often face challenges in accessing quality agricultural inputs and financial resources, limiting their ability

to adopt second-season cropping. Studies have shown that targeted financial interventions, such as subsidies on seeds and fertilizers, access to institutional credit, and crop insurance schemes, can significantly enhance the smallholder participation in diversified cropping systems (Di Bene et al., 2022). Government-backed initiatives like interest-free agricultural loans and weather-based crop insurance have been instrumental in reducing the financial risks and promoting crop intensification in resource-constrained regions (Kumar and Babu, 2021). Strengthening the rural marketing infrastructure is another key factor in incentivizing the farmers to cultivate high-value crops. Research indicates that well-developed supply chains, including the farmer-producer organizations (FPOs), contract farming, and direct market linkages, improve the price realization and reduce post-harvest losses. These evidence-based strategies collectively contribute to the sustainable intensification of rice-fallow systems.

9.11 Safeguarding against stray cattle

Stray cattle, including *Neelgai* (blue bulls), pose a significant threat to crops in fallow areas, discouraging cultivation. Implementing effective policies, such as community fencing, controlled grazing, or alternative fodder management strategies, can help in mitigate the impact of stray cattle, protect the standing crops, and promote second cropping systems.

9.12 Introducing short-duration, high-yielding, climate-resilient pulse varieties

Short-duration pulse varieties are essential for overcoming the terminal moisture stress and heat stress in rice-fallow areas. Successful breeding programs should prioritize traits that enhance the drought tolerance and rapid growth. Providing high-quality seeds with more than 90% germination rates and selecting genotypes with broad canopies can help in reducing soil evaporation and improve crop yields.

9.13 Introducing water-efficient/smart genotypes

Pulse crops can be screened for water efficiency, with their water needs decreasing in the following order: pea > chickpea > lentil > lathyrus. Summer mung bean and urd bean require more water than peas, making them less suitable for drought-prone conditions. Selecting and promoting water-efficient genotypes is a crucial for optimizing crop productivity in the moisture-limited environments.

9.14 Seed pelleting

Seed pelleting with agrochemicals such as superphosphate, *rhizobium* culture, and plant protection chemicals has been shown to improve crop establishment and yields in various trials. Evaluating its cost-effectiveness and performance in rice-fallow conditions is necessary, as it may enhance seed survival and crop growth under the moisture stress conditions.

9.15 Foliar nutrition

In relay cropping systems, where conventional fertilizer application is challenging, seed pelleting and foliar feeding serve as an effective alternatives. Field trials have demonstrated that foliar spraying with 2% urea during flowering and pod formation stages boosts mung bean, urd bean, chickpea, and lentil yields by enhancing the leaf nitrogen concentration and photosynthesis (Anonymous, 2008; Ali and Kumar, 2009). Additionally, seed pelleting with micronutrients such as zinc is beneficial. Addressing widespread molybdenum (Mo) deficiency in Central India caused by insufficient nutrient replenishment can involve soil application of ammonium molybdate (1–1.25 kg/ha), foliar application of 0.1% Mo, or seed inoculation with 1.0 g Mo/kg.

9.16 Timely planting

In rice-fallow areas, delay in planting pulses can be avoided by broadcasting seeds 2–5 days before rice harvesting. Alternatively, zero-tillage drills post-harvesting ensure the sufficient soil moisture for optimal pulse productivity. Timely planting with the adequate soil moisture is a crucial for maximizing the pulse productivity, as it allows crops to efficiently utilize the residual moisture and develop strong root systems to withstand late-season moisture stress.

9.17 Timely plant protection

Low soil moisture in rice-fallow areas limits the effectiveness of post-emergence herbicides, while hard soil conditions make inter-cultivation challenging. Hand weeding should be done early in crop growth stage. Effective pest and disease management includes seed treatment with fungicides such as carbendazim and applying *Trichoderma viride* at 8–10 g/kg of seed to prevent seed rot and protect the young seedlings (Kumar et al., 2022c).

9.18 Supplementary and life-saving irrigation

To manage the limited water resources effectively, implementing supplementary or life-saving irrigation during post-rainy season can help mitigate the moisture stress and sustain the crop productivity. Utilizing farm ponds or natural reservoirs with precision irrigation methods such as drip and sprinkler systems optimizes water use by delivering precise amounts of water and fertilizer at critical crop growth stages (Praharaj et al., 2016a). Technologies such as precision land leveling, zero-tillage, furrow-irrigated raised-bed planting, and residue management are also valuable in reducing water use while improving water productivity and efficiency (Praharaj et al., 2016b). Given the uncertainties of rainfall and climate change, improving resource-use efficiency (RUE) is essential for enhancing pulse crops productivity. Strategic water management in pulses supports sustainable intensification of food production in India, particularly in regions facing natural resource degradation and climatic risks. In rice-fallow areas, intercropping pulses with crops such as linseed or sesame can maximize land utilization and farm income. Planting one or two rows of short-duration pulses between wider rows of strip

crops can enhance the biological nitrogen fixation (BNF), while minimizing the competition for resources.

9.19 Research and development (R&D)

Strategic research and development (R&D) have significantly improved rice productivity in fallow areas. For instance, high-yielding, disease-resistant urd and mung bean varieties have been successfully developed for coastal peninsula. Further targeted research is needed to address disease hotspots and improve seed availability and agronomic management practices. Expanding pulse cultivation to 3.0 million hectares of rice fallow land could yield an additional 1.5–2.0 million metric tons of pulses, as estimated by the Ministry of Agriculture (Anonymous, 2009).

9.20 Actual mapping of rice-fallow areas

A coordinated approach involving all the relevant stakeholders is crucial for mapping and effectively utilizing rice-fallow areas. Satellite image and remote sensing tools are an essential for accurate approach for identifying and updating fallow land records, enabling better planning and intervention strategies.

9.21 Merging all R&D actions on rice-fallows

Consolidating research and development efforts at different levels from farm to state is critical for ensuring the effective implementation of future action plans. Integrating R&D results from various sources will create a cohesive approach to advancing agricultural practices and optimizing the fallow land utilization.

9.22 Implementing model pilot projects

Model pilot projects conducted directly on the farmers' fields are essential for demonstrating and promoting the recently developed technologies. These projects should be implemented in a mission-driven manner to showcase their effectiveness and encourage the widespread adoption among the farming communities.

9.23 Continual addressing of constraints in rice-fallow systems

Assessing and addressing constraints on-site enables faster adoption and dissemination of the proven technologies. Immediate resolution of issues facilitates effective implementation of innovations, and accelerating their acceptance among farmers.

9.24 System-mode approach and tools

Adopting agroecology-based farming systems that integrate the multiple enterprises has been widely recognized as a sustainable

approach to enhancing the farm incomes and resilience. Research indicates that diversified farming systems, including crop-livestock integration, improve resource-use efficiency, soil health, and overall farm productivity (Fatima et al., 2023). Studies have demonstrated that integrating animal husbandry with crop production contributes to long-term sustainability by optimizing nutrient recycling, reducing input costs, and providing an additional income source for smallholder farmers (Fatima et al., 2023). Utilizing rice-fallow lands for strategic residue management further enhances the resource use efficiency. Field experiments suggest that conserving at least 30% of crop residues for animal feed not only supports livestock nutrition but also prevents excessive residue burning, thereby reducing greenhouse gas emissions and improving the soil organic matters (Kumar et al., 2018a,b). These evidence-based strategies contribute to the sustainable intensification of rice-fallow production systems, fostering both the environmental and economic benefits.

9.25 Broad-scale mechanization

Mechanization is a critical driver of farm efficiency, reducing labor dependency and enhancing productivity in rice-fallow systems. Studies have shown that adoption of appropriate mechanization strategies can significantly improve land preparation, sowing, and harvesting efficiency, particularly in the regions with labor shortages. While large-scale machinery is beneficial for consolidated farmlands, research highlights the necessity of small, locally operated equipment for undulating terrains and fragmented smallholder farms (Sims and Kienzle, 2017).

9.26 Scaling-up and scaling-out crop management practices

Innovative technologies and best management practices (BMPs), once tested and refined on the farms, should be scaled up and widely adopted. Expanding these successful interventions will help in increase the production efficiency and total agricultural output by reaching more farmers and extending crop coverage, ultimately enhancing the overall agricultural productivity.

10 Future research and prospects

The effective utilization of rice-fallow lands presents a promising avenue for enhancing agricultural productivity and rural livelihoods. Future research should focus on developing the climate-resilient and short-duration pulses and oilseeds varieties that can thrive well under the residual soil moisture conditions. Emphasis should be placed on improving seed distribution systems, ensuring timely availability of high-quality seeds, and adopting precision agronomic management practices to optimize the crop establishment in these fallow lands. Expanding irrigation infrastructure and promoting efficient water management strategies will be crucial for enhancing the crop yields in these areas. Research should also explore sustainable cropping systems tailored to specific agroecological zones, incorporating conservation agriculture management practices to improve the soil health and long-term crop productivity. Integrating pulses into public food distribution

programs and farmer support initiatives can incentivize their cultivation and contribute to the nutritional security.

Additionally, policy-driven interventions must be informed by data-driven research on economic viability, market linkages, and farmer adoption behavior. Strengthening extension services, digital advisory tools, and financial incentives for farmers transitioning to pulse cultivation will be vital for scaling up this transformation. By addressing these key challenges, rice-fallow areas can be effectively utilized to improve the overall farm incomes, enhance food security, and contribute to a more sustainable agricultural landscape.

11 Conclusion

Despite the identification of numerous technological, institutional, and market-based solutions, integration of evidence-based strategies in designing and implementing fallow land intensification pathways remains limited. Rice-fallow intensification, particularly in risk-prone areas, lacks a cohesive support systems, an active community of practice, and a well-established policy network at various levels, which hampers effective policy reforms.

Research on fallow land management must align with ongoing government schemes and adopt a collaborative approach, involving the multiple partners to assess the investment pathways and sequence interventions for effective winter fallow intensification. Coordination among various stakeholders-including agriculture, water resources, electricity, and public works departments-is essential for successful irrigation management and overall governance.

Rice-fallow systems present the significant opportunities for expanding pulses and oilseeds cultivation through advanced agro-technologies. Key strategies for success includes the soil moisture conservation and mitigating abiotic stress. Focused research is crucial to understand rice-fallow ecology and developing location-specific, short-duration, drought-tolerant cultivars. By addressing site-specific constraints and implementing well-planned cropping strategies, these unutilized lands can be transformed into productive agricultural areas, contributing to poverty reduction and improved nutrition.

Author contributions

RK (1st author): Conceptualization, Data curation, Formal analysis, Resources, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing. AD: Supervision, Writing – original draft, Writing – review & editing. SM: Conceptualization, Data curation, Validation, Writing – original draft, Writing – review & editing. PU: Conceptualization, Formal analysis, Validation, Visualization, Writing – original draft, Writing – review & editing. BB: Writing – original draft, Writing – review & editing. JM: Conceptualization, Data curation, Writing – original draft, Writing – review & editing. AS: Conceptualization, Validation, Writing – original draft, Writing – review & editing. JC: Conceptualization, Validation, Writing – original draft, Writing – review & editing. SanjK: Data curation, Writing – original draft, Writing – review & editing. PS: Conceptualization, Writing – original draft, Writing – review & editing. AB: Data curation, Writing – original draft, Writing – review & editing. SSR: Data curation, Writing – original draft, Writing – review & editing. RS: Validation, Writing – original draft, Writing – review & editing. PP: Validation, Writing – original draft, Writing – review & editing. DS:

Data curation, Writing – original draft, Writing – review & editing. SantK: Data curation, Writing – original draft, Writing – review & editing. AA: Data curation, Writing – original draft, Writing – review & editing. KiS: Data curation, Writing – original draft, Writing – review & editing. KuS: Data curation, Writing – original draft, Writing – review & editing. AK: Conceptualization, Writing – original draft, Writing – review & editing. Manibhushan: Conceptualization, Writing – original draft, Writing – review & editing. PJ: Conceptualization, Writing – original draft, Writing – review & editing. VP: Conceptualization, Writing – original draft, Writing – review & editing. BJ: Conceptualization, Writing – original draft, Writing – review & editing. SN: Conceptualization, Writing – original draft, Writing – review & editing. SSM: Conceptualization, Writing – original draft, Writing – review & editing. RK (27th author): Writing – original draft, Writing – review & editing. SA: Writing – original draft, Writing – review & editing. VS: Writing – original draft, Writing – review & editing. DM: Writing – original draft, Writing – review & editing. MR: Writing – original draft, Writing – review & editing. AC: Data curation, Writing – original draft, Writing – review & editing. SR: Writing – original draft, Writing – review & editing. SC: Writing – original draft, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Generative AI statement

The authors declare that no Gen AI was used in the creation of this manuscript.

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References

- Ali, M., Ghosh, P. K., and Hazra, K. K. (2014). Resource conservation technologies in rice fallow. In: Resource conservation Technology in Pulses, P. K. Ghosh, N. Kumar, M. S. Venkatesh, K. K. Hazra and N. Nadarajan, Eds. Scientific Publishers, Jodhpur pp. 83–89.
- Ali, M., and Kumar, S. (2009). “Major technological advances in pulses-Indian scenario” in Milestones in food legumes research. eds. M. Ali and S. Kumar (Kanpur, India: Indian Institute of Pulses Research), 1–20.
- Ali, M. O., Sarkar, A., Rahman, M. M., Gahoonia, T. S., and Uddin, M. K. (2005). Improvement of lentil yield through seed priming in Bangladesh. *J. Lentil Res.* 2, 54–59.
- Annual Report. (2016–17). Government of India, Ministry of Agriculture & farmers welfare (Department of Agriculture, Cooperation & Farmers Welfare) Directorate of Pulses Development, Vindhyachal Bhavan, DPD/Pub/TR/19/2016-17: 46–47.
- Anonymous (2008). Annual Report of Indian Institute of Pulses Research, 2007–08, IIPR, Kanpur.
- Anonymous (2009). Report of expert group on pulses, Department of Agriculture and Cooperation, Ministry of Agriculture, Govt. of India, New Delhi, pp. 9–10.
- Anonymous (2015). Second advance estimates of food grain production in India, Department of Agriculture and Cooperation and Farmers' Welfare, Ministry of Agriculture, GOI.
- Bandyopadhyay, K. K., Sahoo, R. N., Singh, R., Pradhan, S., Singh, S., Krishna, G., et al. (2015). Characterization and crop planning of rabi-fallows using remote sensing and GIS. *Curr. Sci.* 108, 2051–2062.
- Bandyopadhyay, P. K., Singh, K. C., Mondal, K., Nath, R., Ghosh, P. K., Kumar, N., et al. (2016). Effects of stubble length of rice in mitigating soil moisture stress and on yield of lentil (*Lens culinaris* Medik) in rice–lentil relay crop. *Agric. Water Manag.* 173, 91–102. doi: 10.1016/j.agwat.2016.05.009
- Das, A., Lal, R., Patel, D. P., Ramkrushna, G. I., Layek, J., Ngachan, S. V., et al. (2014). Effects of tillage and biomass on soil quality and productivity of lowland rice cultivation by small scale farmers in north eastern India. *Soil Tillage Res.* 143, 50–58. doi: 10.1016/j.still.2014.05.012
- Di Bene, C., Gómez-López, M. D., Francaviglia, R., Farina, R., Blasi, E., Martínez-Granados, D., et al. (2022). Barriers and opportunities for sustainable farming practices and crop diversification strategies in Mediterranean cereal-based systems. *Front. Environ. Sci.* 10:861225. doi: 10.3389/fenvs.2022.861225
- Fatima, A., Singh, V. K., Babu, S., Singh, R. K., Upadhyay, P. K., Rathore, S. S., et al. (2023). Food production potential and environmental sustainability of different integrated farming system models in Northwest India. *Front. Sustain. Food Syst.* 7:959464. doi: 10.3389/fsufs.2023.959464
- Gangwar, K. S., Singh, K. S., Sharma, S. K., and Tomar, O. K. (2006). Alternative tillage and crop residue management in wheat after rice in sandy loam soils of indo-Gangatic plains. *Soil Tillage Res.* 88, 242–252. doi: 10.1016/j.still.2005.06.015
- Ghosh, P. K., Hazra, K. K., Nath, C. P., Das, A., and Acharya, C. L. (2016). Scope, constraints and challenges of intensifying rice (*Oryza sativa*) fallows through pulses. *Indian J. Agron.* 61, S122–S128.
- Gupta, S., and Bhowmick, M. K. (2005). Scope of growing lathyrus and lentil in relay cropping systems after rice in West Bengal, India. *Lathyrus Lathyrism Newsletter*. 4, 28–33.
- Kar, G., and Kumar, A. (2009). Evaluation of post-rainy season crops with residual soil moisture and different tillage methods in rice–fallow of eastern India. *Agric. Water Manag.* 96, 931–938. doi: 10.1016/j.agwat.2009.01.002
- Kar, G., Singh, R., and Verma, H. N. (2004). Productive and profitable management of rainfed lowland rice through intensive cropping and efficient water use. Research Bulletin No. 17. Water Technology Centre for Eastern Region, Bhubaneswar, Odisha, India, pp: 56.
- Kumar, K., and Babu, S. C. (2021). Can a weather-based crop insurance scheme increase the technical efficiency of smallholders? A case study of groundnut farmers in India. *Sustain. For.* 13:9327. doi: 10.3390/su13169327
- Kumar, R., Choudhary, J. S., Mishra, J. S., Mondal, S., Poonia, S. P., Monobullah, M., et al. (2022c). Outburst of pest populations in rice-based cropping systems under conservation agricultural practices in the middle indo-Gangetic Plains of South Asia. *Sci. Rep.* 12:3753. doi: 10.1038/s41598-022-07760-w
- Kumar, A., Dixit, S., Ram, T., Yadaw, R. B., Mishra, K. K., and Mandal, N. P. (2014). Breeding high-yielding drought-tolerant rice: genetic variations and conventional and molecular approaches. *J. Exp. Bot.* 65, 6265–6278. doi: 10.1093/jxb/eru363
- Kumar, N., Hazra, K. K., Singh, S., and Nadrajan, N. (2016). Constrains and prospects of growing pulses in rice fallows of India. *Ind. Farm.* 66, 13–16.
- Kumar, R., Makarana, G., Mishra, J. S., Choudhary, A. K., Hans, H., Biswas, A. K., et al. (2021). Performance of promising lentil (*Lens culinaris*) cultivars under zero-till condition for sustainable intensification of rice–fallow in eastern India. *Indian J. Agron.* 66, 444–448. doi: 10.59797/ija.v66i4.2891
- Kumar, R., Mishra, J. S., and Hans, H. (2018a). Enhancing productivity of rice–fallow of eastern India through inclusion of pulses and oilseeds. *Ind. Farm.* 68, 7–10.
- Kumar, R., Mishra, J. S., Mali, S. S., Mondal, S., Meena, R. S., Lal, R., et al. (2022a). Comprehensive environmental impact assessment for designing carbon-cum-energy efficient, cleaner, and eco-friendly production system for rice–fallow agroecosystems of South Asia. *J. Clean. Prod.* 331:129973. doi: 10.1016/j.jclepro.2021.129973
- Kumar, R., Mishra, J. S., Naik, S. K., Mondal, S., Meena, R. S., Kumar, S., et al. (2022b). Impact of crop establishment and residue management on soil properties and productivity in rice–fallow ecosystems of India. *Land Degrad. Dev.* 33, 798–812. doi: 10.1002/ldr.4204
- Kumar, R., Mishra, J. S., Rao, K. K., Bhatt, B. P., Hazra, K. K., Hans, H., et al. (2019a). Sustainable intensification of rice fallows of eastern India with suitable winter crop and appropriate crop establishment technique. *Environ. Sci. Pollut. Res. Int.* 26, 29409–29423. doi: 10.1007/s11356-019-06063-4
- Kumar, R., Mishra, J. S., Rao, K. K., Kumar, R., Singh, S. K., and Bhatt, B. P. (2018b). Evaluation of crop establishment techniques in rice–fallow of eastern indo–Gangetic Plains. Paper presented in the National Conference on “organic waste Management for Food and Environmental Security” during 8–10th February 2018; jointly organized by ICAR–Indian Institute of soil science and Bhopal chapter of Indian Society of Soil Science, Bhopal at Nabibagh, Berasia road, Bhopal-462 038 (M.P) pp: 26.
- Kumar, R., Mishra, J. S., Rao, K. K., Mondal, S., Hazra, K. K., Choudhary, J. S., et al. (2020). Crop rotation and tillage management options for sustainable intensification of rice–fallow agroecosystem in eastern India. *Sci. Rep.* 10:11146. doi: 10.1038/s41598-020-67973-9
- Kumar, R., Mishra, J. S., Upadhyay, P. K., and Hans, H. (2019b). Rice fallows in the eastern India: problems and prospects. *Indian J. Agric. Sci.* 89, 567–577. doi: 10.56093/ijas.v89i4.88838
- Manik, S. N., Pengilley, G., Dean, G., Field, B., Shabala, S., and Zhou, M. (2019). Soil and crop management practices to minimize the impact of waterlogging on crop productivity. *Front. Plant Sci.* 10:140. doi: 10.3389/fpls.2019.00140
- Mishra, J. S., and Kumar, R. (2018). Zero tillage options of pulses in rice-based cropping system. Farm mechanization for production. Pp: 122–136. Eds. Khare D, Nahatkar S B, Shrivastava, A. K. Jha A K. Scientific publishers (India), New Delhi.
- Mishra, J. S., Kumar, R., Kumar, R., Rao, K. K., Singh, S. K., Idris, M., et al. (2016). Evaluation of pulses and oilseed under different crop establishment methods in rice–fallow of eastern India. In: Extended summaries Vol. 2: 4th international agronomy congress, 22–26, 2016, New Delhi, India, 1272–1274 pp.
- Mohapatra, B. K., Veetil, P. C., Kumar, A., and Kumar, V. (2022). Rice–fallow management in eastern India: Challenges and opportunities for enhancing system productivity and profitability. *Economic Affairs*, 67, 859–867. doi: 10.46852/0424-2513.5.2022.21
- Mondal, S. S., and Ghosh, A. (2005). Integrated nutrient management on the productivity and nutrient uptake of crops in rice–lathyrus (as utera)–sesame cropping system under rainfed lowland ecosystem. *J. Crop Weed* 1, 12–16.
- NAAS (2013). Improving productivity of Rice fallows. Policy paper no. 64, National Academy of Agricultural Sciences, New Delhi. 16 p.
- Nazir, N., Badri, Z. A., Bhat, N. A., Bhat, F. A., Sultan, P., Bhat, T. A., et al. (2022). Effect of the combination of biological, chemical control and agronomic technique in integrated management pea root rot and its productivity. *Sci. Rep.* 12:11348. doi: 10.1038/s41598-022-15580-1
- Pande, S., Sharma, M., Ghosh, R., Rao, S. K., Sharma, R. N., and Jha, A. K. (2012). Opportunities for chickpea production in rainfed rice fallows of India–baseline survey Report. Grain legumes program Report no. 1. ICRIASAT, Patancheru 502324, Andhra Pradesh, India, 56 pp.
- Praharaj, C. S., Singh, U., Singh, N. P., and Shivay, Y. S. (2016a). Popularizing micro-irrigation in pulses for higher yield and water productivity. *Indian Farming* 66, 71–72. Available online at: <https://epubs.icar.org.in/index.php/IndFarm/article/view/84889>
- Praharaj, C. S., Singh, U., Singh, S. S., Singh, N. P., and Shivay, Y. S. (2016b). Supplementary and lifesaving irrigation for enhancing pulses production, productivity, and water use efficiency in India. *Indian J. Agron.* 61, S249–S261.
- Rautaray, S. K. (2008). Productivity and economics of rice based utera crops for lower Assam. *J. Food Legumes* 21, 51–52.
- Richards, S., Rao, L., Connelly, S., Raj, A., Raveendran, L., Shirin, S., et al. (2021). Sustainable water resources through harvesting rainwater and the effectiveness of a low-cost water treatment. *J. Environ. Manag.* 286:112223. doi: 10.1016/j.jenvman.2021.112223
- Shome, S., Barman, A., and Solaiman, Z. M. (2022). Rhizobium and phosphate solubilizing bacteria influence the soil nutrient availability, growth, yield, and quality of soybean. *Agriculture* 12:1136. doi: 10.3390/agriculture12081136
- Sims, B., and Kienzie, J. (2017). Sustainable agricultural mechanization for smallholders: what is it and how can we implement it? *Agriculture* 7:50. doi: 10.3390/agriculture7060050
- Singh, N. P., Praharaj, C. S., and Sandhu, J. S. (2016). Utilizing untapped potential of rice fallow of east and north-East India through pulse production. *Indian J. Genet.* 76, 388–398. doi: 10.5958/0975-6906.2016.00058.4
- Velasco-Muñoz, J. F., Aznar-Sánchez, J. A., Batlles-de-laFuente, A., and Fidelibus, M. D. (2019). Rainwater harvesting for agricultural irrigation: an analysis of global research. *Water* 11:1320. doi: 10.3390/w11071320

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