
**ROOT SYSTEM COMPLEMENTARITY ENHANCES MINERAL
NUTRIENT ACQUISITION IN CHICKPEA–PEA
INTERSPECIFIC INTERACTIONS**

***Ranvijay Singh and Ajoy Kumar Singh**

Department of Botany, T.D.P.G. College, Jaunpur,
Veer Bahadur Singh Purvanchal University,
Jaunpur, UP, India.

*Corresponding Author: Ranvijay Singh

Abstract

Plant adaptation to a particular environment and evolution depend largely on their ability to acquire nutrients from the soil. Roots play an essential role in nutrient acquisition, thus influencing plant growth and productivity. With the rise in global population, to meet the food demand, several strategies have been adopted worldwide to increase the yield. One such strategy is intercropping, which reduces the land requirement and also positively influences plant growth. To date, numerous studies of intercropping systems have been well reported, which have been known to increase the productivity of the crop. The most common among them are cereals and legumes. However, studies involving legume-legume intercropping system is scarce. In this study, we investigated the effects of interspecific root interaction between chickpea (*Cicer arietinum*) and pea (*Pisum sativum*) on nutrient uptake, rhizosphere nutrient availability, and plant growth performance. Overall, our findings suggest that interspecific root interaction between chickpea and pea promotes rhizosphere modification and nutrient acquisition, ultimately enhancing plant growth. This study highlights the importance of root-mediated processes in legume–legume interactions and provides insights into potential strategies for improving nutrient use efficiency in mixed cropping systems.

Keywords: Legume–legume interactions, Intercropping systems, Rhizosphere nutrient, Kjeldahl digestion.

Introduction

The global population is projected to reach 9.7 billion by 2050, posing significant challenges for ensuring sustainable and sufficient food production (Hamad et al. 2026). One major reason behind this food scarcity is the limited farmland. Thus, to circumvent this problem and ensure that this ever-increasing demand is met, intercropping has been introduced and widely used throughout the globe, contributing almost 50% rise in agricultural productivity in developing countries (Li et al. 2020; Brooker et al. 2021; Li et al. 2024; Zhang et al. 2024). Several studies have demonstrated that intercropping systems can enhance nutrient uptake through modifications in root system architecture, increased rhizosphere microbial activity, and enhanced release of root exudates that facilitate nutrient solubilization (Li et al., 2014; Brooker et al., 2015). Such interactions can improve nutrient availability in the rhizosphere and more efficiently use soil resources.

Most common intercropping systems include cereal-legume combinations, such as maize with cowpea or soybean, and sorghum with pigeon pea. In this interaction, legumes are responsible for fixing atmospheric nitrogen, thereby enhancing soil fertility for the partner-associated cereal crops. Some other widely used combinations are oilseed-pulse, like mustard with chickpea and groundnut with pigeon pea, which are also widely used because they improve nutrient efficiency and reduce pest incidence. In addition, there are studies where cereal-vegetable combination systems have been evaluated, such as maize with beans or pumpkins. In this scenario, the latter helps in better ground cover and weed suppression. Plantation crops like coconut are often intercropped with pineapple or banana to utilize the space between trees and increase the net income. Vegetable-vegetable intercropping systems, such as tomato with onion or carrot with radish, allow efficient use of space and nutrients due to differences in plant growth habits and rooting depths (Willey, 1979; Andrews & Kassam, 1976; Beets, 1982; Francis, 1986; Nair, 1993). Overall, intercropping enhances land productivity, stabilizes yields, reduces pest and disease incidences, and promotes sustainability. However, comparatively very little research has focused on legume-legume intercropping systems and their potential benefits. While legumes are well known for their ability to fix atmospheric nitrogen through symbiotic associations with rhizobia, the interactions between two legume species grown together are not yet fully understood. In particular, limited information is available on how their root architectures differ, how their root systems interact in the rhizosphere, and how these interactions influence nutrient acquisition and resource partitioning. The differences in their root depth, branching patterns, and nutrient uptake

strategies may allow complementary use of soil nutrients such as phosphorus and nitrogen, potentially reduce competition and improve nutrient-use efficiency. Moreover, root interactions may influence symbiotic processes such as nodulation and nitrogen fixation in legumes. The formation of root nodules is a key determinant of nitrogen acquisition in leguminous crops, and this process can be influenced by soil nutrient availability, plant interactions, and rhizosphere conditions. Despite these possibilities, more research is needed to determine whether legume-legume intercropping leads to improved biomass production, yield stability, and productivity, as well as how these systems influence root interactions and nutrient dynamics in the soil (Lithourgidis et al., 2011; Jensen et al., 2020; Brooker et al., 2015; Dakora & Phillips, 2002).

Crops such as chickpea (*Cicer arietinum*) and pea (*Pisum sativum*) are widely cultivated pulse crops and serve as major sources of dietary protein worldwide. In addition to their nutritional importance, these species contribute significantly to soil fertility through biological nitrogen fixation and through the release of root exudates that alter rhizosphere nutrient dynamics individually (Dakora & Phillips, 2002; Hinsinger et al., 2011). In a previous study, chickpea and pea have demonstrated interspecific root interaction across varied soil matrices. And it was observed that chickpea and pea grow best in sandy loam soil from dharmapur (Singh et al. 2025). Despite increasing interest in below-ground interactions in intercropping systems, the interaction between chickpea (*Cicer arietinum*) and pea (*Pisum sativum*) roots and its consequences for nutrient uptake, rhizosphere nutrient availability, and plant performance have been very little studied. The study aims to investigate the root-root interaction between chickpea and pea, regulating nutrient uptake, rhizosphere nutrient availability, root exudation, nodulation, and plant growth performance. By integrating measurements of root morphological traits, rhizosphere nutrient dynamics, and physiological parameters, to provide insights into how root-mediated processes influence nutrient acquisition and productivity in mixed legume cropping systems, thereby influencing overall performance and yield of the plant.

Material and Methods

Plant Material and Experimental Design

Seeds of chickpea (*Cicer arietinum*) and pea (*Pisum sativum*) were used in this study. Seeds were surface sterilized with 1% sodium hypochlorite for 3 min and rinsed thoroughly with sterile distilled water before sowing. Plants were grown in plastic pots (20 cm diameter) filled with sandy

loam soil collected from dharmapur. The experiment consisted of three treatments, namely chickpea monoculture, pea monoculture, and chickpea-pea mixed culture. In the mixed culture treatment, one seedling of each species was grown in the same pot. Each treatment consisted of three biological replicates arranged in a completely randomized design. Plants were grown under controlled greenhouse conditions (25 ± 2 °C, 16 h light / 8 h dark photoperiod) and irrigated regularly with distilled water. Plants were harvested 21 days after sowing for analysis of root traits, nutrient uptake, rhizosphere properties, nodulation, and plant growth parameters.

Mineral Uptake Analysis

Shoots and roots were harvested separately, washed thoroughly with distilled water, and dried at 65 °C for 72 h to obtain constant dry weight. Dried samples were ground into a fine powder using a mortar and pestle. The total nitrogen content of the root and shoot separately was determined using the Kjeldahl digestion method. ~ 0.2 g of dried plant tissue was digested in concentrated sulfuric acid with a catalyst mixture. After digestion, the solution was distilled and titrated to determine total nitrogen content. Phosphorus concentration was determined using the molybdate blue colorimetric assay. Digested samples were reacted with ammonium molybdate reagent, and absorbance was measured at 882 nm using a spectrophotometer. Potassium content was measured using a flame photometer after acid digestion of plant tissue samples. Iron concentration was quantified using a colorimetric method following acid digestion. The absorbance of the Fe-complex was measured spectrophotometrically at 510 nm.

Rhizosphere Nutrient Availability

Rhizosphere soil samples were collected by gently shaking the roots to obtain soil adhering to the root surface. The soil samples were air-dried and passed through a 2-mm sieve before analysis. Available nitrogen was determined using the alkaline permanganate method. Available phosphorus was measured using the Olsen extraction method followed by colorimetric determination using the molybdate reagent. Soil pH was measured using a digital pH meter in a soil–water suspension (1:2.5 w/v).

Root Exudate Analysis

To analyze root exudates, seedlings of chickpea and pea were grown in hydroponic containers containing half-strength Hoagland nutrient solution. Plants were allowed to grow for 10-12 days,

after which roots were gently rinsed with distilled water and transferred to fresh nutrient solution for exudate collection over a 24 h period. The pH of the collected nutrient solution was measured using a digital pH meter. Total organic acids in the root exudate solution were quantified using a spectrophotometric assay based on reaction with appropriate reagents, and absorbance was measured at 210-220 nm. Total phenolic content was determined using the Folin–Ciocalteu method. Absorbance was measured at 765 nm, and phenolic concentration was expressed as gallic acid equivalents.

Nodulation Analysis

At harvest, plants were carefully uprooted and washed to remove soil without damaging the nodules. The total number of nodules present on each plant root system was counted manually. All nodules were detached from the roots and dried at 60 °C for 48 h to determine nodule dry weight, which was expressed as mg per plant.

Plant Growth Performance

Shoot tissues were separated from the roots and dried at 65 °C for 72 h to determine dry biomass. Chlorophyll content was measured using a SPAD chlorophyll meter. Measurements were taken from fully expanded leaves and expressed as SPAD values. Alternatively, chlorophyll can be determined spectrophotometrically after extraction with 80% acetone, and absorbance measured at 645 nm and 663 nm. Leaf nitrogen concentration was determined using the Kjeldahl method after acid digestion of dried leaf samples.

Statistical Analysis

All experiments were conducted with three biological replicates. Data were expressed as mean \pm SE. Statistical differences among treatments were determined using one-way analysis of variance (ANOVA) followed by Tukey's multiple comparison test at $P < 0.05$. Statistical analyses were performed using R software.

Results

Effect of Chickpea-Pea Intercropping on Plant Growth and Physiological Traits

Plant growth and physiological parameters showed clear differences between monoculture and intercropping treatments (Figure 1). The seedling showed better growth when chickpea and pea were grown together (Figure 1A). Shoot biomass were significantly higher in the intercropping

system for both species (Figure 1B). Chickpea grown in the intercrop produced greater shoot biomass (~ 3.3 g) compared to chickpea grown in monoculture (~ 2.9 g). Similarly, pea plants in the intercropping system showed increased shoot biomass (~ 2.6 g) compared to pea monoculture (~ 2.2 g). Leaf chlorophyll content, measured as SPAD values, also increased under intercropping conditions (Figure 1C). Chickpea plants grown in the intercrop exhibited higher chlorophyll content (~ 42–43 SPAD) compared with monoculture plants (~ 39 SPAD). A similar trend was observed in pea, where intercropped plants showed higher SPAD values (~ 39–40) compared to monoculture plants (~ 36–37). Leaf nitrogen concentration followed the same pattern (Figure 1D). Chickpea plants grown in the intercropping system showed higher leaf nitrogen levels (~ 3.4%) compared with monoculture plants (~ 3.1%). Likewise, pea plants exhibited increased leaf nitrogen concentration under intercropping (~ 3.0%) compared with monoculture conditions (~ 2.8%).

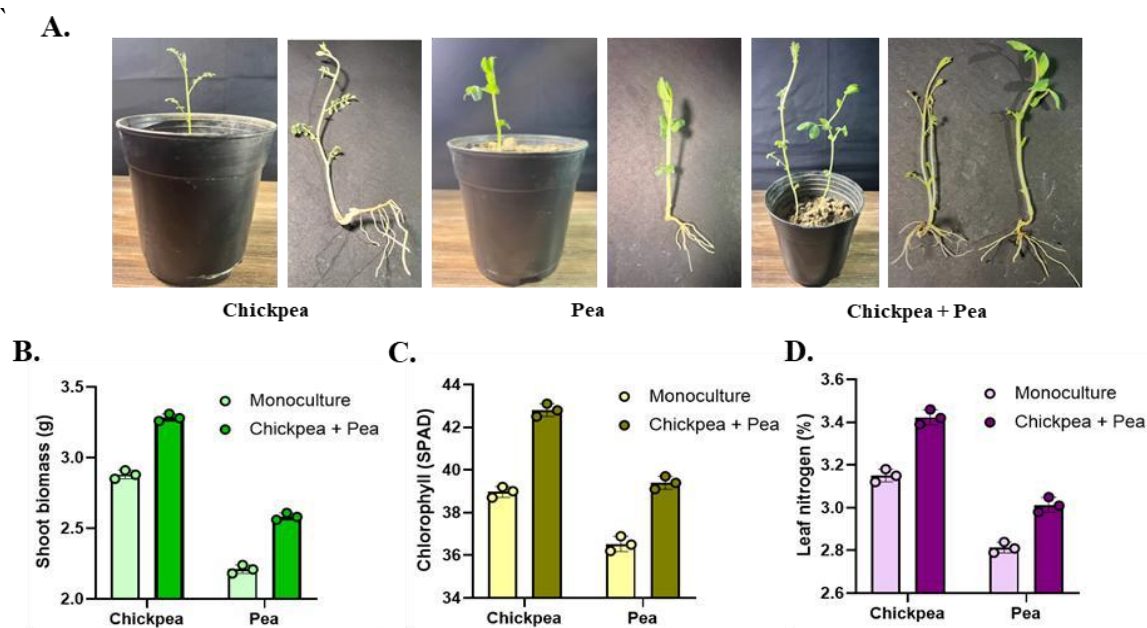


Figure 1. Growth and physiological responses of chickpea and pea under monoculture and chickpea– pea intercropping systems. (A) Chickpea and pea plant growing in monoculture and mixed culture (B) Shoot biomass(g), (C) leaf chlorophyll content measured as SPAD values, and (D) leaf nitrogen concentration (%). Bars represent mean values \pm SE of three biological replicates, and individual points indicate biological replicates. Intercropping enhanced shoot biomass, chlorophyll content, and leaf nitrogen concentration in both chickpea and pea compared with monoculture conditions.

Nutrient analysis demonstrates efficient nutrient acquisition in intercropping

Nutrient uptake analysis has been carried out separately in both the root and the shoot. The data revealed significant differences in nitrogen (N), phosphorus (P), and potassium (K) concentrations

among the treatments (Figure 2). In roots, chickpea plants showed higher nitrogen concentration ($\sim 3.8 \text{ mg g}^{-1} \text{ DW}$) compared to pea ($\sim 3.2 \text{ mg g}^{-1} \text{ DW}$), while the chickpea-pea intercrop exhibited the highest nitrogen concentration ($\sim 4.6 \text{ mg g}^{-1} \text{ DW}$). A similar result was observed for phosphorus and potassium concentrations. Root phosphorus concentration was higher in the intercropping system ($\sim 4.5 \text{ mg g}^{-1} \text{ DW}$) compared to chickpea ($\sim 3.8 \text{ mg g}^{-1} \text{ DW}$) and pea ($\sim 3.2 \text{ mg g}^{-1} \text{ DW}$). Likewise, root potassium concentration was greatest in the intercrop treatment ($\sim 25 \text{ mg g}^{-1} \text{ DW}$), followed by chickpea and pea monocultures (Figure 2 A-C). Further, in the shoots as well, the chickpea-pea intercropping system showed the highest shoot nitrogen, phosphorus, and potassium concentrations (4.9, 4.6, and $26.9 \text{ mg g}^{-1} \text{ DW}$, respectively), whereas pea monoculture displayed the lowest nutrient levels.

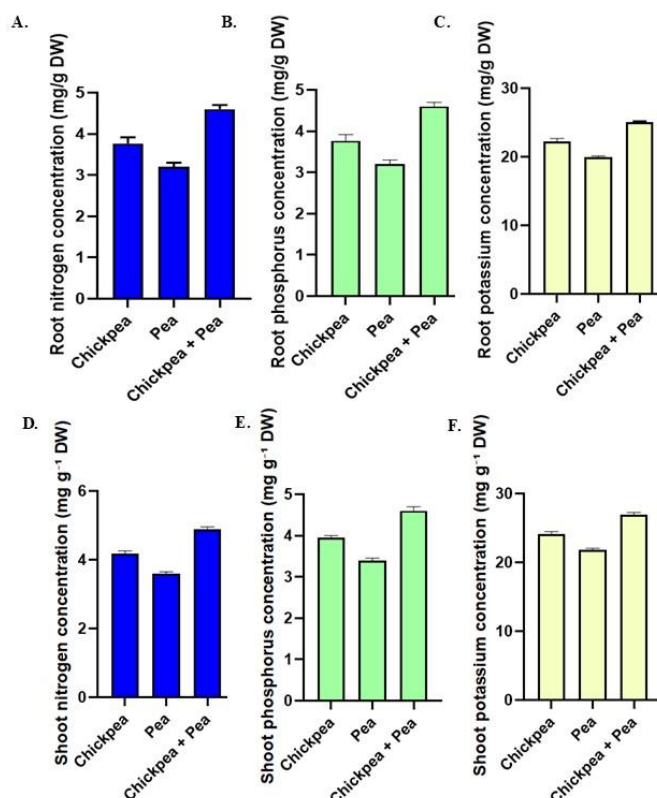


Figure 2. Root and shoot nutrient concentrations in chickpea and pea grown under monocropping and intercropping conditions. (A) Root nitrogen concentration, (B) Root phosphorus concentration, (C) Root potassium concentration, (D) Shoot nitrogen concentration, (E) Shoot phosphorus concentration, and (F) Shoot potassium concentration expressed as mg g^{-1} dry weight (DW). Plants were grown either as monocultures (chickpea or pea) or as a chickpea-pea intercrop. Bars represent mean values \pm SE of biological replicates.

Chickpea monoculture exhibited intermediate nutrient concentrations. These results indicate that intercropping enhanced nutrient uptake and accumulation in both root and shoot tissues, suggesting improved nutrient acquisition and utilization when the two legume species were grown together (Figure 2 D-F).

Effect of Intercropping on Soil Nutrient Availability and Soil pH

The soil nutrient analysis revealed significant differences in available nitrogen, phosphorus, and soil pH among the cropping treatments (Figure 3). The concentration of available nitrogen was highest in the chickpea-pea intercropping system ($\sim 50 \text{ mg kg}^{-1}$), followed by chickpea monoculture ($\sim 46 \text{ mg kg}^{-1}$), while the lowest nitrogen availability was observed in pea monoculture ($\sim 42 \text{ mg kg}^{-1}$) (Figure 3A). A similar pattern was observed for available phosphorus as well, where the intercropping treatment showed the highest phosphorus concentration ($\sim 11 \text{ mg kg}^{-1}$), whereas chickpea monoculture exhibited moderate levels ($\sim 8.3 \text{ mg kg}^{-1}$), and pea monoculture showed the lowest phosphorus availability ($\sim 7.4 \text{ mg kg}^{-1}$) (Figure 3B). Further, soil pH was also determined across treatments (Figure 3C). The result showed pea monoculture with the highest soil pH (~ 6.7), followed by chickpea monoculture (~ 6.5). In contrast, the chickpea-pea intercropping system showed a slightly lower soil pH (~ 6.2). These results suggest that intercropping of chickpea and pea enhanced soil nutrient availability, particularly nitrogen and phosphorus, while slightly reducing soil pH, which may influence nutrient solubility and availability in the rhizosphere.

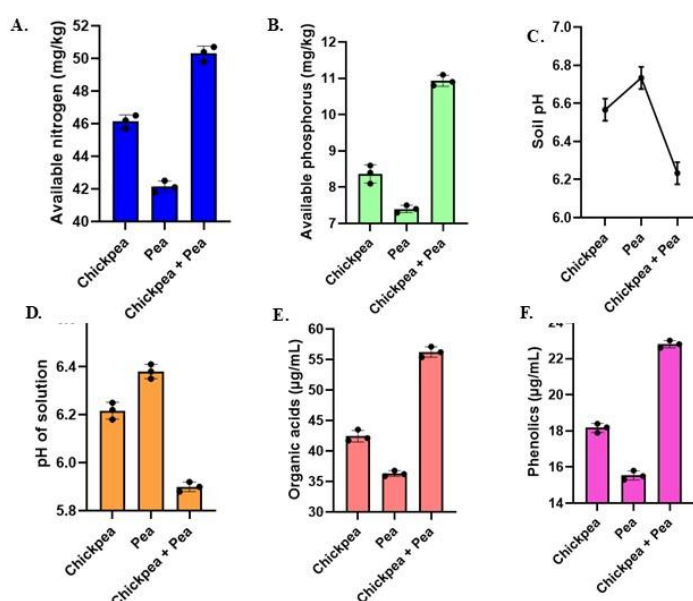


Figure 3. Effect of monocropping and intercropping of chickpea and pea on soil nutrient availability, soil pH and root exudates (A) Available nitrogen (mg kg^{-1}), (B) available phosphorus (mg kg^{-1}), (C) soil pH measured in soils, (D) pH of the root exudate solution, (E) concentration of total organic acids ($\mu\text{g mL}^{-1}$), and (F) total phenolic compounds ($\mu\text{g mL}^{-1}$). Bars represent mean values \pm SE of three biological replicates.

Root Exudate Composition in Chickpea and Pea Under Monocropping and Intercropping

Analysis of root exudate revealed notable differences in pH, organic acid concentration, and phenolic compound release among the cropping treatments. The pH of the root exudate solution varied across treatments, with pea monoculture showing the highest pH (~ 6.4), followed by chickpea monoculture (~ 6.2). In contrast, the chickpea-pea intercropping system exhibited a lower pH (~ 5.9), indicating greater acidification of the rhizosphere (Figure 3D).

The concentration of total organic acids was also determined and was found to be markedly higher in the intercropping treatment ($\sim 56 \mu\text{g mL}^{-1}$) compared with chickpea monoculture ($\sim 42 \mu\text{g mL}^{-1}$) and pea monoculture ($\sim 36 \mu\text{g mL}^{-1}$) (Figure 3E). Similarly, the concentration of released phenolic compounds was also determined and was found to be highest in the chickpea-pea intercropping system ($\sim 23 \mu\text{g mL}^{-1}$), whereas chickpea monoculture showed moderate levels ($\sim 18 \mu\text{g mL}^{-1}$) and pea monoculture recorded the lowest phenolic content ($\sim 15 \mu\text{g mL}^{-1}$) (Figure 3F). These findings suggest that intercropping of chickpea and pea enhances the secretion of root exudates, particularly organic acids and phenolic compounds, which may contribute to rhizosphere acidification and improved nutrient mobilization in the soil.

Effect of Intercropping on Root Nodulation in Chickpea and Pea

Root nodulation differed between monoculture and intercropping systems in both chickpea and pea (Figure 4). In chickpea, plants grown under intercropping conditions produced a higher number of nodules (~ 23 nodules per plant) compared with monoculture plants (~ 19 nodules per plant) (Figure 4A). A similar trend was observed in pea, where intercropped plants formed more nodules (~ 17 nodules per plant) than monoculture plants (~ 14 nodules per plant). Nodule biomass also showed a sharp increase under intercropping conditions (Figure 4B). Chickpea plants grown in the intercropping condition exhibited the highest nodule biomass (~ 94 mg), compared with chickpea monoculture (~ 80 mg). Likewise, pea plants showed greater nodule biomass in the intercropping system (~ 71 mg) relative to monoculture plants (~ 61 mg).

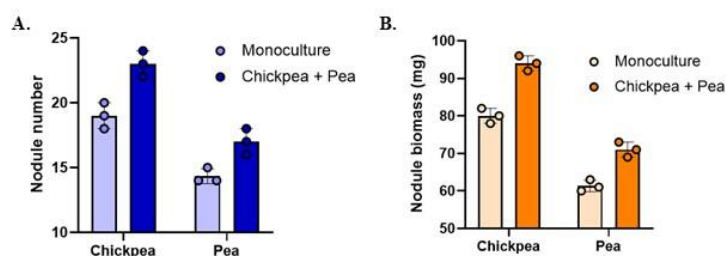


Figure 4. Effect of monoculture and chickpea–pea intercropping on root nodulation parameters. (A) Number of root nodules and (B) nodule biomass (mg) in chickpea and pea plants grown either as monocultures or under chickpea–pea intercropping conditions. Bars represent mean values \pm SE of three biological replicates, and individual data points indicate biological replicates.

Overall, these results indicate that chickpea–pea intercropping enhances nodulation in both species, increasing the number of nodules and total nodule biomass. This enhanced nodulation may contribute to improved biological nitrogen fixation within the intercropping system. In total, these findings illustrate that chickpea–pea intercropping improves plant growth and physiological performance, as reflected by increased shoot biomass, enhanced chlorophyll content, and higher leaf nitrogen concentration in both species. These improvements suggest more efficient nutrient acquisition and enhanced plant productivity under intercropping conditions.

Discussion

The study demonstrates that intercropping chickpea and pea significantly improves nutrient acquisition and accumulation in plant tissues. Both root and shoot concentrations of nitrogen (N), phosphorus (P), and potassium (K) were higher in the intercropping treatment compared with monoculture systems. These results suggest that interspecific interactions between the two legumes improved nutrient uptake efficiency. Intercropping systems are widely known to enhance resource use efficiency through complementary root architecture, niche differentiation, and facilitative interactions in the rhizosphere (Li et al., 2014; Brooker et al., 2015). Such interactions allow coexisting species to exploit soil nutrients more efficiently than when grown individually.

Previous studies have also reported that legume-based intercropping systems improve nutrient uptake and biomass production due to enhanced rhizosphere interactions and improved nutrient mobilization (Zhang and Li, 2003; Brooker et al., 2015). For example, intercropping chickpea with other crops has been shown to increase phosphorus uptake and improve nutrient use efficiency compared with monoculture systems (Alam, 2017). Similarly, increased nutrient uptake in intercropping systems has been attributed to complementary resource acquisition strategies that

reduce direct competition for nutrients and promote more efficient utilization of soil resources (Li et al., 2014). In the present study, the higher nutrient concentrations observed in the intercrop suggest that chickpea and pea may exploit different soil nutrient pools or rooting depths, leading to improved nutrient acquisition. Such complementarity represents a key ecological mechanism underlying the productivity advantages often observed in intercropping systems (Brooker et al., 2015).

Soil analysis revealed that intercropping significantly increased the availability of nitrogen and phosphorus in the rhizosphere compared with monocropping systems. This enhanced nutrient availability may result from several mechanisms, including improved biological nitrogen fixation, increased microbial activity, and greater rhizosphere nutrient mobilization. Legumes possess the ability to fix atmospheric nitrogen through symbiotic interactions with rhizobia, thereby enriching soil nitrogen pools and benefiting neighboring plants (Dakora and Phillips, 2002). In intercropping systems, enhanced biological nitrogen fixation and root turnover can increase nitrogen availability in the rhizosphere, thereby improving nutrient uptake by plants. Previous studies have shown that legume-based intercropping systems enhance soil nitrogen availability and nutrient cycling, contributing to improved crop productivity (Zhang and Li, 2003; Li et al., 2014). In addition to increased nutrient availability, the intercropping treatment resulted in a slight reduction in soil pH. Rhizosphere acidification is a well-known mechanism through which plants mobilize poorly available nutrients, particularly phosphorus (Hinsinger et al., 2011). The lower soil pH observed in the intercropping system may therefore facilitate greater solubilization of phosphorus and other mineral nutrients, contributing to the enhanced nutrient uptake observed in the plants.

One of the most notable findings of this study was the increased secretion of organic acids and phenolic compounds under intercropping conditions. Root exudates play a critical role in shaping rhizosphere chemistry and regulating nutrient availability (Dakora and Phillips, 2002). Organic acids can mobilize mineral nutrients by chelating metal ions and solubilizing phosphate bound to soil particles (Hinsinger et al., 2011). The higher concentrations of organic acids observed in the intercropping treatment likely contributed to the rhizosphere acidification detected in this study. Organic acids such as citrate, malate, and oxalate are known to release phosphorus from insoluble complexes, thereby increasing its availability for plant uptake (Hinsinger et al., 2011). Increased root exudation is frequently observed in intercropping systems where plants respond to neighboring species through chemical signaling and altered root metabolism (Brooker et al., 2015).

Phenolic compounds released by roots can also influence microbial activity and nutrient cycling in the rhizosphere. Moreover, phenolic compounds may participate in signaling processes that influence symbiotic interactions with rhizobia and other beneficial microbes (Dakora and Phillips, 2002). Enhanced root exudation has previously been associated with improved nutrient mobilization and enhanced rhizosphere interactions in legume-based intercropping systems (Zhalnina et al., 2018).

The present study also revealed that intercropping significantly increased both nodule number and nodule biomass in chickpea and pea. Enhanced nodulation suggests that the intercropping system stimulated symbiotic nitrogen fixation in both species. In legumes, root exudates such as flavonoids play a crucial role in initiating symbiosis with rhizobia by activating nodulation genes in rhizobial bacteria (Dakora and Phillips, 2002). Increased root exudation under intercropping conditions may therefore enhance rhizobial signaling and promote nodule formation. Previous studies have demonstrated that intercropping can stimulate the release of signaling molecules in root exudates, thereby promoting rhizobial colonization and nodulation (Zhalnina et al., 2018). The increased nodulation observed in the present study likely contributed to the higher nitrogen concentrations detected in plant tissues and soil in the intercropping system. Enhanced biological nitrogen fixation not only improves plant nitrogen nutrition but also contributes to greater soil nitrogen availability, benefiting the overall cropping system (Li et al., 2014).

The improved nutrient status of plants in the intercropping treatment was reflected in enhanced growth and physiological performance. Both chickpea and pea exhibited increased shoot biomass, higher chlorophyll content, and greater leaf nitrogen concentration under intercropping conditions. Nitrogen is a key component of chlorophyll and plays a central role in photosynthesis. The higher SPAD values observed in intercropped plants therefore likely reflect improved nitrogen nutrition and enhanced photosynthetic capacity. Similarly, increased phosphorus availability can stimulate energy metabolism and root development, further supporting plant growth (Hinsinger et al., 2011). These findings are consistent with previous studies demonstrating that intercropping systems often produce greater biomass and productivity than monocultures due to improved resource utilization and facilitative interactions between species (Li et al., 2014; Brooker et al., 2015). Taken together, the results suggest that chickpea–pea intercropping enhances plant performance through multiple interconnected mechanisms. These include increased root exudation, rhizosphere acidification, improved nutrient mobilization, enhanced nodulation, and

greater nutrient uptake. The synergistic interactions between the two legumes ultimately lead to improved plant growth and nutrient acquisition. Such findings highlight the potential of legume–legume intercropping systems as sustainable agricultural practices that can improve soil fertility, reduce dependence on chemical fertilizers, and enhance crop productivity.

References

1. Alam, M. K. (2017). Nutrient uptake and productivity of chickpea under different intercropping systems. *Legume Research*, 40(2), 354–358.
2. Andrews, D. J., & Kassam, A. H. (1976). The importance of multiple cropping in increasing world food supplies. In R. I. Papendick, P. A. Sanchez, & G. B. Triplett (Eds.), *Multiple Cropping* (pp. 1–10). American Society of Agronomy.
3. Beets, W. C. (1982). *Multiple Cropping and Tropical Farming Systems*. Westview Press, Boulder, Colorado.
4. Brooker, R. W., Bennett, A. E., Cong, W. F., Daniell, T. J., George, T. S., Hallett, P. D., Hawes, C., Iannetta, P. P. M., Jones, H. G., Karley, A. J., Li, L., McKenzie, B. M., Pakeman, R. J., Paterson, E., Schöb, C., Shen, J., Squire, G., Watson, C., Zhang, C., Zhang, F., & White, P. J. (2015). Improving intercropping: a synthesis of research in agronomy, plant physiology and ecology. *New Phytologist*, 206, 107–117.
5. Brooker, R. W., Karley, A. J., Newton, A. C., Pakeman, R. J., & Schöb, C. (2021). Facilitation and sustainable agriculture: a mechanistic approach to reconciling crop production and environmental protection. *Functional Ecology*, 35, 2363–2375.
6. Dakora, F. D., & Phillips, D. A. (2002). Root exudates as mediators of mineral acquisition in low-nutrient environments. *Plant and Soil*, 245, 35–47.
7. Francis, C. A. (1986). *Multiple Cropping Systems*. Macmillan Publishing Company, New York.
8. Hamad, A., Rahman, M., & Karim, M. (2026). Global food demand and sustainable agricultural production under increasing population pressure. *Agricultural Systems*, 195, 103–112.
9. Hinsinger, P., Bengough, A. G., Vetterlein, D., & Young, I. M. (2011). Rhizosphere: biophysics, biogeochemistry and ecological relevance. *Plant and Soil*, 321, 117–152.

10. Jensen, E. S., Carlsson, G., & Hauggaard-Nielsen, H. (2020). Intercropping of grain legumes and cereals improves the use of soil nitrogen resources and reduces the requirement for synthetic fertilizer. *Agronomy for Sustainable Development*, 40, 1–14.
11. Li, L., Tilman, D., Lambers, H., & Zhang, F. (2014). Plant diversity and overyielding: insights from belowground facilitation of intercropping in agriculture. *New Phytologist*, 203, 63–69.
12. Li, L., Zhang, F., & Li, X. (2020). Crop diversification through intercropping enhances agricultural productivity and sustainability. *Nature Plants*, 6, 989–998.
13. Li, L., Zhang, F., & Li, X. (2024). Advances in intercropping research for sustainable intensification of agriculture. *Trends in Plant Science*, 29, 65–78.
14. Lithourgidis, A. S., Dordas, C. A., Damalas, C. A., & Vlachostergios, D. (2011). Annual intercrops: an alternative pathway for sustainable agriculture. *Australian Journal of Crop Science*, 5, 396–410.
15. Nair, P. K. R. (1993). *An Introduction to Agroforestry*. Kluwer Academic Publishers, Dordrecht.
16. Singh, R., & Singh, A. (2025). The Root System Architecture and Interspecific Interactions across Varied Soil Matrices. *Scope*, 15, 4.
17. Willey, R. W. (1979). Intercropping—its importance and research needs. Part 1. Competition and yield advantages. *Field Crop Abstracts*, 32, 1–10.
18. Zhalnina, K., Louie, K. B., Hao, Z., Mansoori, N., da Rocha, U. N., Shi, S., Cho, H., Karaoz, U., Loqué, D., Bowen, B. P., Firestone, M. K., Northen, T. R., & Brodie, E. L. (2018). Dynamic root exudate chemistry and microbial substrate preferences drive patterns in rhizosphere microbial community assembly. *Nature Microbiology*, 3, 470–480.
19. Zhang, F., & Li, L. (2003). Using competitive and facilitative interactions in intercropping systems enhances crop productivity and nutrient-use efficiency. *Plant and Soil*, 248, 305–312.
20. Zhang, T. T., Li, X. F., & Zhang, F. S. (2024). Intercropping systems improve nutrient use efficiency and crop yield under limited farmland conditions. *Agricultural Research*, 13, 112–123.