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Research Article

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**Overcoming Nutrient Asynchrony: Targeted Nitrogen Reduction Drives Plant-
Soil-Enzyme Synergy in an Arid Apricot-Soybean System**

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Abstract

Bckground and aims Intensive agriculture in arid oases relies heavily on excessive nitrogen (N) inputs, driving environmental degradation and resource depletion. While agroforestry systems enhance resource sharing, their ecological potential is often constrained by a lack of targeted nutrient management. This study elucidates how targeting N reduction exclusively to the understory crop regulates plant-soil synergies in a juvenile apricot-soybean intercropping system.

Methods Through a two-year field experiment systematically conducted in Shihezi, Xinjiang, four treatments were evaluated: monoculture with conventional N (MS) and reduced N (MSN), alongside intercropping with conventional N (IS) and reduced N (ISN).

Results Targeted N reduction dynamically regulated soil inorganic N, facilitating early-stage N retention to mitigate monoculture nutrient imbalances. Furthermore, during the critical pod-filling stage (R6), it significantly stimulated belowground microecological potential. Compared to IS, the R6 activities of soil β -glucosidase, N-acetyl- β -D-glucosaminidase, and nitrite reductase increased by 59.87%, 50.03%, and up to

121.96%, respectively. Physiologically, this late-stage enzymatic mineralization alleviated stomatal limitations. At the R6 stage, soybean stomatal conductance was 131.99% higher than MSN, maintaining intercellular CO₂ > 300.00 μmol/mol. This compensatory effect increased R6 dry matter accumulation by 19.98% relative to IS, allocating 28.40%-28.70% of photosynthates to grains. Although interspecific competition reduced absolute soybean yields, the land equivalent ratio of the ISN system consistently exceeded 1.00, and its income equivalent ratio reached 1.25-1.35, demonstrating robust system-level resource synergy.

Conclusion By coupling belowground enzymatic mineralization with aboveground compensation, targeted N reduction provides a highly efficient and sustainable agroforestry paradigm for fragile arid ecosystems.

Keywords: Targeted nitrogen reduction; Apricot-soybean intercropping; Soil fertility; Photosynthetic characteristics; Economic benefit

Introduction

Meeting the food demands of 9.7 billion people by 2050 requires a fundamental paradigm shift in global agriculture toward sustainable intensification, balancing food security with environmental stewardship (Froehlich et al. 2018; Fry et al. 2018; Alexandratos and Bruinsma 2012; Rockström et al. 2017). Modern intensive agriculture remains fundamentally tethered to synthetic nitrogen (N) inputs (Zhang et al. 2015). Yet, the chronic overapplication of N fertilizers not only accelerates soil acidification and reactive nitrogen leaching but also locks agricultural systems into a cycle of high inputs and diminishing returns (Timsina 2018; Ren et al. 2024; Zhang et al. 2022). Thus, optimizing N reduction strategies while sustaining crop yields represents a pressing challenge in contemporary agroecological research.

To address the aforementioned agricultural bottlenecks, agroforestry systems have emerged as a highly promising strategy (Wang et al. 2022), with particularly critical applications in ecologically fragile regions. In the oasis irrigated areas of Xinjiang,

which are characterized by severe water scarcity and limited arable land, these systems play an essential role in mitigating spatial competition for agricultural resources (Dai et al. 2017). The spatial configuration of trees and crops not only optimizes canopy structure and significantly increases the land equivalent ratio but also substantially modifies the soil microenvironment (Pardon et al. 2017; Wang et al. 2022). Within these complex systems, interspecific plant interactions profoundly reshape belowground nutrient cycling dynamics. Research demonstrates that specific tree-crop combinations can effectively stimulate key soil extracellular enzyme activities (Lian et al. 2019; Rolo et al. 2023), accelerate the biochemical turnover of soil organic matter, and subsequently enhance the buffering and retention capacities of soil nutrient pools (Rao et al. 2007; Masebo and Menamo 2016).

Despite the structural advantages of agroforestry systems, optimizing nitrogen (N) management within these complex intercropping systems remains a formidable challenge. Currently, traditional “one-size-fits-all” whole-field N reduction strategies often exacerbate interspecific competition for limited resources (Feng et al. 2021), frequently resulting in severe system-wide yield penalties (Tang et al. 2024). Within the realm of targeted nutrient management, a critical knowledge gap persists: how these systems respond to targeted N reduction applied exclusively to the understory crop while standard fertilization is maintained for the established trees. In such an asymmetric nutrient environment, the sustained productivity of the intercrop depends heavily on localized root adaptations and the temporal regulation of soil carbon and nitrogen cycling (Ren et al. 2023; Mahmud et al. 2025).

Mounting evidence suggests that the homeostasis of belowground ecological functions in these systems relies heavily on robust plant-soil feedbacks, rather than massive external nutrient inputs (Liu et al. 2023a; Xu et al. 2026). Specifically, extracellular hydrolases (e.g., S- β -GC and S-NAG) and particular inorganic nitrogen reductases (e.g., S-NR and S-NiR) directly mediate the pathways of nutrient mineralization and assimilation (Noll et al. 2019; Brück et al. 2023; Zhang et al. 2024a;

Amoah et al. 2026). However, a critical knowledge gap remains twofold: first, whether targeted N reduction can specifically upregulate these key carbon- and nitrogen-cycling enzymes to bridge the spatiotemporal mismatch between nutrient supply and crop demand; and second, how exactly this belowground biochemical turnover mechanistically couples with aboveground carbon assimilation. Resolving this plant-soil decoupling is particularly critical during the pod-filling stage (R6), the definitive period for source-sink translocation and yield formation, when plant-microbe competition for limited resources peaks (Islam et al. 2017). Therefore, evaluating the belowground microecological state during this specific stage is imperative to understand how targeted N reduction sustains late-stage physiological functions.

To elucidate the ecological compensatory mechanisms of these systems, a field experiment was conducted in a typical continental arid oasis region (Shihezi, Xinjiang) utilizing a juvenile apricot-soybean intercropping system. Using a traditional soybean monoculture as a control, we specifically evaluated the system's response to targeted nitrogen (N) reduction applied exclusively to the understory soybean. We hypothesized that: (1) targeted N reduction in the understory crop reshapes the temporal dynamics of soil inorganic N supply, facilitating early-stage N retention and mitigating monoculture nutrient imbalances; (2) specifically during the yield-determining pod-filling stage (R6), this management significantly stimulates the mineralization potential of key soil enzymes (S- β -GC, S-NAG, S-NR, and S-NiR), which serves as the core microecological driver to alleviate late-stage stomatal limitations and sustain photosynthetic capacity; and (3) driven by spatiotemporal niche complementarity, this targeted N reduction strategy yields Land and Income Equivalent Ratios (LER and IER) > 1 , synergistically enhancing both ecological and economic benefits. By integrating soil microecological functions, crop gas exchange, and yield allocation characteristics, this study aims to provide a robust theoretical foundation for precision nutrient management and the sustainable development of agroforestry systems in arid regions.

Materials and Methods

Experimental site

The field experiment was conducted at Shizongchang Farm, Shihezi City, Xinjiang (85°94'E, 44°40'N) from 2024 to 2025. The area has a temperate, continental, semi-arid climate, abundant water resources, and flat terrain. The study area is characterized by a large diurnal temperature range, a mean annual temperature of 6.5°C, and an active accumulated temperature ($\geq 10^{\circ}\text{C}$) of 3662.4°C. The average frost-free period is 162 days, with an annual sunshine duration of 2318-2732 h (62.3% sunshine percentage). Mean annual precipitation is 180-270 mm, contrasting with an annual evaporation of 1000-1500 mm. The soil at the experimental site is classified as a sandy loam (USDA taxonomy). Weather conditions during the crop growing season (April-October) in 2024-2025 are shown in Fig. 1.

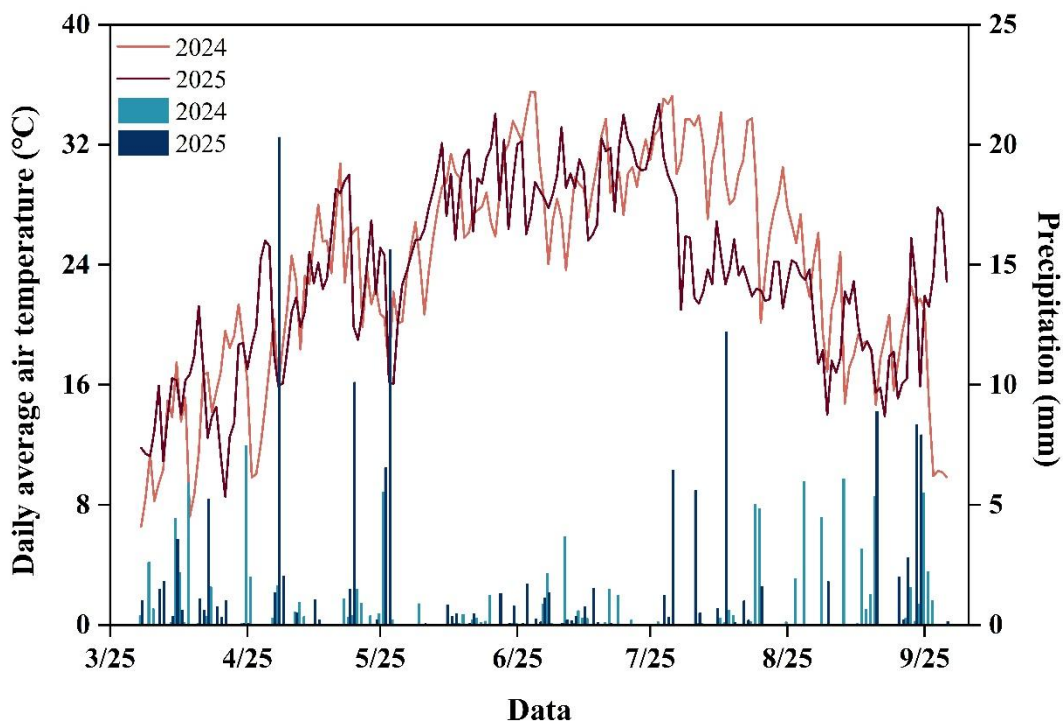


Fig.1 The daily average air temperature and precipitation during experiment periods.

Experimental design

The experiment used a two-factor randomized complete block design. The two factors were cropping pattern (monocropping soybean, MS; apricot-soybean intercropping, IS) and nitrogen application rate (conventional nitrogen: 300 kg ha⁻¹; 25% reduction: 225 kg ha⁻¹). Four treatment combinations were established: monocropping with conventional nitrogen (MS), monocropping with reduced nitrogen (MSN), apricot-soybean intercropping with conventional nitrogen (IS), and apricot-soybean intercropping with reduced nitrogen (ISN). Each treatment had three replicates ($n = 3$), giving 12 plots of 720 m² (24 m × 30 m) each. Apricot trees, transplanted in 2022, were 3 years old and planted in north-south rows with 4 m × 3 m spacing. Soybean was sown in early May each year using a wide-narrow row pattern: wide row spacing 36 cm, narrow row spacing 20 cm, plant spacing 15 cm, and sowing depth 3-5 cm. The monocropping system used the same row spacing, plant spacing, and planting density as the intercropping system. The Planting plane diagram is shown in Fig. 2.

Irrigation and fertilization : For soybean monoculture and intercropped soybean, irrigation used three pipes and six rows. Over the growing season, 12 irrigation events supplied a total of 4820 m³·hm⁻², adjusted by growth stage. Fertilizers were urea (N 46%), monopotassium phosphate (P₂O₅ 52%, K₂O 34%), and potassium sulfate (K₂O 52%). For sole and intercropped apricot trees, the total irrigation volume was 5565 m³·hm⁻² across six events, and 390 kg·hm⁻² of water-soluble fertilizer was applied annually with irrigation. Fertigation was applied with irrigation; soybean fertilizer rates are shown in Table 1.

This experiment employed two nitrogen (N) application levels: conventional fertilization and a 25% N reduction. The former represents standard local farming practices, whereas the latter aligns with the sustainable agricultural goals of reducing fertilizer inputs and enhancing nutrient use efficiency. More importantly, this 25% reduction serves as a critical threshold sufficient to induce significant shifts in interspecific interactions. The primary objective of this study was to elucidate the

mechanisms underlying interspecific interactions and yield compensatory effects within monocropping and intercropping systems under N-restricted conditions, rather than to fit a dose-response curve for determining the optimal fertilization rate. Therefore, this contrasting two-level design was fully adequate to test the scientific hypotheses of this study.

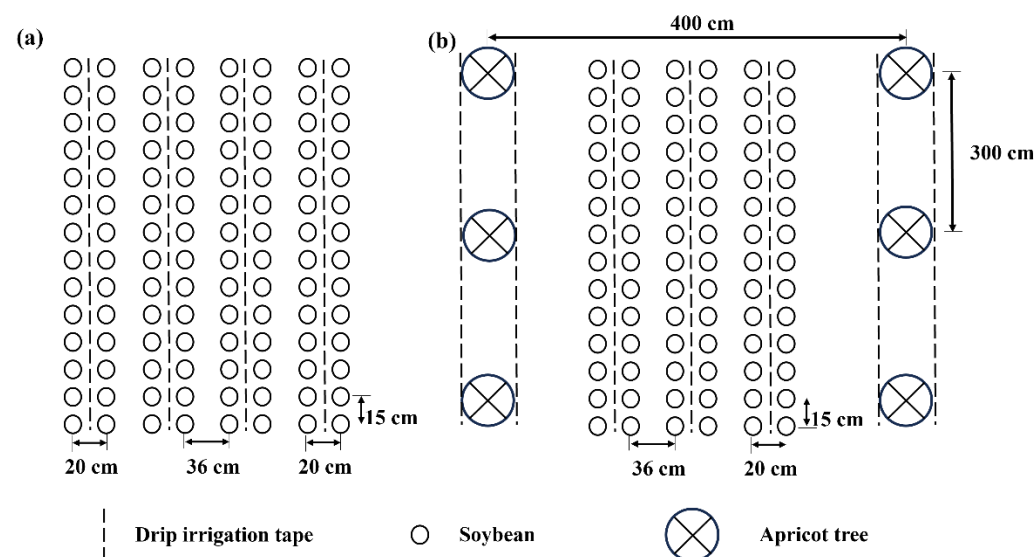


Fig. 2 Planting plane diagram. ((a): MS / MSN: monoculture soybean (conventional N / reduced N); (b): IS / ISN: apricot intercropping soybean (conventional N / reduced N))

Table 1

N, P and K application rates of soybean in different treatments during the whole growth period.

Treatment	N(kg·hm ⁻²)	P ₂ O ₅ (kg·hm ⁻²)	K ₂ O (kg·hm ⁻²)
MS	300	75	49.5
ISN	225	75	49.5
IS	300	75	49.5
ISN	225	75	49.5

Photosynthetic characteristics of soybean

According to the growth stage classification of soybean by Fehr et al. (1977), sampling was conducted at the fourth trifoliolate leaf stage (V4), beginning pod stage (R3), and full seed stage (R6). 10 representative plants were selected in each plot, and

169 the net photosynthetic rate, transpiration rate, stomatal conductance and intercellular
170 CO₂ concentration of soybean leaves were measured by Li-6800 instrument.

171 Determination of dry matter quality of soybean

172 At V4, R3, and R6, 10 representative plants per plot were separated into root, stem,
173 leaf, pod, and grain. Fresh mass was recorded, then samples were oven-treated at 105°C
174 for 30 min and dried at 80°C to constant mass. After cooling, dry mass was measured
175 with a 0.01 g precision balance.

176 Determination of soil nutrients

177 At V4, R3, and R6, in both monocropping and intercropping systems, an S-shaped
178 five-point sampling pattern was used. Prior to sampling, the soil drill (inner diameter
179 4.5 cm; volume 141 cm³) was wiped with 75% ethanol to prevent cross-contamination.
180 The top 2 cm of surface soil (including organic residues such as litter and weeds) was
181 removed, and then a composite soil sample from 0-20 cm depth was collected and
182 placed into a sterile sample bag. Each soil sample was subsequently divided into two
183 subsamples. Each soil sample was split into two parts. One was extracted with 1 mol·L⁻¹
184 KCl (soil: solution = 1:10) to determine inorganic N: ammonium (NH₄⁺-N) by the
185 indophenol blue colorimetric method and nitrate (NO₃⁻-N) by UV dual-wavelength
186 spectrophotometry. The other was air-dried, ground, and sieved (0.153 mm) for total N
187 determination by the Kjeldahl method.

188 Determination of soil enzyme activity

189 At R6, following the same method used for soil sampling. To prevent further
190 changes in soil enzyme activity after sampling, soil samples were stored in portable
191 coolers. Upon returning to the laboratory, the samples were passed through a 2 mm
192 sieve, and roots and other visible debris were removed using sterile forceps. The
193 samples were then refrigerated and measured promptly.

194 Yield and land equivalent ratio

195 In the mature period of soybean, three 1.0 m × 1.0 m harvest plots were randomly
196 selected in each plot to investigate the yield of each plot. According to the survey data
197 combined with the area of the plot, the theoretical yield of each plot was calculated.
198 Although the primary focus of this study was to elucidate the physiological and
199 agronomic responses of understory soybean to nitrogen reduction, the economic yield
200 of apricot was synchronously recorded at maturity. This woody component data was
201 exclusively utilized to calculate the Land Equivalent Ratio (LER) and Income
202 Equivalent Ratio (IER), aiming to comprehensively evaluate the overall land-use
203 efficiency and economic viability of the agroforestry system.

204 Land equivalent ratio (LER): refers to the ratio of land area required for
205 intercropping to land area required for monoculture when obtaining the same yield
206 (Mead and Willey 1980). It is used as an index to measure the yield advantage of
207 intercropping, and the calculation formula is:

$$208 \quad PLER_S = \frac{Y_{IS}}{Y_{MS}} \quad (1)$$

$$209 \quad PLER_A = \frac{Y_{IA}}{Y_{MA}} \quad (2)$$

$$210 \quad LER = PLER_S + PLER_A \quad (3)$$

211 In the formula, $PLER_S$ is the partial land equivalent ratio of soybean, Y_{IS} is the
212 yield of intercropping soybean, Y_{MS} is the yield of monoculture soybean. $PLER_A$ is the
213 partial land equivalent ratio of soybean, Y_{IA} is the yield of intercropping apricot, and
214 Y_{MA} is the yield of monoculture apricot. If $LER > 1$, the apricot-soybean intercropping
215 system has yield advantage; if $LER < 1$, the apricot-soybean intercropping system does
216 not have yield advantage.

217 Income Equivalent Ratio (IER): refers to the ratio of the land area required for
218 intercropping to the land area required for monoculture when the same income is
219 obtained (Demie et al. 2022). It is an index to transform yield benefit into economic
220 benefit. The calculation formula is:

$$IER = \frac{P_s PUY_{IS} + P_t PUY_{IA}}{\max\{P_s PUY_{MS}, P_t PUY_{MA}\}} \quad (4)$$

In the formula, P_s is the unit price of soybean, P_t is the unit price of apricot, PUY_{IS} is the area yield of intercropping soybean, PUY_{IA} is the yield per unit area of intercropping apricot, PUY_{MS} is the yield per unit area of monoculture soybean, PUY_{MA} is the yield per unit area of monoculture apricot.

Statistical analysis

Data collation and preliminary processing were conducted using Microsoft Excel 2019. To evaluate the main and interactive effects of planting pattern, nitrogen application rate, growth stage, and year on soil properties, soybean physiological characteristics, and yield components, data were subjected to multi-way analysis of variance (ANOVA) using SPSS 26.0 (SPSS, Chicago, IL, USA). Means were separated using Fisher's Least Significant Difference (LSD) test, with statistical significance declared at $p < 0.05$. To systematically evaluate the integrated effects of the treatments on physiological and environmental variables, a principal component analysis (PCA) was conducted. Furthermore, a partial least squares path model (PLS-PM) was constructed using the *plspm* package in R 4.3.2 (R Foundation for Statistical Computing, Vienna, Austria) to elucidate the cascading pathways linking nitrogen management, soil microecology, soybean physiological characteristics, and final yield. To preclude temporal confounding in causal inference, this model utilized a cross-sectional dataset strictly obtained at the pod-filling stage (R6). This analytical strategy quantifies the concurrent structural coupling and cascading effects among belowground microecological functions, *in situ* nutrient availability, and aboveground physiological traits during this critical yield-determining window. All data visualizations, including PCA biplots and data distribution charts, were generated using Origin 25 (OriginLab Corporation, Northampton, MA, USA).

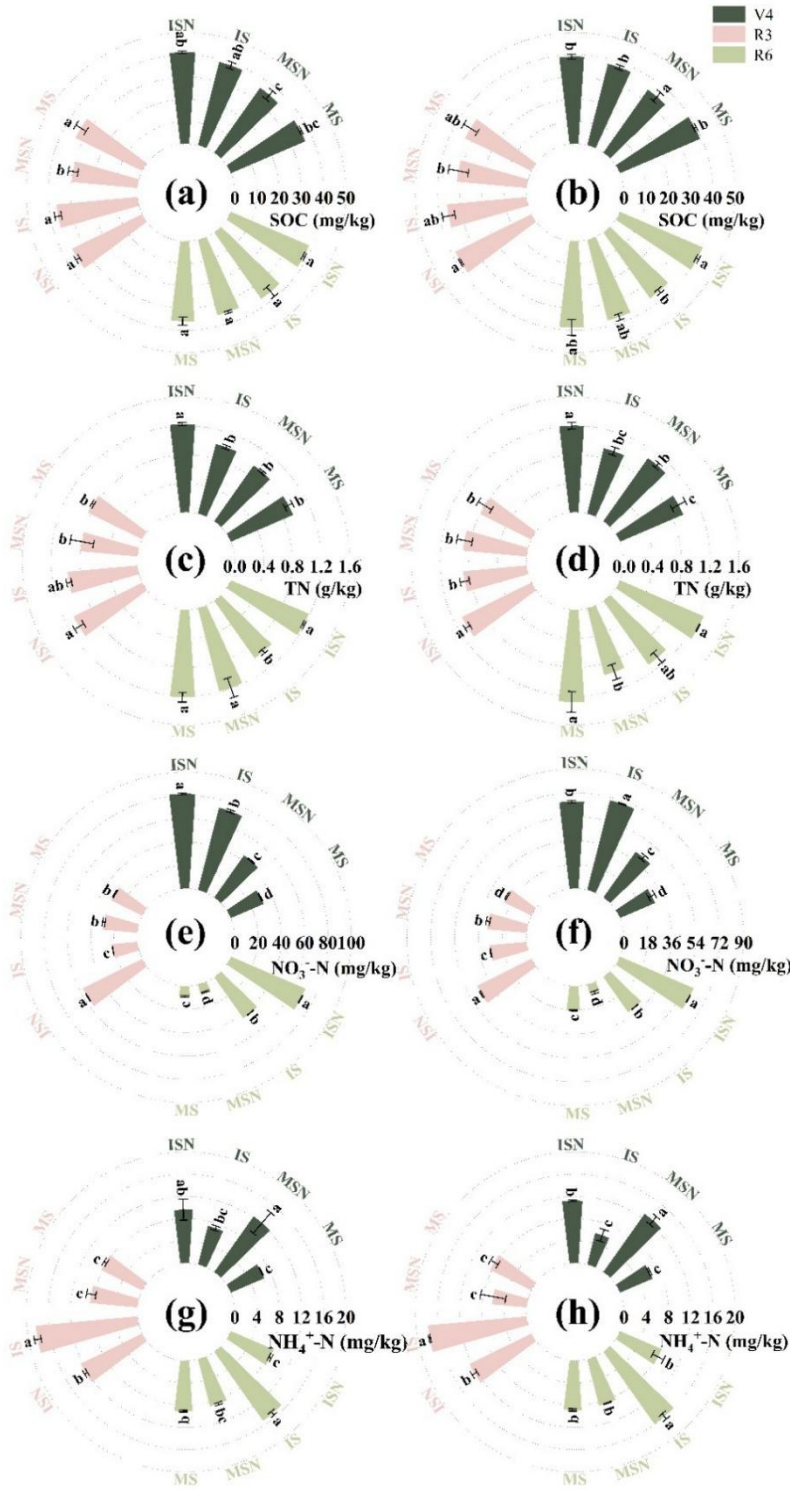
246 **Result**

247 *Soil nutrient*

248 Analysis of variance (ANOVA) revealed that both growth stage (G) and planting
249 pattern (P) had highly significant main effects on soil organic carbon (SOC) and total
250 nitrogen (TN) ($p < 0.001$, Table 2). Although the main effect of nitrogen level (N) on
251 SOC was not significant, the $P \times N$ interaction significantly affected both SOC ($p <$
252 0.01 , Table 2) and TN ($p < 0.001$, Table 2). Under the MSN, SOC decreased by 2.03%
253 to 11.56% compared to MS across multiple growth stages over the two years.
254 Furthermore, MSN led to severe nitrogen depletion during the late growth stages. TN
255 content dropped sharply by 25.00% compared to MS at the R6 stage in 2025. Overall,
256 intercropping significantly enhanced soil carbon and nitrogen sequestration. Compared
257 to MS, the conventional intercropping treatment (IS) consistently increased SOC and
258 TN across multiple growth stages, with notable increases of 9.10% and 15.48%,
259 respectively, at the R3 stage in 2024 (Fig. 3a, c). This advantage was maintained even
260 under ISN. Specifically, SOC increased by 0.13% to 14.80% relative to MS (Fig. 3a,
261 b). The most pronounced increases occurred at the 2024 V4 and 2025 R3 stages,
262 reaching 12.96% and 14.80% respectively, with the 2025 V4 stage being the only period
263 showing no significant difference (Fig. 3a, b). Regarding TN, ISN reached 1.22 g/kg at
264 the V4 stage in 2024, representing a significant 29.79% increase over MS (Fig. 3c).
265 This superiority persisted into the 2025 V4 stage, where TN remained 25.00% higher
266 than that of MS (Fig. 3d).

267 The dynamics of soil inorganic nitrogen were significantly affected by the three-
268 way interaction among growth stage (G), cropping pattern (P), and nitrogen application
269 level (N) ($G \times P \times N$, $p < 0.001$; Table 2). In the monoculture system, MSN only
270 temporarily enhanced the available nitrogen supply during the early growth stages.
271 Compared to MS, nitrate and ammonium nitrogen levels in MSN increased by 44.46%
272 (2024) and 86.91%~100.63%, respectively, during the V4 stage (Fig. 3e, f, g, h).

However, significant deficits occurred in the middle and late growth stages. By the R7 stage, nitrate nitrogen had decreased by 14.38%~60.43%. Similarly, ammonium nitrogen at the R3 stage showed no significant difference or even decreased compared to MS, reflecting a 24.76% decrease in 2025. Intercropping significantly altered the mineralization and temporal dynamics of soil nitrogen. Regarding nitrate nitrogen (Fig. 3e, f), intercropping systems, specifically IS and ISN, exhibited significantly higher levels than monocultures at the V4 stage over two consecutive years. Notably, ISN demonstrated a strong potential for nitrate nitrogen accumulation, maintaining the highest levels across all growth stages except for V4 in 2025, where it was 6.01% lower than IS. Compared to IS, nitrate nitrogen in ISN increased by 160.50% and 63.84% at the R3 stage, and by 61.36% and 86.11% at the R7 stage across the two years. Conversely, ammonium nitrogen dynamics were strongly regulated by the growth stage (Fig. 3g, h). In IS, the nitrogen supply peaked at the R3 stage with a significant increase of 98.11%~122.55% compared to the concurrent monoculture. This supply remained elevated through the R7 stage, where it was 67.14% higher than MS. In contrast, ISN exhibited early accumulation during the V4 stage, increasing significantly by 34.08%~87.17% compared to IS. However, it subsequently experienced significant decreases of 30.12%~32.84% and 44.71% during the R3 and R7 stages, respectively, relative to IS. Notably, the ammonium nitrogen supply in ISN and MSN displayed significant temporal variations. At the V4 stage, ISN effectively mitigated the excessive early accumulation seen in monocultures, resulting in levels 12.54%~21.50% lower than those in MSN. Furthermore, during the R3 stage, ISN demonstrated a stronger capacity for sustained nitrogen conservation and supply. Its ammonium levels were significantly higher, ranging from 38.44%~43.71% above those of MSN during the same period.



298

299 **Fig. 3** Effects of planting patterns and nitrogen application levels on soil nutrient.
 300 (Different lowercase letters indicated significant differences between treatments ($p <$
 301 0.05). (a,c,e,g): 2024; (b,d,f,h): 2025. MS / MSN: monoculture soybean (conventional
 302 N / reduced N); IS / ISN: apricot intercropping soybean (conventional N / reduced N))

Table 2

Analysis of variance of planting patterns and nitrogen application levels on soil nutrients.

Items	SOC (g/kg)	TN (g/kg)	NO ₃ ⁻ -N (mg/kg)	NH ₄ ⁺ -N (mg/kg)
Growth stages (G)	***	***	***	***
Planting patterns (P)	***	***	***	***
N treatment (N)	NS	***	**	***
G × P	***	**	***	***
G × N	NS	**	***	***
P × N	**	***	***	***
G × P × N	NS	NS	***	***

The significance levels are denoted as follows: ^{ns} no significant difference, * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$)

Soil enzyme

Planting pattern (P) and nitrogen application level (N) exhibited a significant interactive effect ($P \times N$, $p < 0.001$) on the activities of key enzymes regulating soil carbon and nitrogen turnover (S-β-GC and S-NAG) (Table 3). Across both years, S-β-GC activity in the MSN and IS treatments remained at baseline levels with no significant difference between them (Fig. 4). In contrast, the ISN treatment significantly increased S-β-GC activity by 48.84% and 59.87% relative to IS ($p < 0.05$). Concurrently, S-NAG activity exhibited a highly significant three-way interaction involving year ($Y \times P \times N$, $p < 0.001$), indicating a cumulative temporal effect. While there were no significant differences in S-NAG activity among treatments in 2024, the responses diverged significantly by 2025. Specifically, S-NAG activity under the MSN treatment decreased significantly by 24.65% compared with MS, whereas activity under the ISN treatment peaked at 259.92 nmol/h/g, representing a significant 50.03% increase over IS ($p < 0.05$).

Nitrate reductase (S-NR) and nitrite reductase (S-NiR), as the core enzymes driving soil inorganic nitrogen transformations, were also significantly affected by the $P \times N$ interaction ($p < 0.05$, Table 3). The two cropping systems exhibited opposite

response trajectories to nitrogen reduction. Under monocropping, the MSN treatment significantly decreased S-NiR activity by 19.59% in 2024 and 43.75% in 2025 compared with MS ($p < 0.05$). Conversely, under intercropping, the ISN treatment significantly enhanced S-NiR activity, which was 50.37% and 121.96% higher than that of IS in 2024 and 2025, respectively. Similarly, S-NR activity reached its highest levels under the ISN treatment across both years (21.08 and 20.54 $\mu\text{g/d/g}$).

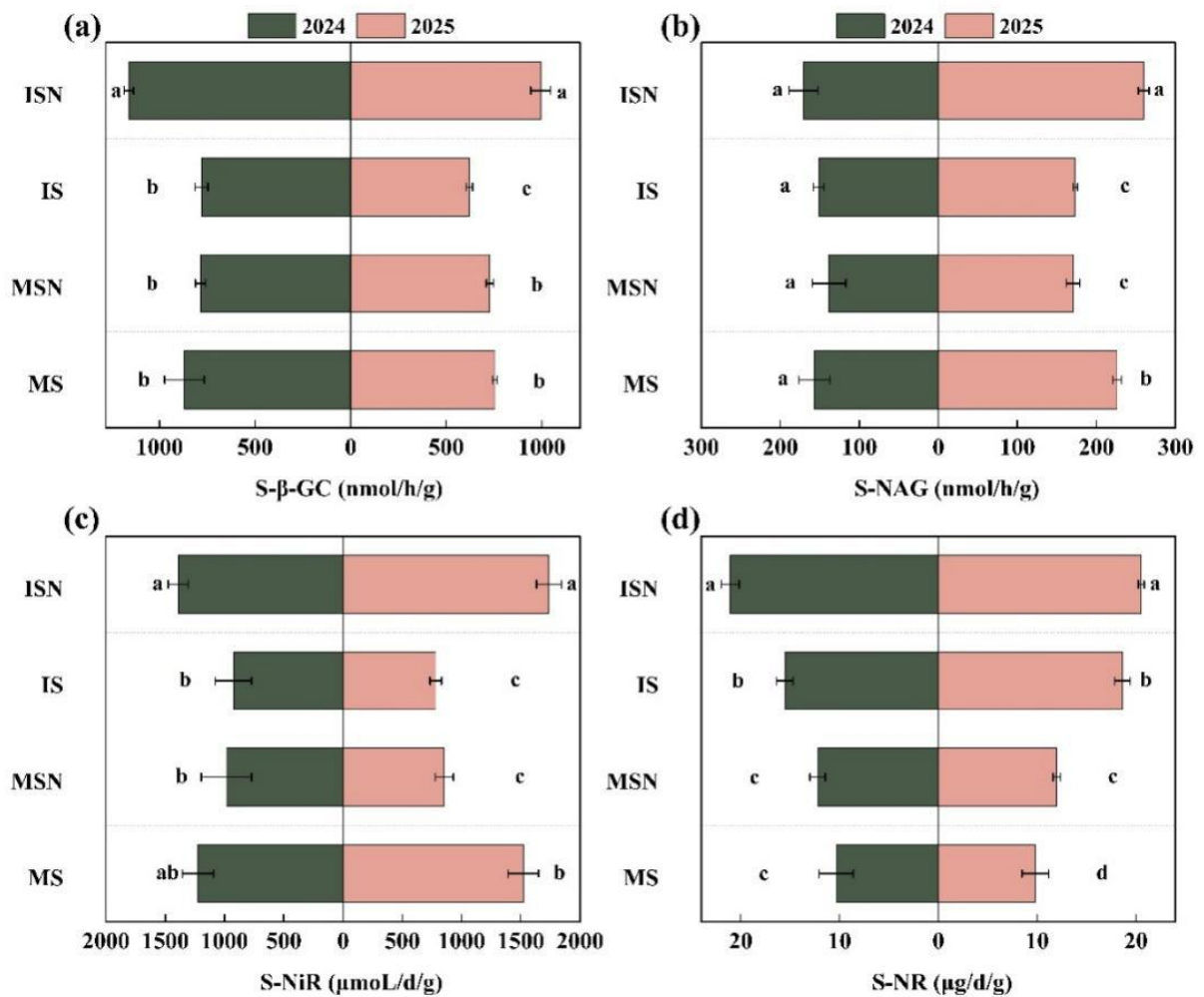


Fig. 4 Effects of planting patterns and nitrogen application levels on soil enzymes. (Different lowercase letters indicated significant differences between treatments ($P < 0.05$). MS / MSN: monoculture soybean (conventional N / reduced N); IS / ISN: apricot intercropping soybean (conventional N / reduced N))

Table 3

Analysis of variance of planting patterns and nitrogen application levels on soil

338 enzymes.

Items	S-β-GC (nmol/h/g)	S-NAG (nmol/h/g)	S-NR (μg/d/g)	S-NiR (μmol/d/g)
Year (Y)	***	***	NS	NS
Planting pattern (P)	***	**	***	NS
N treatment (N)	***	NS	***	*
Y × P	NS	NS	NS	NS
Y × N	NS	NS	NS	NS
P × N	***	***	*	***
Y × P × N	NS	***	*	***

339 The significance levels are denoted as follows: ^{ns} no significant difference, * $p \leq 0.05$,
340 ** $p \leq 0.01$, *** $p \leq 0.001$. MS / MSN: monoculture soybean (conventional N / reduced
341 N); IS / ISN: apricot intercropping soybean (conventional N / reduced N)

342 Photosynthetic characteristics of soybean leaves

343 Analysis of variance (ANOVA) indicated that growth stage (G) exerted a highly
344 significant main effect on all photosynthetic parameters ($p < 0.001$, Table 4).
345 Furthermore, the interaction between planting pattern and nitrogen application rate (P
346 × N) significantly influenced all measured parameters ($p < 0.01$ or $p < 0.001$, Table 4).
347 The three-way interaction (G × P × N, Table 4) was significant only for transpiration
348 rate (Tr) ($p < 0.05$, Table 4), suggesting that most photosynthetic traits responded
349 additively to the treatment combinations. During the vegetative stage (V4), IS
350 significantly enhanced Tr, stomatal conductance (Gs), and intercellular CO₂
351 concentration (Ci) compared with monocropping (MS) ($p < 0.05$). Specifically, in 2025,
352 IS increased Tr and Gs by 49.82% and 73.40%, respectively, relative to MS. However,
353 this trend reversed during the early reproductive stage (R3), at which point MS
354 exhibited significantly higher Tr and Gs than IS, showing average increases of 62.19%
355 and 99.47%, respectively, across both years (Fig. 5e, h). This stage-dependent reversal
356 remained consistent across both growing seasons (Table 4). Although the main effect
357 of nitrogen rate (N) on Gs and Ci was not significant, its interaction with planting
358 pattern (P × N) was highly significant. During the late reproductive stage (R7), the

reduced-nitrogen intercropping treatment (ISN) maintained significantly higher Gs and Tr ($p < 0.05$). For example, at the R7 stage in 2025 (Fig. 5e, h), ISN increased Gs and Tr by 131.99% and 25.63% relative to MSN, and by 30.55% and 26.87% compared with IS. This indicates that intercropping fully compensated for the inhibitory effects of nitrogen reduction on late-stage gas exchange. Furthermore, Ci remained consistently above $300 \mu\text{mol mol}^{-1}$ under the intercropping treatments (both IS and ISN), whereas it plummeted to $135.5 \mu\text{mol mol}^{-1}$ under MSN in 2025. Over the two study years, ISN significantly increased Ci by 84.27% and 130.88% compared with MSN ($p < 0.05$), demonstrating that intercropping effectively prevents the depletion of intercellular CO_2 supply under nitrogen-restricted conditions.

Table 4

Variance analysis of planting patterns and nitrogen levels on photosynthetic characteristics of soybean leaves.

Items	Transpiration rate Tr ($\text{mmol m}^{-2} \text{s}^{-1}$)	Net photosynthetic rate Pn ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	Intercellular concentration Ci ($\mu\text{mol mol}^{-1}$)	CO_2 Stomatal conductance Gs ($\text{mmol m}^{-2} \text{s}^{-1}$)
Growth stages (G)	***	***	***	***
Planting patterns (P)	NS	NS	***	*
N treatment (N)	*	**	NS	NS
G $\times$ P	***	**	***	***
G $\times$ N	***	NS	*	*
P $\times$ N	**	**	**	**
G $\times$ P $\times$ N	NS	*	NS	NS

The significance levels are denoted as follows: ^{ns} no significant difference, $*p \leq 0.05$, $**p \leq 0.01$, $***p \leq 0.001$.

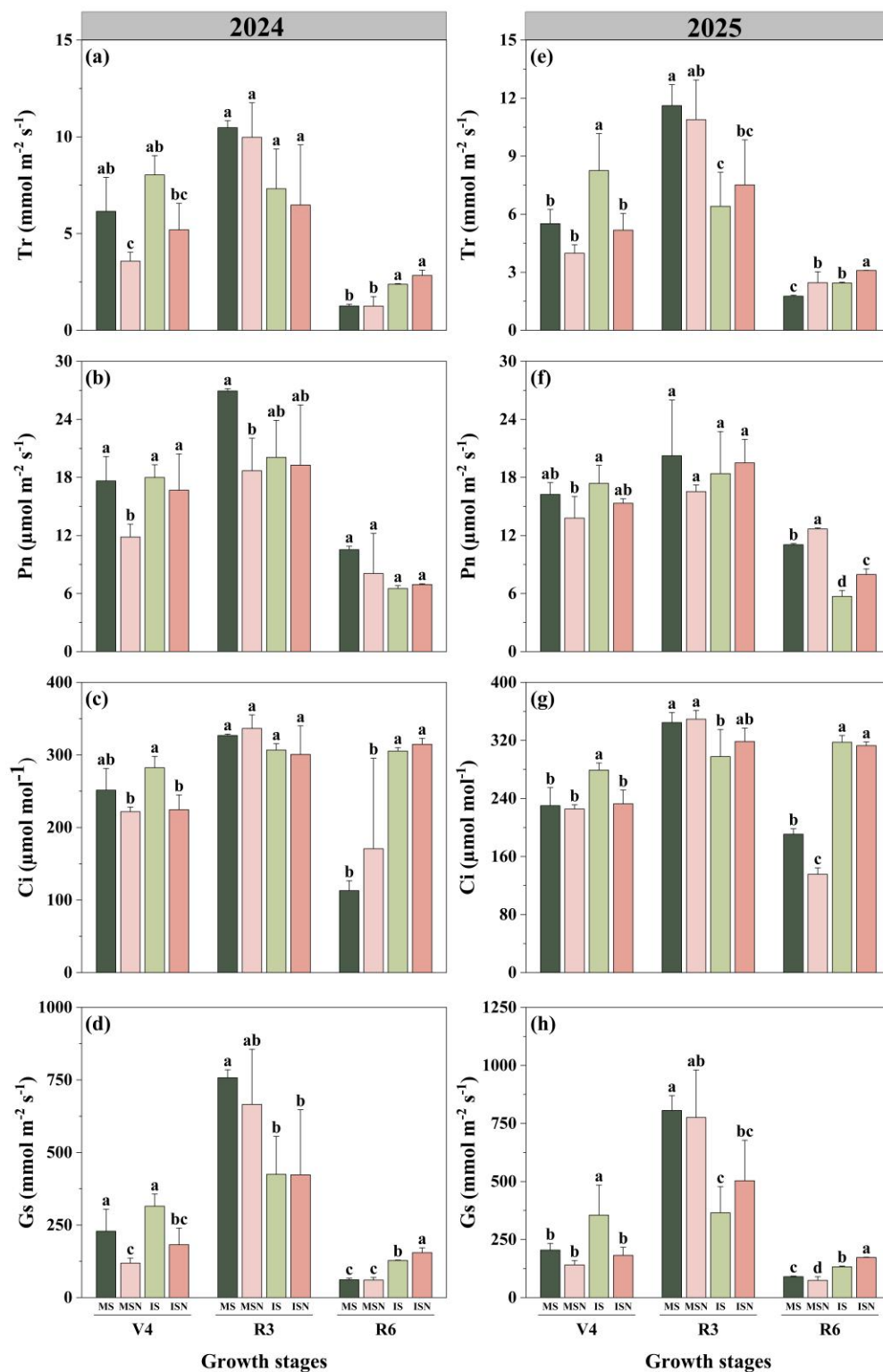


Fig. 5 Effects of planting patterns and nitrogen levels on photosynthetic characteristics of soybean leaves. (Different lowercase letters indicated significant differences between treatments ($p < 0.05$). MS / MSN: monoculture soybean (conventional N / reduced N); IS / ISN: apricot intercropping soybean (conventional N / reduced N))

Dry matter ratio and dry matter accumulation

Over the two-year experiment, planting pattern and nitrogen application level exhibited a significant interactive effect on dry matter accumulation. Dry matter accumulation per soybean plant increased progressively from the V4 to the R6 stage. Concurrently, biomass partitioning shifted from vegetative organs during the V4-R3 stages to reproductive organs during the R3–R6 stages (Fig. 6a, b). At the V4 stage, shading and initial interspecific competition significantly reduced the total dry matter of intercropped soybeans compared with monocultured soybeans. However, MSN treatment exhibited an early stimulatory effect, increasing dry matter by 48.05% relative to MS. This suggests that low nitrogen levels induced compensatory root foraging growth during the seedling stage. By the R3 stage, the growth responses among treatments diverged significantly. The negative impacts of nitrogen reduction in the MSN treatment became evident, resulting in a 16.67% decrease in dry matter compared with MS. Conversely, the ISN treatment effectively alleviated resource competition between the companion trees and soybeans, increasing dry matter by 18.85% relative to IS. At the R6 stage, although the total dry matter of intercropped soybeans remained significantly lower than that of monocropping, the planting patterns exhibited contrasting responses to nitrogen reduction. Specifically, the total dry matter of MSN was significantly lower than that of MS, whereas the compensatory growth effect in ISN was further amplified, resulting in a 19.98% increase in total dry matter compared with IS ($p < 0.05$).

Beyond altering total biomass accumulation, the treatments significantly reshaped the partitioning of carbon assimilates between vegetative and reproductive organs at the R6 stage. Following the R6 stage, reproductive organs (pods and seeds) became the primary carbon sink (Fig. 6c, d). Compared with monocropping, the intercropping systems (IS and ISN) altered the allocation strategy for photosynthetic products: biomass allocation to leaves decreased, while allocation to seeds significantly increased from 25.35%~25.77% in MS to 28.40%~28.70% in intercropping. This preferential

resource allocation to sink organs represents a typical adaptive mechanism for plants to cope with shading stress and maintain reproductive capacity. Furthermore, the ISN treatment optimized the spatial distribution of dry matter, with biomass allocation to stems peaking at 24.32%, while allocation to roots decreased to 9.48%.

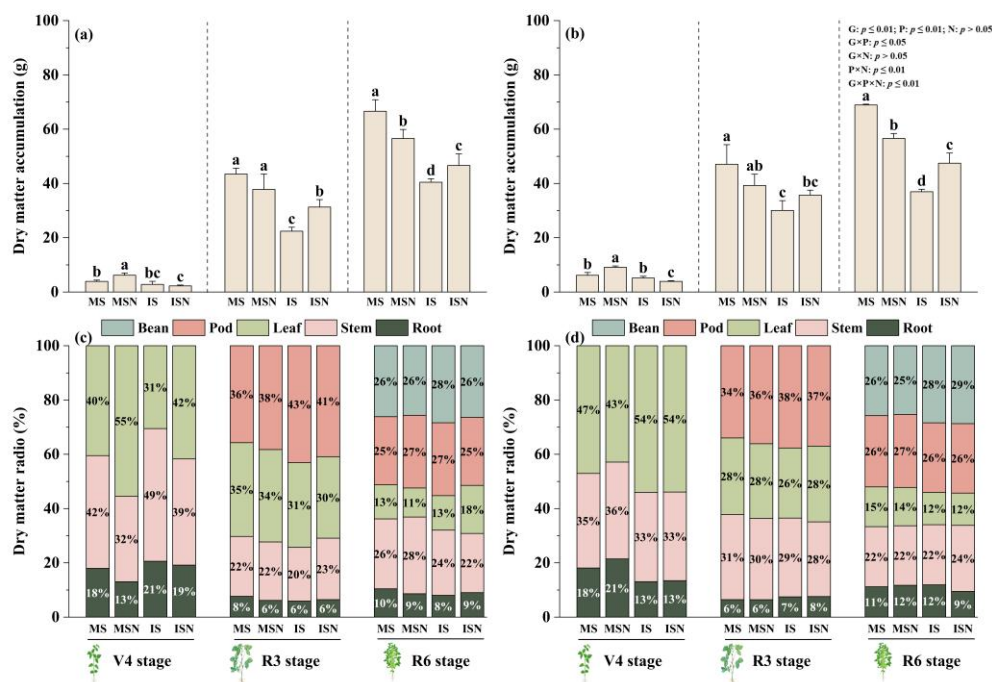


Fig. 6 Effects of planting pattern and nitrogen application level on dry matter distribution rate and accumulation of soybean. (Different lowercase letters indicated significant differences between treatments ($p < 0.05$). (a,c): 2024; (b,d): 2025. MS / MSN: monoculture soybean (conventional N / reduced N); IS / ISN: apricot intercropping soybean (conventional N / reduced N))

Yield and yield components

Planting pattern (P) and nitrogen application level (N) exhibited a significant interactive effect on soybean yield and its components (Table 5). Analysis of variance (ANOVA) revealed that the $P \times N$ interaction significantly affected the number of effective pods per plant ($p < 0.01$), the number of seeds per pod ($p < 0.01$), 100-seed weight ($p < 0.001$), and final yield ($p < 0.001$). The three-way interaction involving year ($Y \times P \times N$) was not significant, indicating that the treatment effects remained

424 consistent across both years.

425 Interspecific competition significantly limited the yield of intercropped soybeans.

426 Yields in the intercropping treatments (IS, ISN) were significantly lower than those in

427 the monocropping treatments (MS, MSN) ($p < 0.05$). Under normal nitrogen

428 application, the yield of the IS treatment accounted for only 44.84% and 46.88% of the

429 MS yield in the two respective years. In terms of yield components,

430 microenvironmental changes within the intercropping system primarily caused a

431 significant reduction in 100-seed weight ($p < 0.05$). Conversely, reduced intraspecific

432 competition promoted an increase in the number of effective pods per plant.

433 Furthermore, the different planting patterns exhibited distinct responses to reduced

434 nitrogen application.

435 Table 5

436 Effects of planting patterns and nitrogen application levels on yield and yield

437 components and variance analysis of soybean.

Year	Treatment	Plant number per ha (plant·ha ⁻¹)	Effective Pods per Plant (pod·plant ⁻¹)	Seeds per Pod (seed·pod ⁻¹)	100 grain weight (g)	Yield (kg·ha ⁻¹)
2024	MS	2.4×10 ⁵	34.33±1.53 ab	2.61±0.06 a	20.89±0.54 a	4496.25±328.13 a
	MSN	2.4×10 ⁵	32.73±1.62 bc	2.54±0.03 a	20.17±0.43 ab	4001.29±109.15 b
	IS-S	1.1×10 ⁵	38.27±1.42 a	2.57±0.04 b	18.63±0.42 c	2016.11±84.79 c
	ISN-S	1.1×10 ⁵	42.33±3.51 a	2.72±0.06 b	19.57±0.58 b	2472.57±240.63 d
2025	MS	2.4×10 ⁵	33.10±1.01 b	2.71±0.07 bc	22.12±0.77 a	4762.40±222.15 a
	MSN	2.4×10 ⁵	30.96±2.50 b	2.61±0.04 c	20.90±0.68 b	4060.86±478.00 b
	IS-S	1.1×10 ⁵	37.13±2.20 a	2.78±0.03 ab	19.67±0.52 c	2232.46±184.75 c
	ISN-S	1.1×10 ⁵	39.60±2.23 a	2.87±0.09 a	20.87±0.17 b	2610.85±162.90 c
Variation source						
Year (Y)			NS	***	***	NS
Planting pattern (P)			***	***	***	***
N treatment (N)			NS	NS	NS	NS
Y × P			NS	*	NS	NS
Y × N			NS	NS	NS	NS
P × N			**	***	***	***
Y × P × N			NS	NS	NS	NS

438 The significance levels are denoted as follows: ^{ns} no significant difference, * $p \leq 0.05$,

439 ** $p \leq 0.01$, *** $p \leq 0.001$. MS / MSN: monoculture soybean (conventional N / reduced

N); IS / ISN: apricot intercropping soybean (conventional N / reduced N)

LER and IER of the system

To comprehensively evaluate the land-use efficiency and economic viability of the agroforestry systems, the land equivalent ratio (LER) and income equivalent ratio (IER) were analyzed for each treatment (Fig. 7). As depicted in Fig. 7a, the total LER values across all intercropping treatments consistently exceeded 1.0. This demonstrates a significant land-use advantage over monocropping, indicating that interspecific complementarity outweighed competition within the system. Notably, reduced nitrogen application significantly altered the interspecific competitive dynamics. Compared with IS, the ISN significantly increased the partial LER of soybean, indicating enhanced land-use efficiency for the understory crop. Regarding system economic returns (Fig. 7b), the IER of the intercropping treatments similarly exceeded 1.0 (ranging from 1.25 to 1.35), with ISN tending to outperform IS. These findings confirm that moderate nitrogen reduction in agroforestry systems can improve the land-use efficiency of understory soybeans and maintain overall system productivity, thereby striking an optimal balance between ecological sustainability and economic profitability.

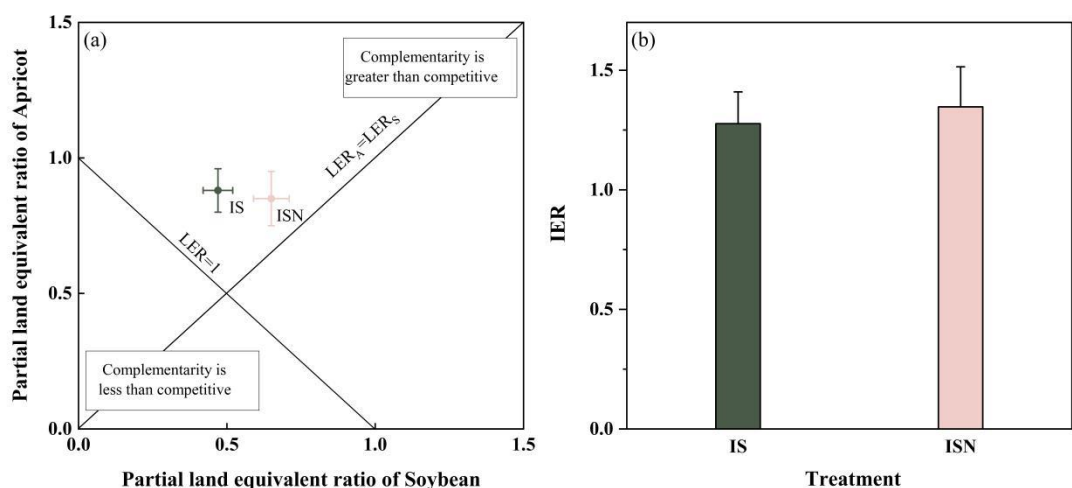


Fig. 7 LER and IER of intercropping system. (Since there is no yield of apricot trees in 2024, LER and IER only calculate 2025. Soybean were priced at 5 yuan·kg⁻¹. Apricots were priced at 25 yuan·kg⁻¹ IS / ISN: apricot intercropping soybean (conventional N /

460 reduced N))

461 Principal Component Analysis of Environmental Factors

462 Principal component analysis (PCA) was conducted to systematically evaluate the
463 integrated effects of planting patterns and nitrogen levels on soybean photosynthetic
464 physiology, soil carbon and nitrogen pools, and enzyme activities (Fig. 8). Along the
465 first principal component (PC1), the monocropping (MS, MSN) and intercropping (IS,
466 ISN) treatments were distinctly separated. The monocropping treatments clustered
467 along the negative PC1 axis, which was significantly and positively correlated with
468 total dry matter (TDM) and net photosynthetic rate (Pn), reflecting a stronger capacity
469 for carbon assimilation and biomass accumulation in monocultured soybeans. In
470 contrast, the intercropping treatments were primarily distributed along the positive PC1
471 axis, showing strong correlations with stomatal conductance (Gs), intercellular CO₂
472 concentration (Ci), transpiration rate (Tr), soil nitrate-nitrogen (NO₃⁻-N), and nitrate
473 reductase (S-NR) activity. Furthermore, TDM and Pn were negatively correlated with
474 Ci and Gs. The second principal component (PC2) captured a significant interactive
475 effect between nitrogen application and planting pattern. Under monocropping
476 conditions, the MS and MSN treatments showed no clear spatial separation. However,
477 within the intercropping system, IS and ISN diverged significantly along the PC2 axis.
478 The ISN treatment clustered along the positive PC2 axis, closely associating with soil
479 organic carbon (SOC), nitrite reductase (S-NiR), β -glucosidase (S- β -GC), and N-
480 acetyl- β -D-glucosaminidase (S-NAG) activities. Meanwhile, the IS treatment was
481 positioned along the negative PC2 axis, driven primarily by its positive correlation with
482 soil ammonium-nitrogen (NH₄⁺-N).

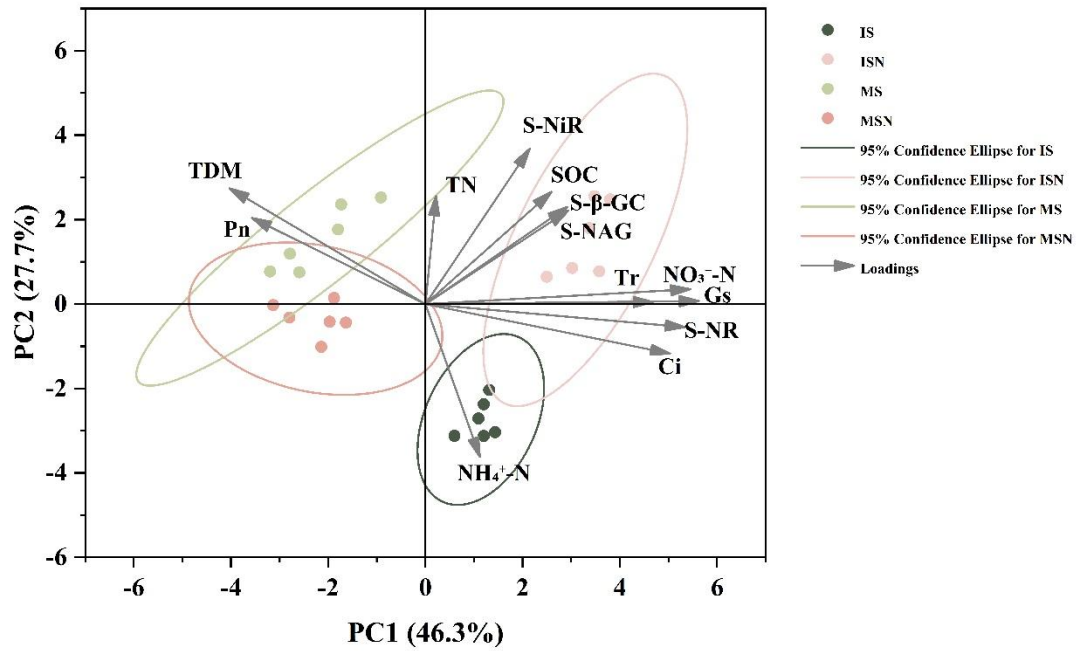


Fig. 8 PCA analysis of environmental factors under planting patterns and nitrogen application levels.

System cascade path analysis of yield formation

A partial least squares path model (PLS-PM) mapped the cascading pathways among nitrogen management, soil microecology, soybean physiology, and yield (Fig. X). The intercropping model exhibited a substantially higher goodness-of-fit ($GOF = 0.7741$) than the monoculture system ($GOF = 0.5952$), indicating tighter structural coupling among variables. In monoculture (Fig. 9a), distinct inhibitory cascading effects were observed. While nitrogen treatments stimulated soil enzymes ($0.843, p < 0.001$), this activity negatively impacted soil nutrients ($-0.883, p < 0.001$). This belowground barrier cascaded upward, severely constraining source-sink dynamics ($-0.977, p < 0.001$) and revealing a severe supply-demand mismatch, although source-sink traits ultimately benefited yield ($0.876, p < 0.001$).

Conversely, the intercropping system (Fig. 9b) established a synergistic positive feedback loop. Here, nitrogen inputs negatively affected soil enzymes ($-0.975, p < 0.001$), suggesting that moderate nitrogen limitation effectively stimulated belowground enzymatic potential. These upregulated enzymes then strongly enhanced

soil nutrients ($0.987, p < 0.001$). This optimized microenvironment restored the positive coupling between belowground nutrients and aboveground traits, significantly benefiting photosynthesis (0.614) and source-sink dynamics (0.731), which ultimately drove final yield ($0.942, p < 0.001$).

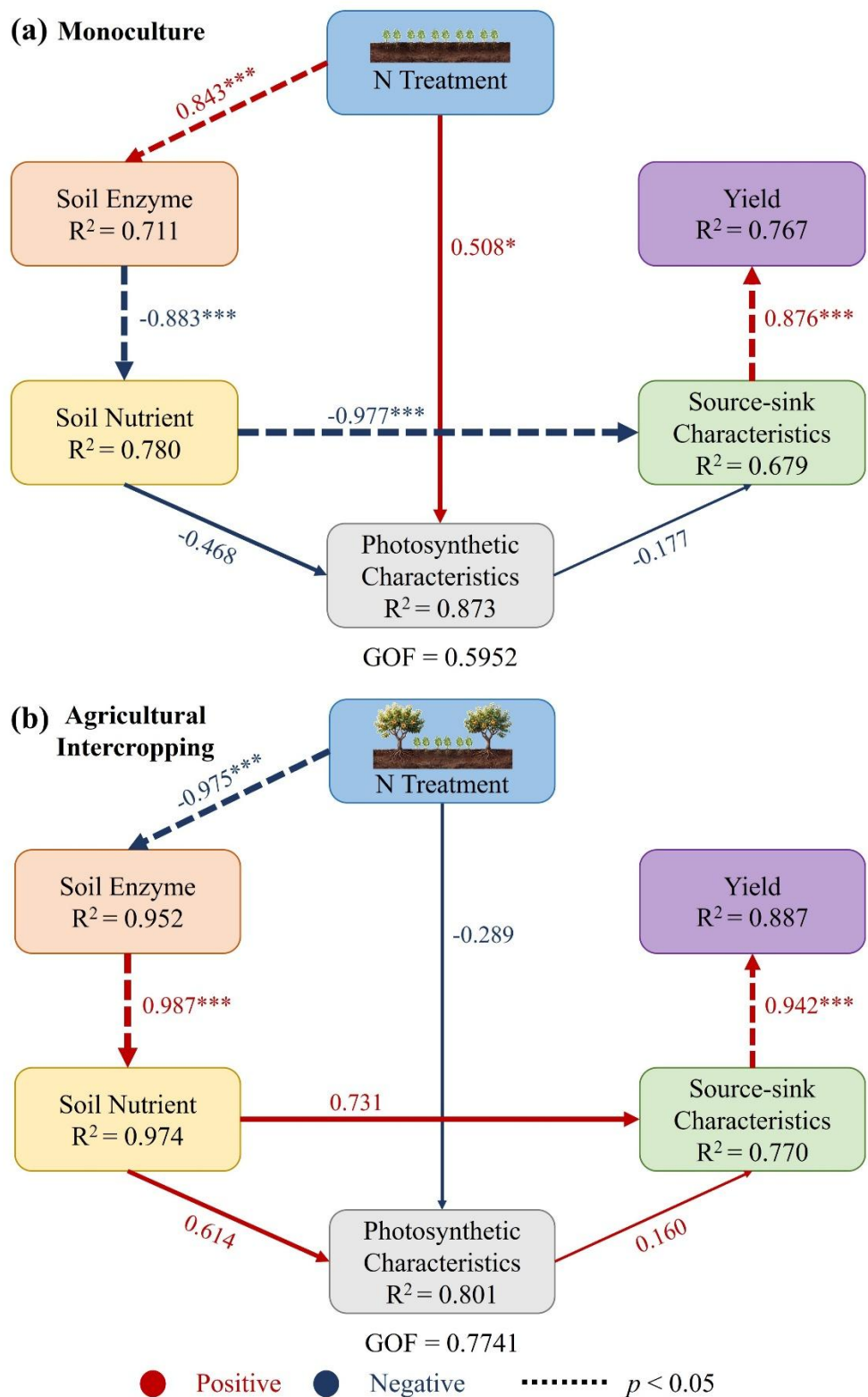


Fig. 9 The cascade relationship between nitrogen management, soil microecology, soybean physiological characteristics (R6 stage) and yield. (* $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$)

Discussion

Drivers of soil C and N cycling and nutrient availability under reduced-N intercropping

The baseline soil fertility of oasis agricultural systems in arid regions, such as Shihezi in Xinjiang, is inherently low and highly susceptible to nutrient loss due to intense evaporation and sandy soil textures. Consequently, excessive reliance on exogenous nitrogen fertilizers frequently disrupts nutrient cycling (Gillani et al. 2024; Pandian et al. 2024). This study demonstrates that reducing N inputs in monocultures exacerbates supply-demand asynchrony. In arid environments, the rapid accumulation of inorganic nitrogen during the V4 stage is highly susceptible to leaching and volatilization, leading to critical nutrient deficits during mid-to-late growth stages. Consequently, this mismatch causes total soil nitrogen (TN) under reduced nitrogen (MSN) to decline by 25.00% relative to conventional fertilization (MS) by the R6 stage. This phenomenon highlights that, in the absence of interspecific interactions and spatial niche differentiation, soil nitrogen cycling in monoculture systems remains heavily dependent on synthetic nitrogen inputs (Jensen et al. 2020; Brooker et al. 2015). Furthermore, the shallow, homogeneous root architectures of monocropped legumes fail to intercept deep soil N, instead exacerbating nitrate leaching risks (You et al., 2023). Conversely, intercropping mitigates this late-stage N depletion through resource complementarity and spatiotemporal root stratification (Moreira et al. 2024).

Crucially, our targeted nitrogen reduction strategy (ISN), where N is limited for the understory crop but maintained for the companion tree, creates an asymmetric nutrient environment that reshapes the temporal dynamics of nitrogen supply, thereby enhancing system stability and nutrient buffering (Xu et al. 2020). During early

vegetative growth (V4), heightened enzymatic responses accelerated nitrogen immobilization, mitigating ammonium accumulation and deep leaching to secure early nutrient retention (Ardenti et al. 2022).

During the late reproductive stage (R6), when crop nutrient demands peak, the nitrogen-deficient monoculture (MSN) system exhibits a severe decoupling of nutrient supply and demand, accompanied by suppressed soil enzyme activities. In contrast, the reduced-nitrogen intercropping (ISN) system triggers a profound belowground compensatory response, effectively unlocking the enzymatic potential of the soil microenvironment to cope with localized nitrogen limitation. This mechanism is quantitatively corroborated by our PLS-PM analysis (Fig. 9b). Specifically, the ISN system significantly upregulates key enzymes driving carbon and nitrogen (C-N) cycling (Liu et al. 2023b). The activities of β -glucosidase (S- β -GC) and N-acetyl- β -D-glucosaminidase (S-NAG) increased by 59.87% and 50.03%, respectively, accelerating the turnover of complex organic substrates into labile nutrients. Concurrently, the significant upregulation of nitrate reductase (S-NR) and nitrite reductase (S-NiR) activities facilitates inorganic nitrogen assimilation and the nitrate reduction pathway.

This pronounced enzymatic acceleration elucidates how the reduced-nitrogen intercropping (ISN) system sustains a higher inorganic nitrogen supply during the late growth stages (as evidenced by R3 and R6 nutrient data, Fig. 3). In response to targeted nitrogen limitation, the intercropping system inherently stimulates robust enzymatic activity, driving the continuous mineralization of soil organic matter under low-N conditions (Zhou et al. 2024). The PLS-PM analysis (Fig. 9b) quantitatively corroborates this highly coupled cascading mechanism: although nitrogen limitation exerts a strong direct negative effect on soil enzymes (-0.975), it paradoxically unlocks belowground enzymatic potential. This "enzyme-nutrient" pathway (0.987) effectively synchronizes nutrient supply and demand, mitigating the decoupling observed in monoculture systems (Liao et al. 2026), and significantly enhances the soil organic carbon (SOC) and total nitrogen (TN) pools during critical periods. Ultimately, this

sustained belowground nutrient provisioning directly bolsters late-stage stomatal conductance and carbon assimilation capacity (0.614, Fig. 9b), triggering a physiological compensatory mechanism to overcome nutrient limitations. Consistent with previous findings in cereal-legume systems (Xu et al. 2020), these results further substantiate the synergistic benefits of the ISN system in improving nutrient use efficiency and overall soil fertility.

Physiological mechanisms alleviating soybean photosynthetic decline under reduced-nitrogen intercropping

Photosynthetic characteristics form the critical physiological basis for crop growth and development (Luo et al. 2023) and are significantly regulated by limiting factors, such as light and nutrients, within intercropping systems (Huang et al. 2020; Zheng et al. 2022). Soybean photosynthetic parameters showed a notable stage-dependent reversal, reflecting spatiotemporal niche differentiation within the young tree-crop system. During the V4 stage, intercropping significantly enhanced stomatal conductance (G_s) and intercellular CO_2 concentration (C_i) compared to monoculture. Moderate shading from the young apricot canopy improved the local microclimate (Bai et al. 2016; Zheng et al. 2022), effectively alleviating the severe stomatal limitations typically induced by high temperatures and intense sunlight in arid-environment monocultures (Liu et al. 2022). By the R3 stage, however, monocultured soybeans outperformed intercropped plants. This reversal stemmed from the rapid canopy and root expansion of both species, which intensified interspecific competition for photosynthetically active radiation and soil nutrients. Consequently, the intercropped soybeans were forced to reduce their stomatal conductance to adapt to these environmental resource constraints (Zhu et al. 2026).

Furthermore, planting patterns and nitrogen levels interacted significantly during late growth. Under monoculture, reduced nitrogen (MSN) triggered a sharp decline in C_i and severe stomatal limitation. This confirms that late-stage nitrogen deficiency

accelerates premature leaf senescence and restricts both stomatal opening and carbon assimilation (Mu and Chen 2021; Sakuraba 2022). Conversely, ISN treatment fully offset low-nitrogen stress, maintaining C_i levels above $300 \mu\text{mol mol}^{-1}$ and significantly increasing G_s . In the high-evaporative-demand environment of an arid oasis, maintaining late-stage stomatal conductance is a crucial indicator of robust physiological resilience.

PLS-PM analysis provides quantitative evidence that belowground compensatory responses mitigate low-nitrogen stress (Fig. 9b). Specifically, moderate nitrogen reduction upregulates soil enzymatic potential (-0.975), which optimizes nutrient availability (0.987) to sustain aboveground photosynthetic maintenance. This sustained mineralization of organic nitrogen by key soil enzymes (e.g., S- β -GC and S-NAG), coupled with enhanced root nodulation (Lin et al. 2024), establishes a continuous nitrogen supply pipeline to the leaves. This improved belowground microenvironment shows a strong positive coupling with the maintenance of aboveground photosynthetic capacity (0.614), confirming the existence of a robust plant-soil synergy.

Biochemically, this sustained nitrogen influx is essential for the continuous synthesis of photosynthetic enzymes, particularly Rubisco, during the late reproductive stages (Zhang et al. 2024b; Liu et al. 2025). By preventing the degradation of these key enzymes, the ISN system effectively delays nitrogen-starvation-induced leaf senescence. This finding challenges the traditional assumption that nitrogen reduction inevitably causes late-stage photosynthetic decline. Physiological evidence indicates that the intercropping with reduced nitrogen strategy does not impair the late-stage photosynthetic potential of soybeans, but rather enhances their adaptability to resource constraints. Crucially, this resilient carbon assimilation capacity serves as the physiological engine for subsequent yield formation. By maintaining a strong photosynthetic "source," the plants are empowered to dynamically shift photosynthate partitioning towards reproductive "sinks" under competitive stress, which acts as the ultimate system-level driver of final yield.

Synergistic mechanisms of dry matter partitioning across cropping systems under reduced-nitrogen intercropping

Crop dry matter accumulation serves as the physiological basis for yield formation (Sun et al. 2025). The dynamics of its accumulation and partitioning directly reflect interspecific interactions and resource competition patterns within the cropping system, providing a comprehensive indicator of population productivity and resource utilization efficiency (Lu et al. 2023). Our results indicate that monoculture soybean (MS) exhibited the highest dry matter accumulation across nearly all growth stages and plant organs, particularly during the seed-filling stage, which directly determines the final yield (Wu et al. 2016; Wang et al. 2023). This advantage primarily stems from unrestricted access to light, water, and nutrients in the absence of interspecific competition. Interestingly, at the V4 stage, the reduced-nitrogen monoculture (MSN) treatment demonstrated significantly enhanced early growth, with dry matter accumulation reaching 48.05% higher than that of the MS treatment. This aligns with the “nitrogen limitation-induced root nodulation compensatory growth” mechanism observed in *Medicago truncatula* by Jeudy et al. (2010), suggesting that low-nitrogen conditions can trigger an early root compensatory response in legumes. However, upon reaching the R3 stage, as nutrient demands for reproductive organ development rapidly increased, the negative effects of nitrogen limitation began to manifest, leading to a significant decline in dry matter accumulation. This shift from early growth promotion to subsequent decline demonstrates that the ecological compensation and nodulation advantages gained during the vegetative stage are insufficient to offset the resource limitations caused by absolute nitrogen deficiency during the reproductive stage (Zambon et al. 2023).

These results are consistent with previous studies (Chen et al. 2017), indicating that the conventional nitrogen application rates commonly used in monocropping systems may be inefficient or even detrimental when applied to intercropping systems. Excessive nitrogen application not only leads to resource waste (Yuan et al. 2017; Fan

et al. 2022) but also promotes luxury nitrogen uptake by fruit trees, thereby exacerbating the competition between the trees and soybeans (Liang et al. 2023) and ultimately reducing soybean yield. Because resource competition is inevitable in intercropping systems (Khalid and Khalil 2020), both intercropping treatments exhibited lower overall dry matter accumulation. This competitive inhibition became evident as early as the soybean branching stage. However, the reduced-nitrogen intercropping (ISN) treatment consistently outperformed the standard intercropping (IS) treatment in dry matter partitioning, particularly to reproductive organs (pods and seeds).

In highly competitive intercropping environments, moderate nitrogen reduction mitigates nitrogen excess and enhances the use efficiency of limited nitrogen resources (Li et al. 2018). Furthermore, our PLS-PM analysis (Fig. 9b) quantitatively validates this structural shift, confirming that the optimized belowground microenvironment directly drives aboveground source-sink dynamics (0.731). These results demonstrate that under the ISN treatment, 28.40%–28.70% of photosynthates are preferentially partitioned to the grains. Rather than being an isolated agronomic trait, this phenomenon serves as a physiological manifestation of a positive plant-soil feedback mechanism. Specifically, the enzymatic mineralization of organic nitrogen during late growth stages effectively sustains the aboveground photosynthetic source (Xu et al. 2023). This process drives plants to dynamically regulate carbon allocation under competitive stress, facilitating the translocation of resources from vegetative tissues to reproductive organs (Guo et al. 2025). By coupling soil enzymatic mineralization (Jia et al. 2023) with the precise spatial reconfiguration of plant resource allocation, the ISN system establishes a robust synergistic pathway that ultimately ensures system-level yield formation (0.942).

Yield compensation and comprehensive system benefits under reduced-nitrogen
intercropping

In this study, soybean yields ranked as follows: MS > MSN > ISN > IS. Although the ISN treatment outperformed the MS treatment in key yield components (such as the number of effective pods per plant) and exhibited a compensatory yield effect, total yield remained constrained. These constraints were primarily driven by insufficient photosynthetically active radiation due to canopy shading (Sudmeyer and Speijers 2007; Qiao et al. 2019) and resource limitations arising from interspecific competition (Zhang et al. 2019). However, crop yield alone is insufficient to fully evaluate overall system performance. System-level indicators, such as the land equivalent ratio (LER) and income equivalent ratio (IER), more accurately capture the synergy between productivity and economic benefits within this system (Wang et al. 2022). Unlike the severe yield penalties in the MSN treatment, ISN consistently maintained an LER > 1.0 and an IER > 1.25 (Fig. 8).

Viewed through the lens of plant-soil feedbacks, the integrated superiority in land utilization and economic profitability is essentially a macro-scale response driven by belowground microecological synergies. This indicates that the system's superiority stems from a synergistic effect: moderate nitrogen reduction acts not as a limiting factor, but as a catalyst that reshapes interspecific interactions (Zhu et al. 2023; Khashi u Rahman et al. 2025). Consequently, the ISN system effectively buffers against nutrient stress, achieving an optimal balance of land-use efficiency and economic returns. Extending traditional intercropping theory, our findings demonstrate that targeted N reduction unlocks ecological potential beyond basic resource efficiency. While moderate N reduction improves N-use efficiency (Tao et al. 2025), severe deficiency under intense competition still constrains yield (Nasar et al. 2024). Therefore, targeted N reduction acts as an ecological lever, stimulating belowground enzymatic potential and enhancing plant-soil nutrient synergy rather than simply managing fertilizer inputs. By coupling these microecological processes with systemic yield stability, ISN

optimizes the competition-facilitation trade-off, providing a precise, mechanism-based framework for sustainable arid agroforestry

Conclusion

This study demonstrates that targeted understory nitrogen reduction (ISN) in an arid apricot-perilla intercropping system effectively mitigates the nutrient supply-demand mismatch typical of monocultures. By significantly upregulating key soil C- and N-cycling enzymes (e.g., S- β -GC, S-NAG, S-NiR), ISN enhances early-stage nitrogen retention and sustains late-stage mineralization. This belowground microecological priming directly drives aboveground physiological resilience: it alleviates late-stage stomatal limitations, maintains robust carbon assimilation, and optimizes assimilate partitioning to reproductive organs, successfully buffering the understory crop against low-nitrogen stress. Crucially, ISN functions as a proactive ecological lever rather than a mere yield-limiting constraint. It reshapes interspecific interactions, transforming competitive stress into complementarity to achieve superior land-use ($LER > 1.0$) and economic ($IER > 1.25$) efficiencies. This mechanism-driven approach offers a highly sustainable intensification paradigm for arid oasis agriculture. Future research integrating long-term monitoring and multi-omics is needed to elucidate “plant-soil-microbe” pathways as companion trees mature, further advancing precise, biology-driven nutrient management.

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Data availability Not applicable.

Code availability Not applicable.

Declarations

Conflict of interest The authors declare no conflicts of interest.

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