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Synergizing root growth and carboxylate release enhance seed yield in maize-soybean intercropping on acidic karst soils

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ABSTRACT

Context: Southwest China is one of the largest karst regions, where nitrogen (N) deficiency and poor management limit crop productivity. Maize-soybean intercropping is a widely adopted planting model used by farmers across China. Therefore, innovative crop management practices to improve productivity in this region are essential to ensure China's food security.
Objective and methods: Ridge-furrow with film mulching (RFM) combined with N supply was introduced for the first time into the maize-soybean intercropping system. Eight treatment combinations (maize and soybean monocultures (M), maize-soybean intercropping with RFM and with ridge-furrow (RF) under 0 (N0) and 150 (N150) kg N ha^{-1} supply) were used to investigate changes in seed yield, land use efficiency, biomass, N uptake, and root morphological and physiological traits from 2020 to 2023 in Southwest China.
Results: The results showed that introduction of RFM into the maize-soybean intercropping system significantly increased maize (13 %) and soybean (42 %) seed yields and land equivalent ratio (LER) (25 %) compared to ridge-furrow without film mulching. Meanwhile, N150 significantly increased maize (33 %) and soybean (24 %) seed yields compared to N0 across four years. The high LER was attributed to the increased yields of maize and soybean, which were associated with higher biomass and N uptake under RFM. The promotion of root growth, such as increased root length and carboxylate release with RFM, enhanced N uptake in both maize and soybean was observed across three years (2021–2023). In addition, N application significantly increased biomass accumulation, N uptake, root length, and carboxylate release at two developmental stages across two years (2022 and 2023), thus contributing to higher seed yields in maize and soybean.
Conclusion: RFM combined with N supply can further increase crop yield and land use efficiency in maize-soybean intercropping systems in karst areas. This improvement is explained by the enhancement of the "N-capture", related to root morphological traits, and "N-mining", related to carboxylate release, which together increase N uptake, biomass, and ultimately seed yield.
Implications: RFM combined with N addition could be considered an efficiency strategy to increase crop productivity in maize-soybean intercropping systems in karst agroecosystems. Our results provided insights into the effects of crop management practices and N addition on N-acquisition strategies and their roles in nutrition uptake and yield formation.

1. Introduction

Legume-based intercropping systems, such as maize-soybean intercropping, are widely used globally (Zhao et al., 2022) and can increase crop production on a global scale while minimizing negative environmental impacts (Ditzler et al., 2021). Maize-soybean intercropping is a widely adopted planting model across China, which can improve seed yield and resource use efficiencies such as nitrogen-use efficiency (NUE)

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and land use efficiency, often expressed as the land equivalent ratio (LER; Nasar et al., 2023; Raza et al., 2019; Zhang et al., 2025). A global meta-analysis indicated that the average LER of maize-soybean intercropping was 1.32, suggesting significant land-sparing potential for two of the world's major food crops (Xu et al., 2020) and a strong capacity to reduce reliance on soybean and maize imports. The high LER highlights that intercropping is a promising practice for improving land productivity while reducing the environmental impacts of nitrogen fertilizer usage worldwide. Therefore, maize-soybean intercropping is a sustainable approach to enhancing crop productivity, and further improving the productivity of this system is crucial to ensuring food security.

Southwest China is one of the largest karst regions (0.54 millionkm^2), which is highly sensitive to human activities and environmental change (Oliver et al., 2020). Soybean and maize are two major grain crops in the karst lands of Southwest China, accounting for approximately 75 % of the cultivated area and 82 % of total grain production (Zhang et al., 2017). Nutrient scarcity, particularly nitrogen (N), seasonal drought and poor management limit crop productivity in karst regions (Fenton et al., 2017; Li et al., 2021; Song et al., 2020). Nitrogen deficiency occurs in over 80 % of karst soils in Southwest China (Zhang et al., 2017) and is considered a major limiting factor for crop production (Du et al., 2011; Qi et al., 2013). This is because in Karst agroecosystems, the poor soil structure, high calcium content, and land low soil organic content limited the transformation of the soil N, and thereby lowering soil N availability and N-use efficiency (Wen et al., 2024). Besides, seasonal drought-induced water stress also affects the soil N cycle by restricting N mineralization rate, which further limits soil N availability (Deng et al., 2021). While nitrogen fertilizer application significantly increases maize and soybean seed yields (Zhang et al., 2017), the supplied N showed a low retention rate and high leaching in karst areas (Zhang et al., 2021), which not only lowers nitrogen use efficiency but also contributes to nitrate pollution (Yue et al., 2019; Zhang et al., 2015). Thus, sustainably using nitrogen is key to boosting seed yields while minimizing nitrogen loss. Improved farm management practices, including intercropping, fertilizer optimization, and tillage management have proven effective in enhancing crop productivity (Agnolucci et al., 2020; Williams et al., 2019; Zhang et al., 2017). Zhang et al. (2017) reported that maize-soybean intercropping improves nitrogen uptake in Southwest China's karst regions.Furthermore, agricultural intensification in these karst areas is relatively low compared to other regions in China (Tang et al., 2019). Thus, innovation crop managements to alleviate the adverse effects of N deficiency and seasonal drought are urgently needed to increase the crop productivity in this area is essential to ensure the food security of China.

Ridge-furrow with film mulching (RFM) is considered a sustainable management practice to improve crop yield in monoculture systems in arid and semi-arid areas (Liao et al., 2022b; Zhang et al., 2025; Zheng et al., 2021). Previous studies have shown that RFM significantly increase crop yields by inhibiting water evaporation, reducing nutrient loss, and enhancing N uptake in monoculture systems (Liao et al., 2022a; Zhang et al., 2025). However, the maize-soybean intercropping systems of karst agroecosystems in southern China are highly susceptible to drought stress (Song et al., 2020), whether and how the potential changes in nutrients uptake caused by mulching affect yield have not yet been reported. Maize-soybean intercropping can improve leaf N status and nitrogen use efficiency by regulating nitrogen assimilation enzymes, thereby enhancing maize growth and yield (Nasar et al., 2023). Yong et al. (2018) found that maize-soybean intercropping significantly improved maize N uptake and NUE by modifying rhizosheath processes (Yong et al., 2018). Increased nitrogen transfer from soybean to maize also contributed to the high NUE of maize in intercropping systems (Raza et al., 2019; Zhang et al., 2017). Roots are the primary organs for nutrient uptake, including N, and promoting root growth is essential for improving yields and nutrient uptake (Li et al., 2023b), especially in Southwest China's karst regions where nutrient resources are scarce and nitrogen utilization is low (Qi et al., 2013). An eight-year field experiment confirmed that mean maize root dry mass under RFM was 34.7 % higher than that under ridge-furrow without film mulching in monoculture maize systems (Yang et al., 2024). Furthermore, root length, diameter, surface area, and volume were all significantly higher under RFM than under ridge-furrow without mulching ($P < 0.05$). However, the effects of RFM on root traits, seed yield, and their correlations in maize-soybean intercropping systems in China's karst areas have not been fully investigated. Similarly, the impacts of RFM on root morphological and physiological traits as well as N uptake in intercropping systems remain largely unexplored.

In this study, to the best of our knowledge, we first introduced the ridge-furrow (RF) system into a maize-soybean intercropping system in a karst agroecosystem located in southern China, where low plant-available soil N concentrations and seasonal drought events limit crop productivity (Du et al., 2011; Qi et al., 2013; Song et al., 2020; Zhang et al., 2017). We aimed to investigate the effects of RFM and N addition on N-acquisition strategies and its role in N uptake and yield formation in the maize-soybean intercropping system, offering insights into the underlying mechanisms of RFM's impact on N-acquisition efficiency and yield improvement. The following hypotheses were tested: (1) the introduction of RFM into maize-soybean intercropping significantly increases seed yield and land-use efficiency compared to conventional maize-soybean intercropping; (2) the RFM could enhance the "N-capture" related to root morphological and "N-mining" related to physiological traits contributes to increase N uptake to increase biomass accumulation and seed yield.

2. Materials and methods

Field experiment was set in 2020, located in Lianxing Village, Jichang Town, Anshun, Guizhou Province (106° 5′ 59" E, 26° 6′ 29" N). The soil type at the test site is yellow soil (Shi et al., 2004). The basic chemical properties of the surface layer of the soil (0–20 cm) at the site are as follows: pH= 4.54, organic carbon = 17.06 g/kg, alkali-hydrolyzed nitrogen = 126.73 mg/kg, available phosphorus = 20.92 mg/kg, available potassium = 159.50 mg/kg. The crop growth period was from April to October each year, with no crop growth during other times. The weather data were obtained from the weather station located 1.2 km away from the field. The mean temperatures were 21.1℃, 21.3℃, 20.9℃ and 22.7℃ while the precipitations were 1065 mm, 729 mm, 496 mm and 408 mm for 2020, 2021, 2022 and 2023 across the whole growth season, respectively (Fig. 1).

2.1. Experimental design

This experiment was a two-factor split-zone design (film mulching × nitrogen application). The N treatment is the main plot and cropping system as the sub-plots. There are three subplots (replicates) for each N treatment and each subplot was considered as a block; the four cropping systems were randomized arranged in each block. Each plot (replicate) was 60 m^2 (6 m wide × 10 m long). Maize and soybean monoculture (M) with 0 (N0) and 150 (N150) kg N ha^{-1}, maize-soybean intercropping with ridge-furrow with film mulching (I+RFM, as shown in Fig. S1) at 0 and 150 kg N ha^{-1}; maize-soybean intercropping with ridge-furrow without film mulching (I+RF) at 0 and 150 kg N ha^{-1}. Black plastic film was used. The maize variety was Jinyu 908 and the soybean variety was Fendou 97. The planting pattern of intercropping was two rows of maize intercropped with two rows of soybeans. The plant spacing in maize-soybean intercropping was as follows: the row spacing for maize was 40 cm (1 plant per hole), for soybeans was 40 cm (2 plants per hole); the row spacing between maize and soybeans was 60 cm. The row spacing for maize and soybean monoculture was 60 cm and 40 cm, respectively. Superphosphate (P: 7.1 %) was used as the phosphorus fertilizer at a rate of 45 kg P ha^{-1}, all P fertilizer was applied as basal fertilizer (equally for maize and soybean). Urea (N: 46.2 %) was applied as the nitrogen fertilizer at a rate of 150 kg N ha^{-1}, with 50 % applied before sowing as

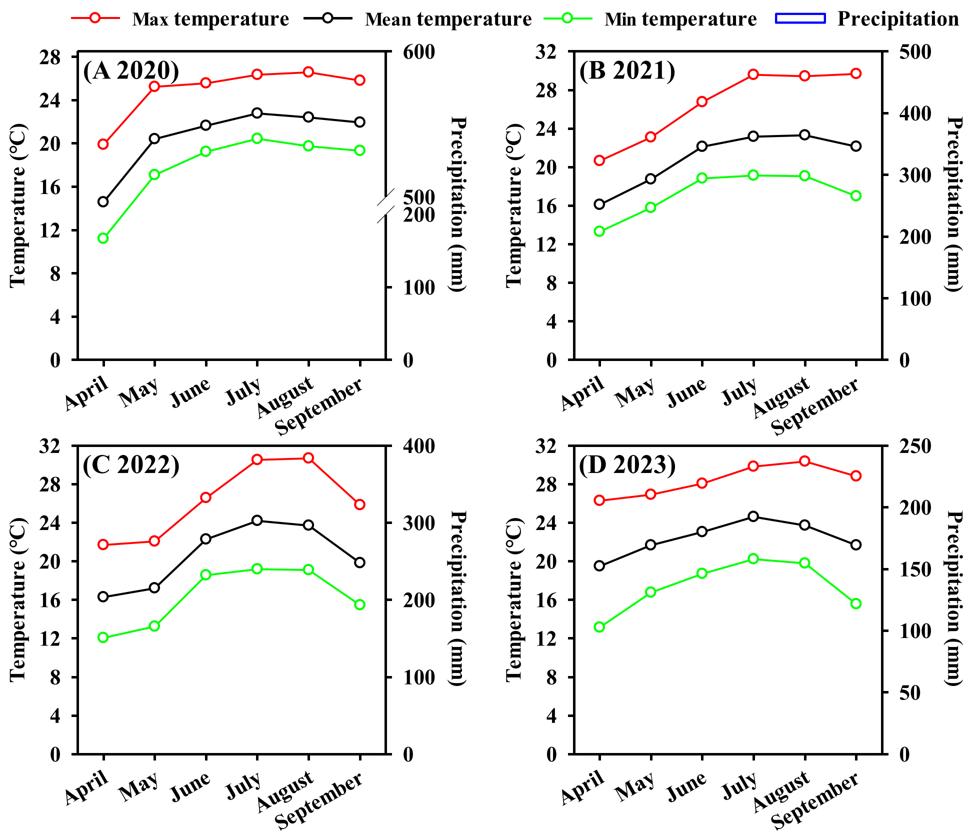

Fig. 1. The monthly temperature (max, mean and min) and precipitation during the growth stage from April to September in Lianxing Village, Jichang Town, Anshun, Guizhou Province from 2020 to 2023.

basal fertilizer (equal for maize and soybean) and 50 % at the maize silking stage (N fertilizer was top-dressed to maize).

2.2. Sample collection

The plant samples used to determine the biomass and P uptake were collected at 70 and 106 days after sowing over three consecutive years (2021–2023), corresponding to the full flowering and late grain filling stages of soybean, and the jointing and early grain filling stages of maize. Five represented consecutive maize plants and ten soybean plants were collected from each plot as samples; all plants were selected in the central plot to avoid the border effects and the five maize/ten soybean plants were combined to one sample for each plot. The shoots were collected and dried at 75 ℃ for 48 h, then finely powdered with a ball mill (CEBO-24, Shanghai Cebo Biotechnology Development Center, Shanghai, China) and stored for shoot P concentration determination.

After removing the shoot, the shovelomics method (Trachsel et al., 2011) was used to dig out the roots (0–20 cm soil depth where most roots were grown to determine the root traits from 2021 to 2023), then shaken to remove loose soil and the soil adhere to roots were defined as rhizosheath soil. The carboxylates in rhizhsheath soil (the soil adhered to roots) were collected in 2022 and 2023. Briefly, the roots were placed into a 100 mL conical flask with 0.1 mmol/L $CaCl_2$ solution (50 mL for soybean roots and 100 mL for maize roots). The flask was shaken for 5 min to allow the solution to fully rinse the plant roots and remove all the soil adhered to roots. Removing the plant roots, and then poured the rinsing solution into a 50 mL centrifuge tube, labelled, and placed in an ice box. All collected samples were brought back to the laboratory and centrifuged at 4000 rpm, and the supernatants were collected, two drops of thymol solution were added and then stored for carboxylate determination. The washed roots were brought back to the lab and scan using a scanner (Epson PV850 Pro, Epson Corporation, Long Beach, CA, USA). After scanning, the roots for each plot were collected and dried at 75 ℃ for 48 h. The dried roots were then finely ground as before for N concentration determination following (He et al., 2019). The soil core (5 cm diameter) method was used to collect the soil samples (0–20 cm soil depth) at 106 DAS to determine the soil water contents followed Feng et al. (2022). Five randomized soil samples were obtained in each plot and combined to one soil sample, which was dried at 85°C for 72 h, then weighted and calculated the soil water content.

2.3. Determination of root morphological traits, dry matter and N concentrations

The root images obtained from the scanning were analyzed using WinRhizo 2019 Pro software (Regent Instruments Corporation, Québec, Canada) to obtain root length, root surface area, root volume, and root diameter. The finely ground samples described previously were used to shoot N concentration analysis. Briefly, plant samples were digested with sulfuric acid and hydrogen peroxide, then the total N concentration was determined using the Kjeldahl method (SKD-800, Shanghai Peiou Analytical Instruments Co. Ltd, Shanghai, China) following He et al. (2017)

2.4. Analysis of the root released carboxylates anions

The supernatants were filtered through a 0.22 µm syringe filter (Biosharp, Shanghai Yanhui Biotechnology Co., Ltd) before determination. A subsample (20 µL) was used to determine the seven organic acids (oxalate, tartrate, citrate, malate, fumarate, lactate, and succinate) for each sample and summed to obtain the total root organic anions. The calibration curve was established for each organic acid and the units is express as µmol L^{-1}. The carboxylates for each plant were obtained by multiplying the concentration with its volume. The organic anions were determined by high performance liquid chromatography (Agilent 1260 Infinity II, Agilent Corporation, Santa Clara, CA, USA) following (Shen et al., 2003).

2.5. Determination of seed yield and land equivalent ratio

The seed yields of maize and soybean were determined when the crops attained the maturity stage. A subplot (2 ×2 =4 m^2) was used to collect all maize cobs and soybean seeds. The maize cobs were manually threshed, dried at 75 ℃ for 48 h, and weighed. The seed yield in monoculture was calculated based on the harvest area. The land equivalent ratio (LER) was calculated as follows:

LER = intercropping maize seed yield/monoculture maize seed yield + intercropping soybean seed yield/monoculture soybean seed yield.

2.6. Statistical analysis

The data were analysed by three-way ANOVA (RFM, N supply rate, and year were fixed factors and block was used as random factor) using the GenStat 19.0 statistical software (VSN International Ltd., Rothamsted, England, 2019), and the Tukey test was used to analyze whether there were significant differences among various treatments at $P = 0.05$. The mean squares based on the results of three-way ANOVA were used to calculate the percentages explained by the treatment factors and their interactions. The data were tested for normality and heteroscedasticity (Brown-Forsythe test), and no transformations were required. The correlation matrix generated with Sigma Plot 15.0 (Grafiti LLC, Waverley St, Palo Alto, CA) was used to show the correlation among the seed yield, LER, biomass, root morphological and physiological traits based on Spearman correlation and included three years data (2021–2023). R software (version 4.4.2) was used to perform the partial least squares path modelling (plspm) to reveal the effects of FM and N addition on root traits, N uptake and seed yield. The sample size is 36. All variables are dependent variables and there are no latent variables.

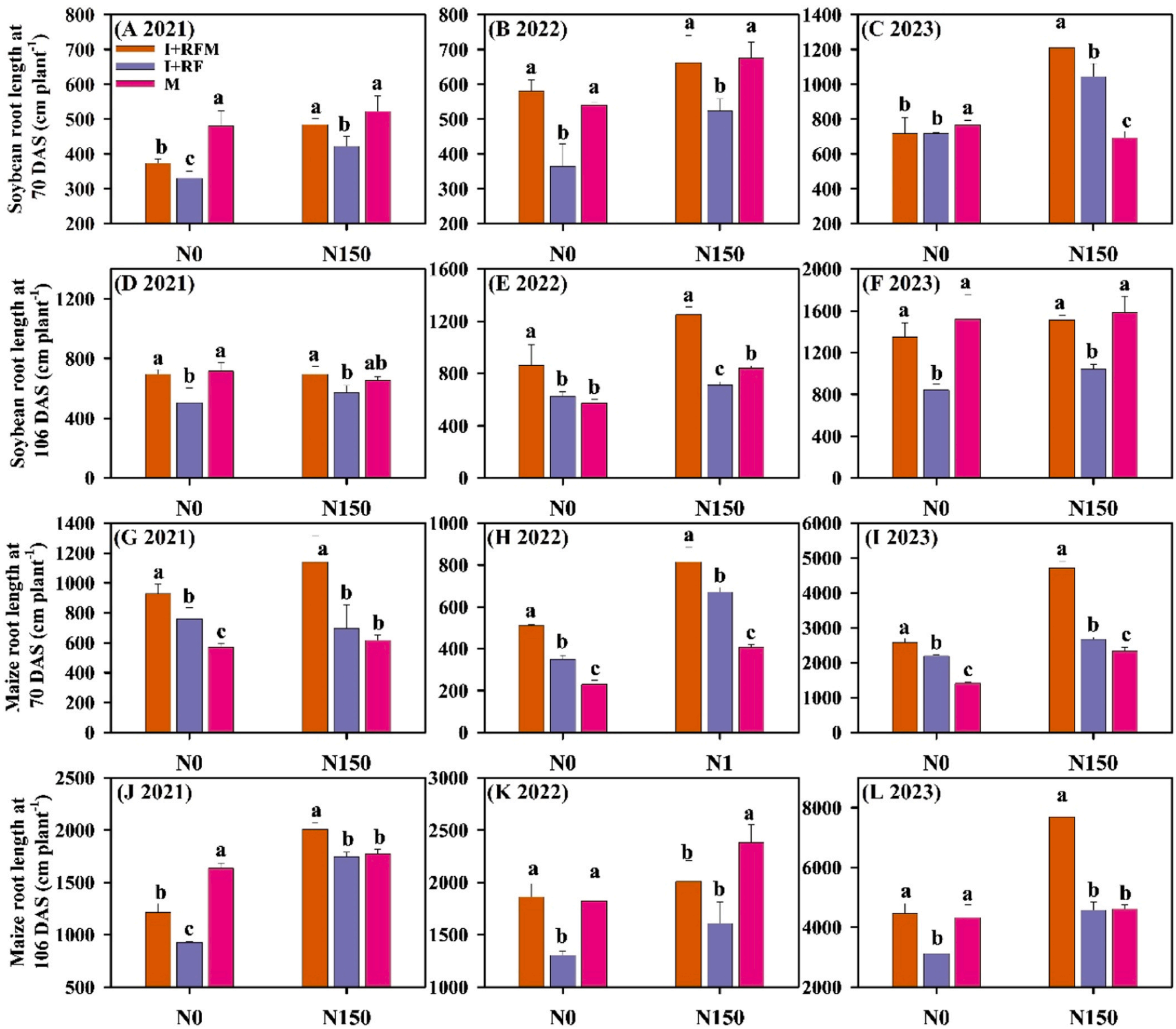

Fig. 2. Root length of soybean at (A-C) 70 and (D-F) 106 days after sowing, maize root length at (G-I) 70 and (J-L)106 days after sowing over consecutive three years in a soybean and maize monoculture (M), maize-soybean intercropping system with ride-furrow film mulching (I+RFM) and ride-furrow (I+RF) under two nitrogen (N) supply rates: (0 (N0) and 150 (N150) kg N ha^{-1}). The different low case letters indicated significantly differences among I+RFM, I+RF and M at the same N levels at $P = 0.05$.

3. Results

3.1. N-acquisition related root morphological and physiological traits

The film mulching (FM), N supply rate (N), year, and their interactions significantly affected maize and soybean root morphological and physiological traits in the maize-soybean intercropping system (Figs. 2 and 3, Figs. S2–S4, Tables 1 and S1). In maize-soybean intercropping system and across three years and two N supply rates, the soybean averaged root length, root surface area, and root volume in treatment with FM were 21 %, 28 % and 57 % higher than those without FM at 70 DAS, and 43 %, 46 % and 51 % higher at 106 DAS, respectively (Fig. 2, Figs. S2 and S4); maize averaged root length, root surface area, and root volume with FM were 41 %, 47 % and 71 % higher than without FM at 70 DAS, and 37 %, 39 % and 42 % higher at 106 DAS, respectively. Root diameter mainly varied among years (Fig. S3; Table S1). The N supply (N150) significantly increased root length of maize (46 % and 50 %) and soybean (37 % and 21 %), root surface area of maize (44 % and 42 %) and soybean (21 % and 18 %), and root volume of maize (49 % and 35 %) and soybean (19 % and 20 %) for 70 and 106 DAS across three years and management practices, respectively.

In the maize-soybean intercropping system, FM significantly increased soybean (16.2 % and 43.6 %) and maize (15.5 % and 66.4 %) root carboxylates at 106 DAS for 2022 and 2023 across two N supply rates, respectively (Fig. 3); while N150 significantly increased averaged root carboxylates of soybean (202 % and 174 %) and maize (111 % and 279 %) for 2022 and 2023, respectively (Fig. 3; Table 1).

3.2. Biomass accumulation and N uptake at different development stage

The film mulching (FM), N supply rate (N), year, and their interactions significantly affected maize and soybean biomass and N uptake in the maize-soybean intercropping system (Figs. 4–7; Tables 1 and 2). The effects of FM on biomass were greater in soybean (averaged 47 % vs 18 %) than in maize (Table 2).

Across three years and two N supply rates in the maize-soybean intercropping system, soybean shoot and root biomass with FM were on average 109 % and 53 % higher than without FM at 70 DAS, 57 % and 49 % higher at 106 DAS, respectively (Fig. 4). Maize shoot and root biomass with FM were 59 % and 54 % higher than without FM at 70 DAS, and 32 % and 38 % higher at 106 DAS, respectively (Fig. 5). Similarly, soybean shoot and root N contents with FM were 122 % and 39 % higher than without FM at 70 DAS, 81 % and 76 % higher at 106 DAS, respectively (Fig. 6). For maize, shoot and root N contents with FM

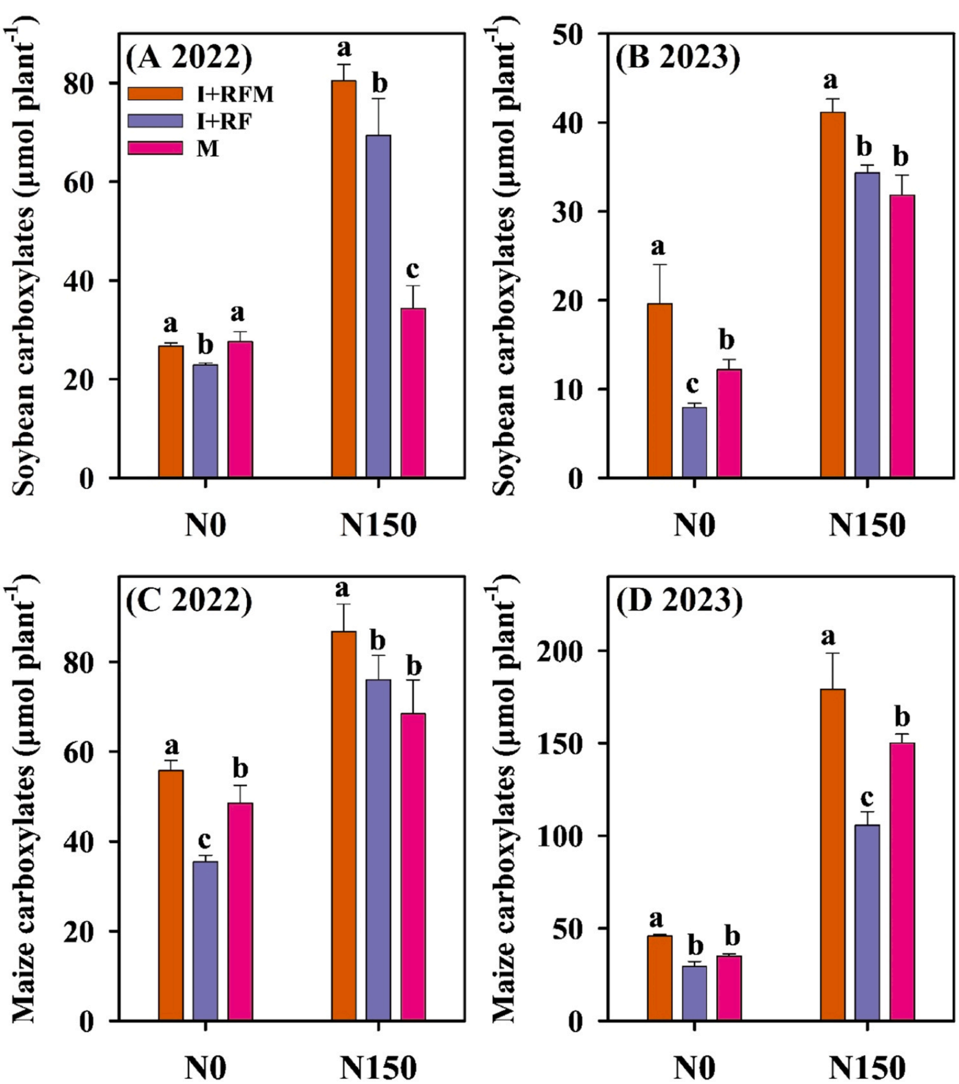

Fig. 3. The carboxylates of (A-B) soybean and (C-D) maize in soybean and maize monoculture (M), maize-soybean intercropping system with ride-furrow film mulching (I+RFM) and ride-furrow (I+RF) at 106 days after sowing in 2022 and 2023 under two nitrogen (N) supply rates: (0 (N0) and 150 (N150) kg N ha^{-1}). The different low case letters indicated significantly differences among I+RFM, I+RF and M at the same N levels at $P = 0.05$.

Table 1
The effects of management practice (MP), nitrogen supply rate (N), year (Y), and their interactions on root traits, carboxylates and biomass of soybean and maize. DAS: days after sowing. The numbers in the parentheses represent the percentage of the total mean square. n.s. not significant; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Parameter	Significance of sources of variability							
	MP	**N**	**Y**	**MP×N**	**MP×Y**	**N × Y**	**MP×N × Y**	**Error**
Soybean root length at 70 DAS	n.s. (3.5)	***(21.5)	***(60.3)	n.s. (3.2)	n.s. (4.1)	n.s. (2.4)	n.s. (2.9)	2.1
Soybean root length at 106 DAS	**(18.8)	n.s. (5.0)	***(65.3)	n.s. (0.1)	n.s. (4.8)	n.s. (1.8)	n.s. (0.6)	3.6
Maize root length at 70 DAS	***(9.8)	***(9.8)	***(70.2)	*(1.4)	***(2.9)	***(4.6)	*(0.9)	0.3
Maize root length at 106 DAS	***(5.6)	***(12.5)	***(72.8)	n.s. (1.6)	**(2.7)	*(2.8)	n.s. (1.5)	0.6
Soybean root carboxylates at 106 DAS	**(5.4)	***(57.2)	***(24.5)	*(4.3)	n.s. (1.7)	n.s. (2.9)	*(3.1)	0.9
Maize root carboxylates at 106 DAS	*(4.0)	***(61.7)	***(10.9)	n.s. (0.6)	n.s. (1.0)	***(19.6)	n.s. (1.4)	0.8
Soybean shoot biomass at 70 DAS	***(43.2)	*(6.1)	***(42.9)	n.s. (1.8)	n.s. (0.7)	n.s. (2.1)	n.s. (1.3)	1.9
Soybean root biomass at 70 DAS	***(55.4)	n.s. (9.0)	n.s. (17.4)	n.s. (4.9)	n.s. (4.3)	n.s. (1.1)	n.s. (2.1)	6.0
Soybean shoot biomass at 106 DAS	***(53.9)	***(22.3)	*(6.9)	n.s. (0.8)	***(13.7)	n.s. (0.3)	n.s. (0.4)	1.7
Soybean root biomass at 106 DAS	***(36.4)	n.s. (5.8)	***(34.7)	n.s. (3.7)	***(14.4)	n.s. (1.4)	n.s. (1.3)	2.3
Maize shoot biomass at 70 DAS	***(11.8)	***(10.7)	***(72.5)	n.s. (0.9)	n.s. (1.0)	n.s. (1.7)	n.s. (0.6)	0.6
Maize root biomass at 70 DAS	***(18.6)	***(23.5)	***(48.9)	n.s. (0.9)	n.s. (1.4)	*(3.2)	* (2.6)	0.9
Maize shoot biomass at 106 DAS	***(19.2)	***(29.5)	***(45.9)	n.s. (0.0)	n.s. (1.6)	n.s. (1.6)	n.s. (1.4)	0.7
Maize root biomass at 106 DAS	***(23.4)	***(24.8)	***(34.5)	n.s. (0.3)	*(4.6)	*(8.2)	n.s. (2.5)	1.6

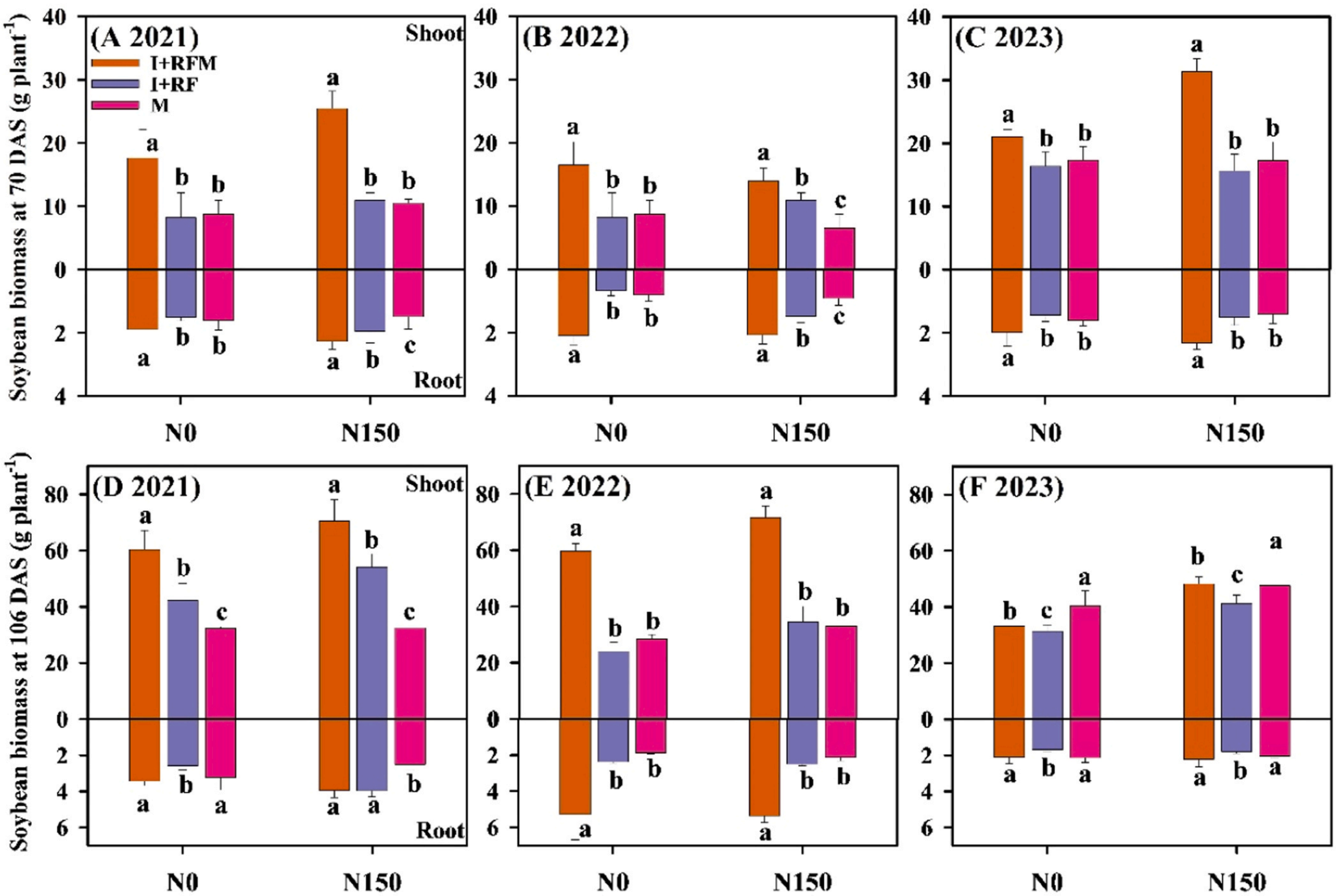

Fig. 4. Biomass of soybean shoots (above zero) and roots (below zero) at (A-C) 70 and (D-F) 106 days after sowing over consecutive three years in soybean and maize monoculture (M), maize-soybean intercropping system with ride-furrow film mulching (I+RFM) and ride-furrow (I+RF) under two nitrogen (N) supply rates: (0 (N0) and 150 (N150) kg N ha^{-1}). The different low case letters indicated significantly differences among I+RFM, I+RF and M at the same N levels at $P = 0.05$.

were 62 % and 48 % higher than without FM at 70 DAS, 62 % and 38 % higher at 106 DAS, respectively (Fig. 7). In addition, N150 significantly increased shoot biomass of maize (24 % and 36 %) and soybean (24 % and 36 %), root biomass of maize (18 % and 29 %) and soybean (21 % and 15 %), shoot N content of maize (88 % and 64 %) and soybean (47 % and 45 %), as well as root N content of maize (67 % and 71 %) and soybean (35 % and 39 %) at 70 and 106 DAS (Figs. 4–7; Tables 1 and 2).

3.3. Maize and soybean seed yield and land equivalent ratio

The film mulching (FM), N supply rate (N), year, and their interactions significantly affected maize and soybean yield in the maize-soybean intercropping system (Fig. 8 and Table 2). The maize and soybean averaged seed yields and land equivalent ratio (LER) in the maize-soybean intercropping system with FM were 13 %, 43 %, and 25 % higher than without FM across four years and two N supply rates, respectively. The N supply significantly increased maize (33 %) and

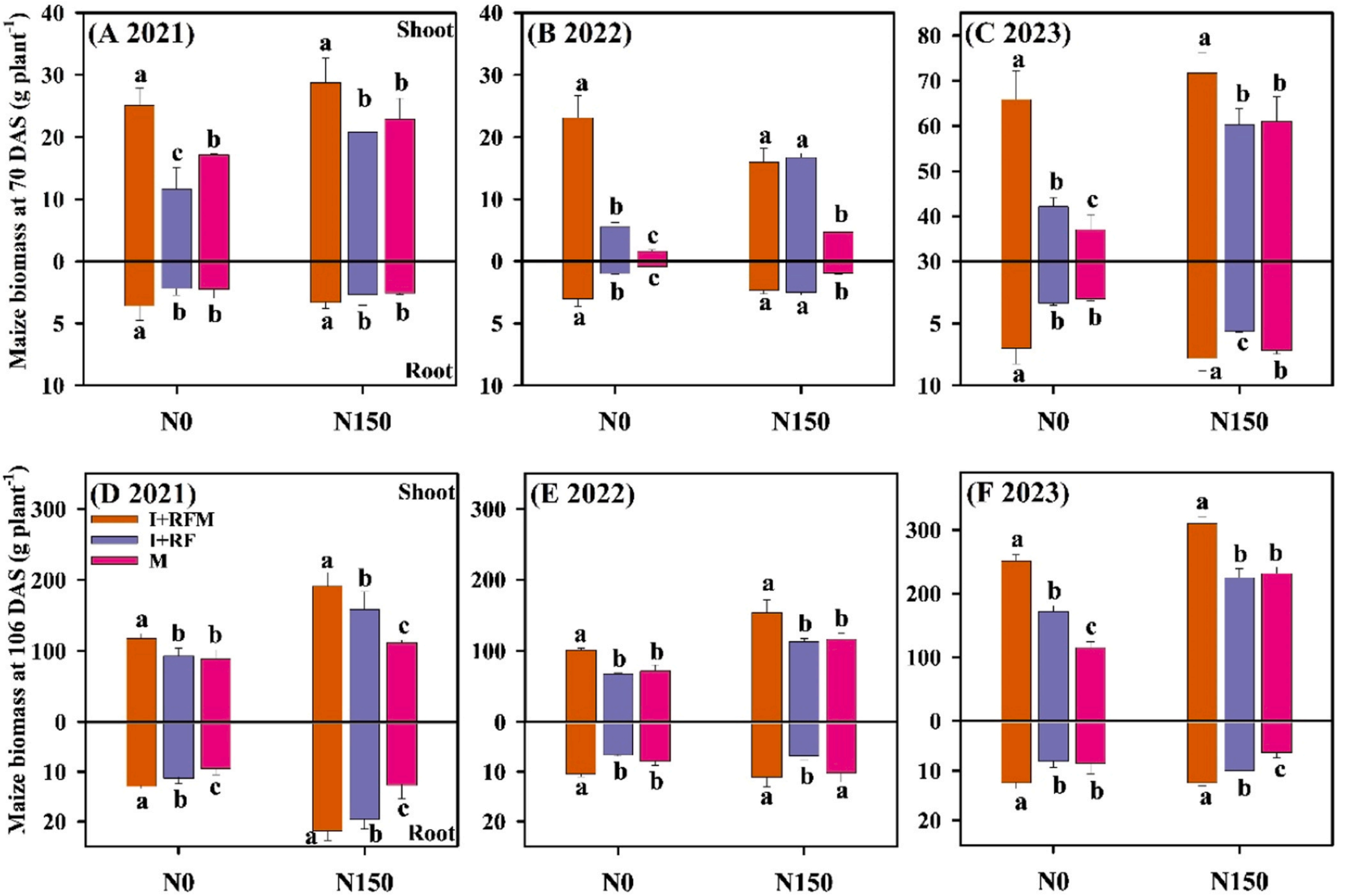

Fig. 5. Biomass of maize shoots (above zero) and roots (below zero) at (A-C) 70 and (D-F) 106 days after sowing over consecutive three years in soybean and maize monoculture (M), maize-soybean intercropping system with ride-furrow film mulching (I+RFM) and ride-furrow (I+RF) under two nitrogen (N) supply rates: (0 (N0) and 150 (N150) kg N ha^{-1}). The different low case letters indicated significantly differences among I+RFM, I+RF and M at the same N levels at $P = 0.05$.

soybean seed yields (24 %), and LER (9 %, not significant) in the maize-soybean intercropping system across four years and management practices. FM and N supply could explain 81 % and 9 % of the improvement in soybean seed yield, respectively, while they accounted for 30 % and 50 % of the improvement in maize seed yield (Table 1). The increase in LER was mainly attributed by FM (56 %). In addition, soil water content under FM was higher than without FM (Fig. S5).

3.4. Correlation analysis

The maize and soybean yields were positively correlated with LER ($r = 0.51$, $P < 0.01$ for maize; $r = 0.74$, $P < 0.001$ for soybean; Figs S6 and S7). Positive correlations were also observed between maize and soybean seed yields and shoot biomass, root biomass (except maize at 106 DAS), shoot N content, root length (except maize 70 DAS), root surface area (except maize at 106 DAS) and root volume at 70 and 106 DAS (Figs S6 and S7), as well as root carboxylates at 106 DAS (Fig. S7). Shoot biomass in maize and soybean was positively correlated with shoot N content, root length, and root surface area at 70 DAS (Fig. S6), and positively correlated with shoot N content, root surface area, root volume, and root carboxylates at 106 DAS (Fig. S7). Shoot N content in maize and soybean was positively correlated with root length and root surface area at 70 DAS (Fig. S6), and positively correlated with root surface area, root volume, and root carboxylates at 106 DAS (Fig. S7).

The Partial Least Squares Path modelling indicates that both film mulching and N addition could significantly promote the root growth and carboxylates releasing, which increased the biomass accumulation and N uptake to increase the seed yield, and thus the land use efficiency in the maize-soybean intercropping system (Fig. 9).

4. Discussion

4.1. Effects of RFM on N-acquisition strategies and its roles in N uptake and biomass accumulation

Crop productivity in karst agroecosystem of southwest China is limited by the combined effects of N scarcity and seasonal drought (Song et al., 2020; Zhang et al., 2017). In this study, we confirmed the positive effects of RFM on N uptake in a maize-soybean intercropping system through a four-year consecutive field experiment. Such effects were previously observed in monoculture systems (Liao et al., 2023; Yang et al., 2024) and help allivate the adverse impacts of N deficiency.

Roots are the primary organs responsible for nutrient uptake. The significant increase in root length under RFM increases root-soil contact area and soil exploration volume, thereby improving N uptake (Figs. 6, 7, 9) (Lynch, 2019). The simulation of root growth by RFM may be attributed to improved soil characteristics, particularly soil moisture, which was 15 % higher under FM than without FM, helping to alleviate the negative effects of seasonal drought (Li et al., 2023b). This effect is particularly evident in dry years, such as 2022 in our study. In addition, N addition exhibited stronger effects on N uptake in maize (averaged 46 %) than in soybean (30 %), primarily promoting maize root growth. One explanation for this difference is that soybean root growth is relatively insensitive to N addition, as excess N can reduce dry matter allocation to roots (Wang et al., 2009). In contrast, optimal N application (153–220 kg N ha^{-1}, compared with 150 kg N ha^{-1} in this study) can

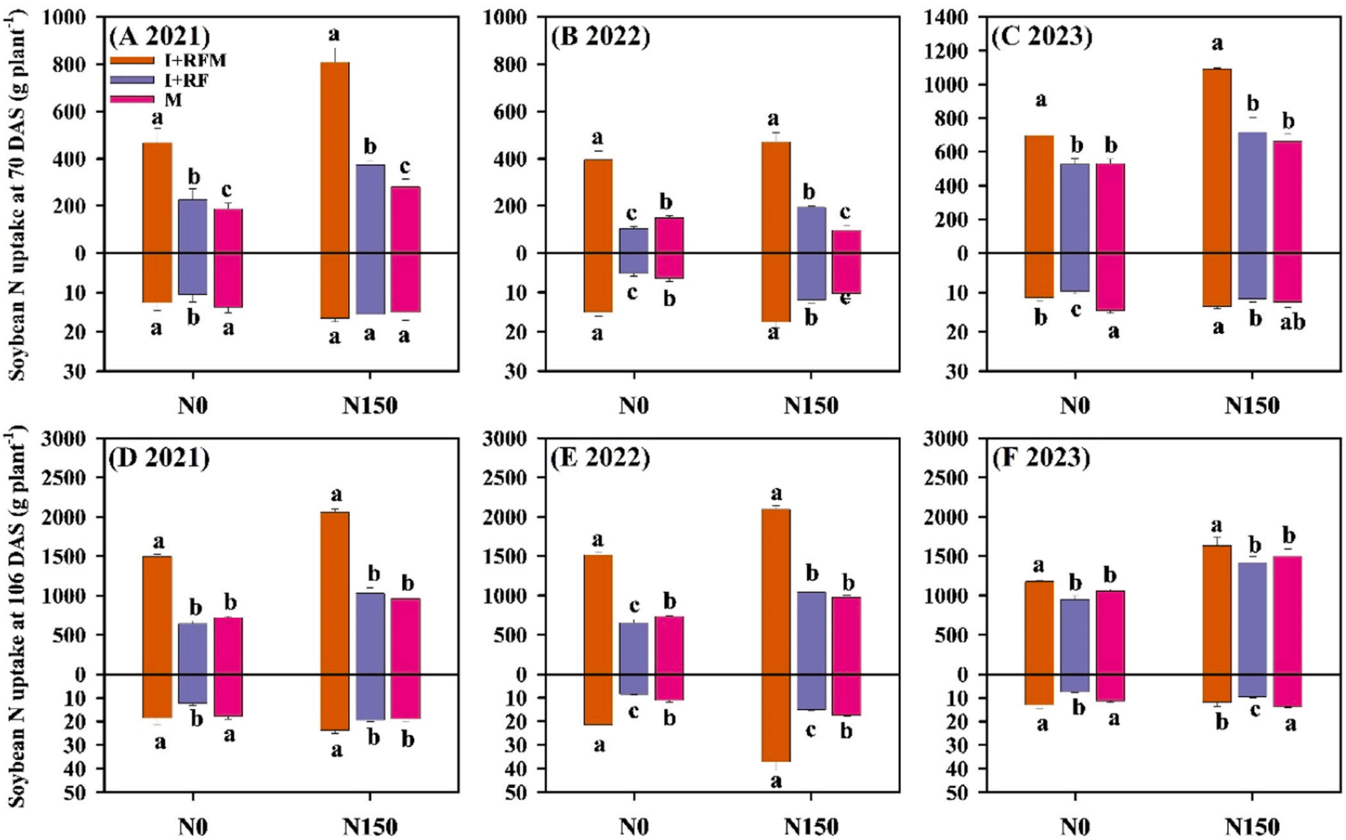

Fig. 6. Soybean shoots (above zero) and roots (below zero) N uptake at (A-C) 70 and (D-F) 106 days after sowing over consecutive three years in soybean and maize monoculture (M), maize-soybean intercropping system with ride-furrow film mulching (I+RFM) and ride-furrow (I+RF) under two nitrogen (N) supply rates: (0 (N0) and 150 (N150) kg N ha^{-1}). The different low case letters indicated significantly differences among I+RFM, I+RF and M at the same N levels at $P = 0.05$.

stimulate root growth in maize (Ren et al., 2024; Shen et al., 2025). Overall, our results confirm that RFM stimulates root growth, while the effects of N addition on root growth are species-dependent. The enhanced "N-capture" strategy, achieved through root growth promotion by RFM or N addition, increased N uptake in the maize-soybean intercropping system.

Root carboxylate release also plays an important role in N transformation and uptake (Coskun et al., 2017; He et al., 2025; Meier et al., 2017). In our study, we found that both introduction of RFM and N addition could increase root carboxylate release (Table 2). In addition, we found that the effects of N addition on carboxylates are higher than FM in soybean (57 % vs 5 %) and maize (63 % vs 4 %), while the underlying mechanisms remain largely unknown. These results indicated that although the introduction of RFM has improved the roots' ability to release carboxylates, the N deficiency determines that N addition remains the most effective way to enhance root carboxylate release. Carboxylates can increase plant-available soil N concentration by enhancing organic N mineralization (Liu et al., 2022) and decomposing labile soil organic matter to release N (Meier et al., 2017) to increase soil N availability. The enhanced "N-capture" strategy by stimulating carboxylate release induced by RFM and N addition could accelerate soil N transformation to promote N uptake in the maize-soybean intercropping system, which is another reason of higher N uptake with FM than without FM (Figs. 6, 7, 9). Furthermore, the synergy between the "N-capture" related root growth and "N-mining" related carboxylate release was observed, which further promote N uptake in soybean-maize intercropping system.

The increase of N uptake caused by FM and N addition could enhance biomass, as supported by the positive correlation between N uptake and biomass at two development stages in soybean-maize intercropping system. As noted earlier, N deficiency occurs in over 80 % of karst soils in Southwest China, significantly restricting crop growth (Zhang et al., 2017). The increase of N uptake induced by FM and N addition can alleviate the adverse effects of N deficiency, thereby promoting biomass accumulation. Higher N uptake can improve leaf N status, enhancing photosynthetic rate and further contributing to biomass increase (Bassi et al., 2018). In addition, high N uptake may be associated with superior root traits, which also increase water uptake to support biomass accumulation (He et al., 2019). These results indicate that RFM promotes biomass accumulation by increasing root growth and N uptake. However, further studies are warranted to clarify underlying mechanisms related to the N uptake process, such as the roles of microbials in N transformation in the rhizosheath. In addition, although both FM and N addition showed positive effects on shoot biomass, but we did not observe an interaction between FM and N addition (Table 1), indicating that the effects of management practice and N addition on shoot growth were independent.

4.2. Effects of RFM on crop productivity and land-use efficiency

In this study, we first introduced the ridge-furrow (RF) system in the maize-soybean intercropping system in a karst agroecosystem located in south China, where low plant-available soil N concentration and seasonal drought (e.g., in 2022 in our study) events limited crop productivity (Du et al., 2011; Qi et al., 2013; Song et al., 2020; Zhang et al., 2017). Substantial improvements in crop productivity with RFM in soybean-maize intercropping system is observed, which can be explained by the increase of biomass and N uptake (Zhang et al., 2024). Firstly, the high N uptake induced by FM could help to alleviate the adverse effects of N deficiency on crop yield which widely observed in karst acidic soils (Wang et al., 2025). Secondly, the high biomass could provide more assimilates to support the seed development to increase

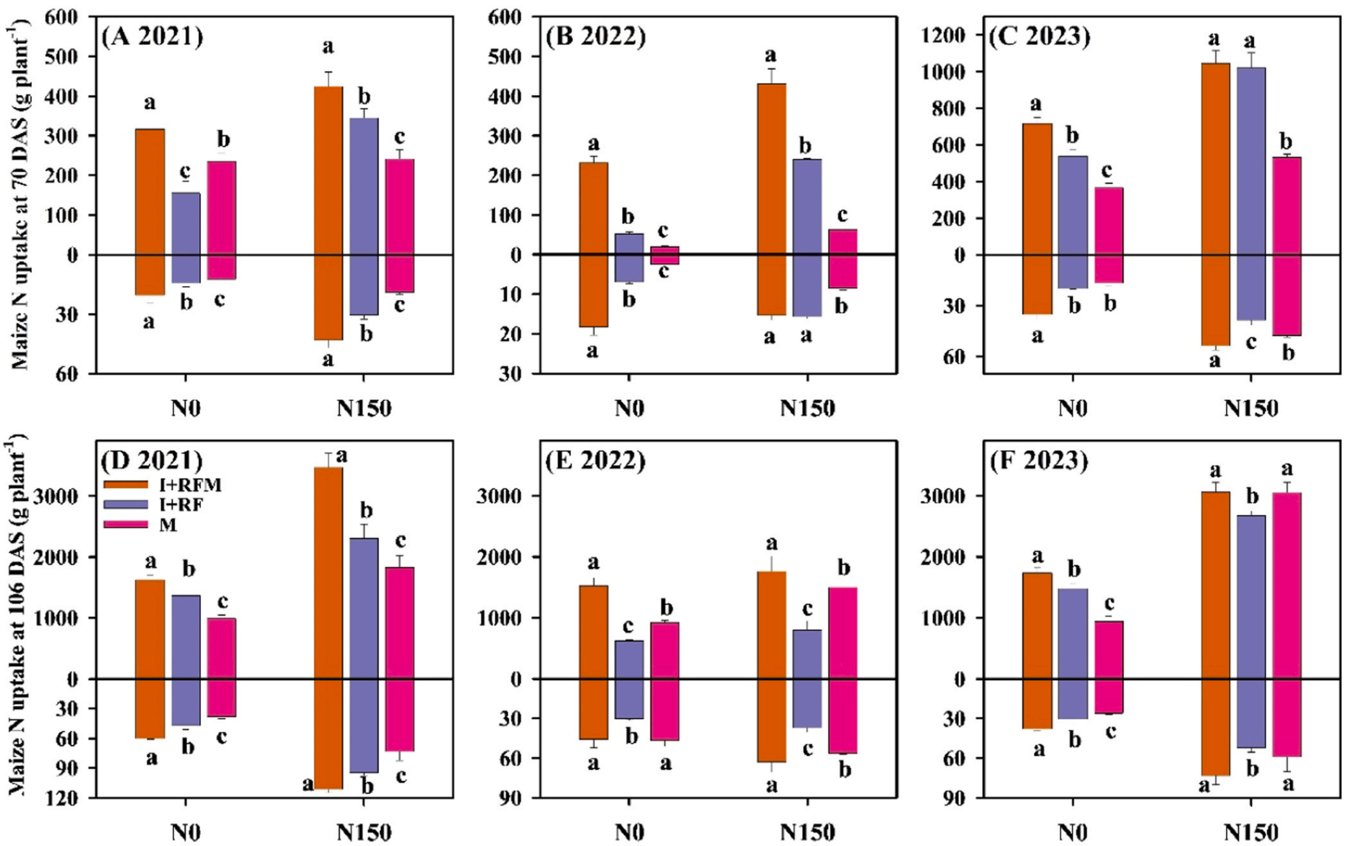

Fig. 7. Maize shoots (above zero) and roots (below zero) N uptake at (A-C) 70 and (D-F) 106 days after sowing over consecutive three years in soybean and maize monoculture (M), maize-soybean intercropping system with ride-furrow film mulching (I+RFM) and ride-furrow (I+RF) under two nitrogen (N) supply rates: (0 (N0) and 150 (N150) kg N ha^{-1}). The different low case letters indicated significantly differences among I+RFM, I+RF and M at the same N levels at $P = 0.05$.

Table 2
The effects of management practice (MP), nitrogen supply rate (N), year (Y), and their interactions on seed yield and N uptake of soybean and maize. DAS: days after sowing. The numbers in the parentheses represent the percentage of the total mean square. n.s. not significant; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Parameter	Significance of sources of variability							
	MP	N	Y	MP×N	MP×Y	N × Y	MP×N × Y	Error
Soybean seed yield	***(80.8)	***(8.6)	***(4.1)	n.s. (0.0)	***(4.6)	**(1.2)	n.s. (0.4)	0.3
Maize seed yield	***(30.0)	***(49.6)	***(15.7)	n.s. (0.5)	n.s. (1.1)	n.s. (1.6)	n.s. (0.3)	1.0
Land equivalent ratio	***(56.2)	n.s. (9.9)	***(23.7)	n.s. (0.0)	n.s. (5.6)	n.s. (0.8)	n.s. (0.3)	3.5
Soybean shoot N content at 70 DAS	***(29.5)	***(16.5)	***(47.1)	n.s. (2.5)	n.s. (0.2)	n.s. (2.6)	n.s. (0.3)	1.4
Soybean root N content at 70 DAS	n.s. (19.0)	*(35.9)	n.s. (13.3)	n.s. (5.1)	n.s. (12.9)	n.s. (5.4)	n.s. (1.2)	7.3
Soybean shoot N content at 106 DAS	***(40.2)	***(41.0)	*(6.3)	n.s. (2.6)	**(7.0)	n.s. (0.4)	n.s. (1.1)	1.4
Soybean root N content at 106 DAS	*** (24.4)	***(27.0)	***(28.9)	n.s. (1.0)	** (8.8)	n.s. (5.1)	n.s. (2.6)	2.2
Maize shoot N content at 70 DAS	***(14.6)	***(20.0)	***(57.5)	* (2.5)	*(2.0)	* (2.5)	n.s. (0.1)	0.7
Maize root N content at 70 DAS	***(12.6)	***(39.5)	***(38.8)	n.s. (0.1)	n.s. (0.8)	***(5.9)	n.s. (1.6)	0.8
Maize shoot N content at 106 DAS	***(11.6)	***(62.8)	***(15.9)	n.s. (0.3)	n.s. (2.3)	*(4.3)	n.s. (1.8)	1.0
Maize root N content at 106 DAS	*** (7.4)	***(61.0)	***(19.0)	n.s. (0.6)	n.s. (2.8)	**(7.4)	n.s. (0.3)	1.4

the yield components such as increasing the seed number and size (He et al., 2019). Thirdly, the increase of the soil water content with FM observed in this and previous studies (Liao et al., 2022a; Zhang et al., 2021) could help to alleviate the adverse effects of seasons drought on seed yield. We further observed the distinct yield responses of soybean and maize in maize-soybean intercropping system to FM and N fertilizer management. The high soybean yield response to FM may be explained by improved soil temperature promoting crop growth to alleviate the shading effects, while the low soybean yield response to N application was mainly associated with the adverse effects of chemical N fertilizer on soybean N_2-fixation ability (Almeida et al., 2023; Epie et al., 2022; Qiang et al., 2025); but further studies are warranted to clarify the underlying mechanisms.

Intercropping can increase productive performance and a recent meta-analysis indicated the global LER of maize-soybean intercropping systems varied from 0.95 to 1.48 with a mean of 1.32 (Li et al., 2023a; Xu et al., 2020). In this study, the mean LER with RF was 1.15, indicating that land use efficiency of the maize-soybean intercropping system in the karst agroecosystem was low, likely due to limiting effects of low plant-available soil N concentration (Zhang et al., 2017) and seasonal drought events (Song et al., 2020). However, the LER with RFM was 1.42, which was 23 % higher than LER with RF and 8 % higher than the global mean LER and mainly explained by the increase of the seed yield. In summary, the introduction of RFM into the maize-soybean intercropping system could significantly increase crop productivity and land use efficiency by alleviating the combination of N deficiency and seasonal drought.

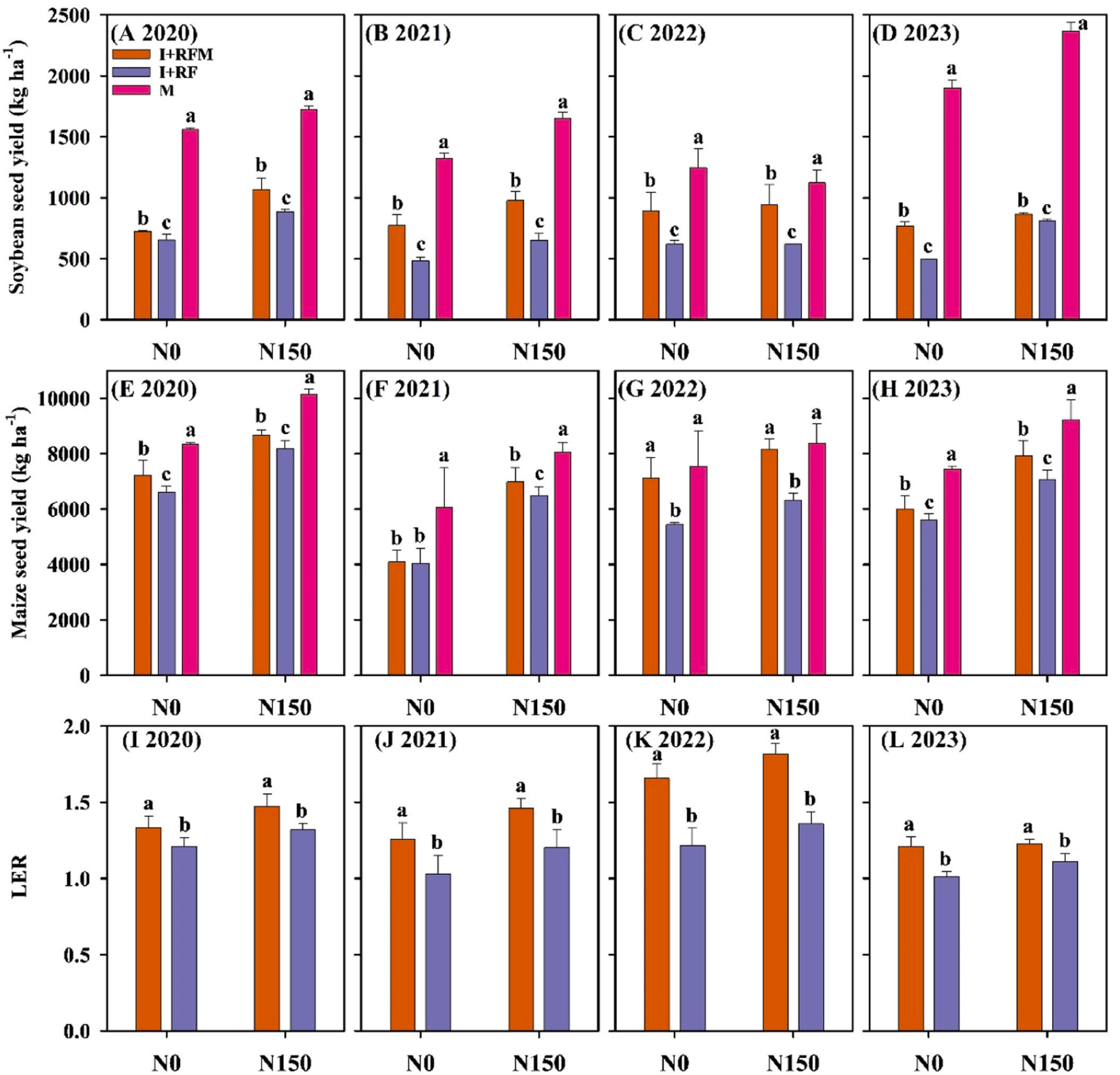

Fig. 8. Seed yield of (A-D) soybean, (E-H) maize, and (I-L) land equivalent ratio (LER) over four consecutive years in soybean and maize monoculture (M), maize-soybean intercropping system with ride-furrow film mulching (I+RFM) and ride-furrow (I+RF) under two nitrogen (N) supply rates: 0 (N0) and 150 (N150) kg N ha^{-1}. Different lowercase letters indicate significant differences among I+RFM, I+RF, and M treatments at the same N levels at $P = 0.05$.

5. Conclusion

In this study, we first introduced ridge-furrow with film mulching (RFM) into a maize-soybean intercropping system and confirmed that RFM promotes N uptake by enhancing root growth to increase soil exploration and by stimulating carboxylate release to improve soil N transformation. These processes help overcome low N availability and frequent seasonal droughts in southwest China, thereby stimulating shoot growth and increasing maize and soybean seed yield (Fig. 8). The distinct effects of management practices and N addition on root growth and carboxylate release were evident; however, the underlying mechanisms remains unclear. Our findings suggest that RFM combined with N addition is a promising strategy to enhance crop productivity in maize-soybean intercropping systems in karst agroecosystems, highlighting the pivotal roles of enhanced “N-capture” (root morphological traits) and “N-mining” (physiological traits) in improving N uptake and yield formation. However, our study was only conducted in one experiment site and further study conducted in multiple experiment sites with contrasting weather conditions were needed to further strength our results.

CRediT authorship contribution statement

Qiao Zhu: Writing – review & editing, Investigation. **Xiao-Li Wang:** Writing – review & editing. **Yinglong Chen:** Writing – review & editing. **Xiao-Min Wu:** Writing – review & editing. **Yi Jin:** Writing – original draft, Methodology, Investigation, Formal analysis. **Long-Gui Li:** Writing – review & editing, Investigation. **Yu-Mei Wang:** Writing – review & editing, Investigation. **Yu Dai:** Writing – review & editing,

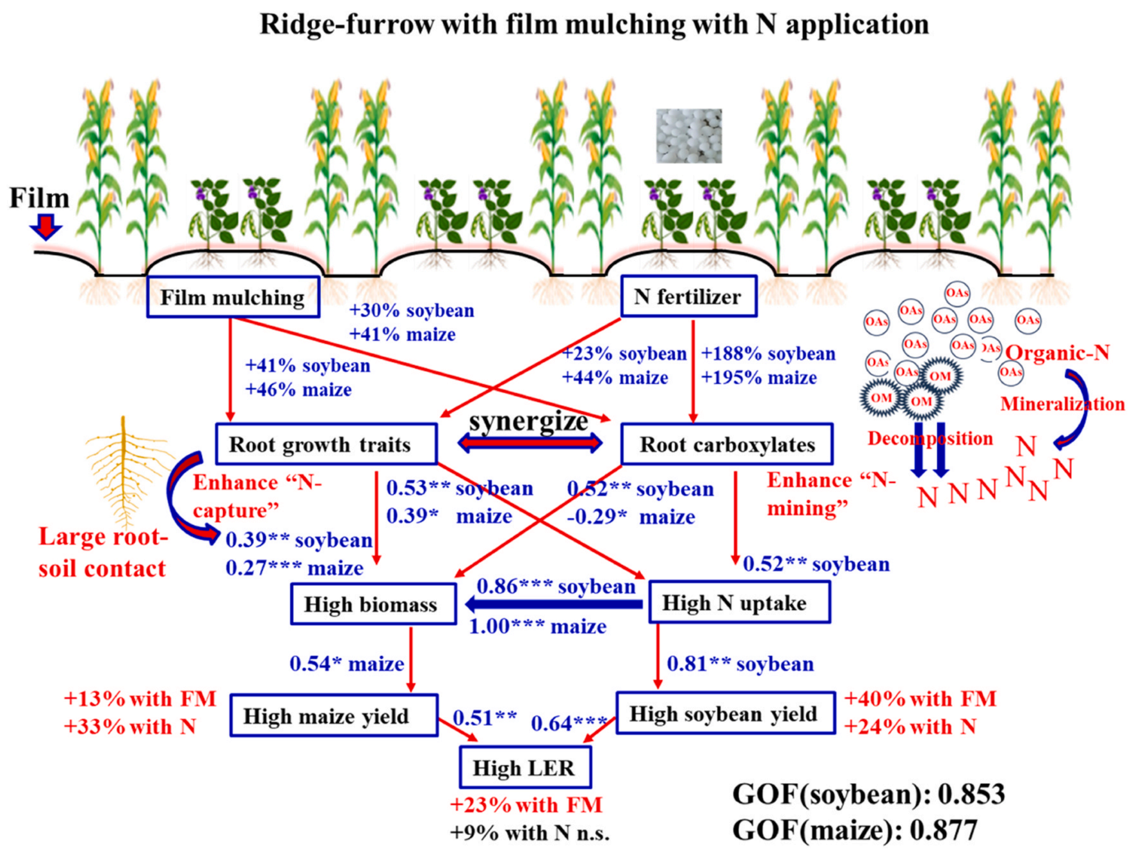

Fig. 9. The conceptual framework to indicate the potential mechanisms contributed to high crop productivity and land use efficiency in maize-soybean intercropping system with ridge-furrow with film mulching and N application. The proportions derived from the results to determine the influence of film mulching and N application on root trait, carboxylates and LER (land equivalent ratio). GOF: goodness of fit for the model; N: inorganic-N. The numbers were the coefficients of the path; n.s. not significantly; $^{**}P < 0.01$; $^{***}P < 0.001$.

Investigation. **Sanwei Yang:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization. **Jin He:** Writing – review & editing, Writing – original draft, Supervision, Funding acquisition, Conceptualization. **Cheng-Xi Yi:** Writing – original draft, Methodology, Investigation, Formal analysis.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.fcr.2025.110286.

Data availability

Data will be made available on request.

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