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Intercropping-driven nitrogen trade-off enhances maize productivity in a long-term experiment

Yizhe Wang[a,b], Yuping Zhang[a,b,*], Hanfeng Zhang[a,b], Ziyu Yang[a,b], Qirui Zhu[a,b], Bojing Yan[a,b], Jiangchi Fei[a,b], Xiangmin Rong[a,b], Jianwei Peng[a,b], Gongwen Luo[a,b,*]

[a] College of Resources and Environment, Hunan Agricultural University, Hunan Provincial Key Laboratory of Farmland Pollution Control and Agricultural Resources Use, Changsha 410128, China

[b] National Engineering Laboratory for Efficient Utilization of Soil and Fertilizer Resources, Changsha 410128, China

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ABSTRACT

Intercropping improves land productivity by exploiting species complementarities to achieve sustainable agriculture. Intercropping systems, therefore, require a nitrogen (N) management approach that matches temporal and spatial N supply with crop requirements. Present field-based study (started in 2013) explored the effects of intercropping of maize (*Zea mays L.*) with legumes [peanut (*Arachis hypogaea*) and soybean (*Glycine max*)] and non-legumes [gingelly (*Sesamum indicum L.*) and sweet potato (*Dioscorea esculenta*)] on maize productivity and N trade-off. Compared with maize monoculture, intercropping with gingelly, peanut, soybean, and sweet potato all significantly improved maize average yield (2013 and 2021), average N use efficiency (NUE), average N partial factor productivity (PFPN), and plant N uptake by 8–29%, 28–49%, 20–80%, and 16–35%, respectively. The N losses via ammonia volatilization and runoff in intercropping systems decreased by 12–19% and 11–43% respectively, compared with monoculture. Soil total N, inorganic N (NH_4^+-N and NO_3^--N), and microbial biomass N (MBN) contents as well as the urease, β-1,4-N-acetyl-glucosaminidase (NAG), and leucine aminopeptidase (LAP) activities varied among different intercropping systems and maize growth periods. Maize productivity (yield, PFPN, and NUE) was positively correlated with plant N uptake ($R^2 = 0.66$–0.92, $P < 0.001$) and soil MBN content ($R^2 = 0.41$–0.47, $P < 0.01$), while it was found negatively associated with N losses ($R^2 = 0.35$–0.56, $P < 0.05$), soil N availability ($R^2 = 0.27$–0.67, $P < 0.05$), and NAG activity ($R^2 = 0.36$–0.55, $P < 0.05$). These findings collectively indicated that regulating the balance between soil N supply and plant N uptake in an intercropping system with low N fertilization could achieve high productivity. This study highlighted the importance of understanding the complex interaction between crop development and intercropping practices in improving maize productivity and N trade-off.

1. Introduction

Maize (*Zea mays L.*) is cultivated worldwide as food, feed or raw materials of the alcohol and energy industry. Maize is a major cereal crop that requires high water and fertilizer inputs for increased productivity. Long-term monoculture is the main mode of maize planting, accompanied by high inputs of fertilizer and water, which results in decreasing nutrient use efficiency and increasing nutrient loss from croplands. Additionally, continuous maize cropping often leads to a decline in soil fertility and plant nutrient uptake (Sanginga, 2003; Feng et al., 2021), which may increase the risk of crop failure (Kermah et al., 2017). Under such a situation, intercropping of maize with other crops, especially leguminous crops, has gained attention.

Intercropping, a feature of traditional farming, has been the focus of sustainable agriculture (Renard and Tilman, 2019). Under an intercropping system, competition, complementarity, or facilitation may occur among species (Glaze-Corcoran et al., 2020). Plant species can be complementary when there is a significant time lag between their needs. Importantly, intercropping increases the utilization efficiency of light, heat, water, fertilizer, and other resources and effectively improves the primary productivity (Ofori and Stern, 1987; Duchene et al., 2017). Nitrogen (N) is an essential nutrient for plant growth and crop

* Corresponding authors at: College of Resources and Environment, Hunan Agricultural University, Hunan Provincial Key Laboratory of Farmland Pollution Control and Agricultural Resources Use, Changsha 410128, China.

E-mail addresses: zhyp2003@126.com (Y. Zhang), gongwenluo@hunau.edu.cn (G. Luo).

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productivity. Farmers have started applying excessive N fertilizers for high yield in recent years, leading to serious environmental issues (Wang et al., 2017). Under such situations, intercropping can help maintain a relatively high yield by reducing N input (Du et al., 2020). Generally, when leguminous crops are intercropped with non-leguminous crops, N gets transferred from the leguminous to the non-leguminous crop (Stern, 1993; Tang et al., 2018). Legumes depend more on their own-produced N and therefore take up less fertilizer N (Hu et al., 2020). Intercrops roots in mobilizing limited or unavailable nutrients such as phosphorus (P) also could influence N trade-off in low N condition (Duchene et al., 2017). Intercropping affects N retained in the biomass and/or soil, and thereby may offer a mechanism for improving maize productivity.

Numerous studies have demonstrated that intercropping could increase plant N uptake, residue biomass and maize yield, leading to high land production efficiency (Du et al., 2020; Marques et al., 2020). Through a complementary N absorption strategy, intercrops increase the N that plants can absorb (Cong et al., 2015; Yang et al., 2018). Hu et al. (2020) found that maize intercropping with pea (*Pisum sativum L*) maintained a high yield under reduced N input. The high N fixing ability of the legume contributed to this advantage (Stern, 1993). Although most studies focus on the maize/legume or maize/non-legume systems, there have been relatively few field-based studies comparing the degree of advantages in maize productivity and N trade-offs between the two systems simultaneously. Additionally, intercropping plays a critical role in maintaining soil biodiversity by selecting microbial populations that drive N fixation and transformation, such as azotobacter and nitrifier (Duchene et al., 2017). Intercropping is reported to change soil microbiomes to promote N assimilation, absorption, and transformation (Dang et al., 2020; Liu et al., 2020a) and promote N cycling by influencing enzyme activity (Xiao et al., 2018). Apparent N loss may be reduced by intercropping through strengthening the ammonifying and nitrifying capacities to increase soil N residue (Liu et al., 2014) and N losses (Chen et al., 2019). However, previous studies on the transfer of N into, within, and/or out of the soils are based on post-harvest data without any dynamic monitoring of plant-soil N trade-off across crop development. Nitrogen transformation and utilization by soil and plants are different at different plant growth periods (Yun et al., 2020). Thus, there is a need to analyze the interaction between plant development and intercropping practice, which modulates maize productivity and N trade-off.

The main objective of present study was to explore the effects of intercropping of maize with legumes [peanut (*Arachis hypogaea*) and soybean (*Glycine max*)] and non-legumes [gingelly (*Sesamum indicum L.*) and sweet potato (*Dioscorea esculenta*)] on maize productivity and N trade-off, based on a long-term field experiment (Fig. S1). The interannual variations in maize yield, N-use efficiency (NUE), and N partial factor productivity (PFPN) were evaluated to assess the effectiveness of intercropping on maize productivity. Meanwhile, the variations in plant N accumulation, soil N losses, soil N pool and availability, soil microbial biomass N, and soil N-acquirement enzyme activity were investigated to understand N trade-offs across four maize growth stages. Promising strategies were compiled to assess the relationship between maize N trade-offs and productivity. Our field-based results would highlight the different benefits in maize productivity and N trade-offs between maize/legumes and maize/non-legumes systems, and decipher the relationships of plant-soil N balance with maize productivity.

2. Materials and methods

2.1. Site description and experimental design

The long-term field experiment of this study was established in 2013 in Liuyang County, Hunan Province, China (28°19′ N, 113°49′ E). The climate type of this region belongs to Cfa according to Koppen-Geiger climate classification (Peel et al., 2007). The distribution of annual precipitation and temperature in 2013 and 2021 was shown in Fig. S2. The average precipitation and average temperature were 1429 mm and 24 ℃ during the experiment, respectively. The soil of this region was classified as fluvisols developed in fluvial and lacustrine deposits (WRB, 2015). The diameters of soil aggregate were mainly within 2–0.053 mm, followed by > 0.053 mm. The soil properties (0–0.2 m) at the beginning of the field experiment were as follows: 5.69 pH, 11.30 g kg^{-1} organic matter, 1.56 g kg^{-1} total N, 0.48 g kg^{-1} total phosphorus (P), 12.2 mg kg^{-1} available P, and 152.2 mg kg^{-1} available K.

The experiment was conducted using the following five treatments: (1) M-M, maize monoculture; (2) M-G, maize and gingelly intercropping; (3) M-P, maize and peanut intercropping; (4) M-S, maize and soybean intercropping; (5) M-SP, maize and sweet potato intercropping. The experiment was carried out in a randomized block design using three replicate plots of 20 m^2 (4 m × 5 m) per treatment. Fertilizer application rates and fertilizer types were summarized in Table S1; N, P_2O_5, and K_2O were applied following the conventional fertilization approach. Nitrogen fertilizer was applied at 40% before maize planting, 30% at maize seedling stage, and 30% at maize flowering stage; All P fertilizer was used before maize planting; And K fertilizer was applied at 50% before maize planting and 50% at maize flowering stage. All crops in the experiment were rain-fed.

The maize variety *Qiandan12* was planted in April, maintaining 30 cm × 40 cm spacing between maize plants. The *Yuzhi4*, *Huayu16*, *Hefeng61*, and *Guangshu135* were the gingelly, peanut, soybean, and sweet potato varieties. Gingelly, peanut, and soybean were sown simultaneously as maize. In the M-M, M-G, M-P, M-S, and M-SP, the sowing quantity of maize crop was 140, 84, 84, 84, and 140 plants/plot, respectively. In four intercropping plot, the sowing quantity of gingelly, peanut, soybean, and sweet potato were 108, 56, 56, and 126 plants/plot, respectively. The details of experimental design and crop community were shown in Fig. S1. The harvest time of maize crop in all treatments was consistent, and that of the intercrops was subject to their actual maturity period. When maize and intercrops were harvested, all plots were treated with winter-fallowing to avoid the effects of crop rotation. Fertilization, planting, and other management practices had been maintained since 2013.

2.2. Determination of maize yield, nitrogen-use efficiency, and partial factor productivity

At maize physiological maturity, plants from each plot were separately harvested, and grains were threshed and dried to obtain the actual yield in 2013 and 2021. Grains were threshed and dried at 70 ℃ for 4 day and weighed to calculate water content. In order to unify the calculation standard, the number of intercropped crops planted per square meter was unified with that of monoculture crops in the actual calculation, which was 140 plants per plot (20 m^2), or 7 plants per square meter (Yan et al., 2017; Schwerdtner and Spohn, 2021). The yield per square meter is then converted to yield per hectare. In 2021, in the seedling, elongation, flowering, and mature stages of maize crop, three plants were randomly selected from each plot, and then the roots were separated from soil by using a shovel without destroying the root system. Above-ground parts and roots were separated and then brought back to the laboratory, and dried in an oven at 70 ℃ for 48 h to a constant weight, and then detected the aboveground biomass and plant N content. Total N content was measured using the Kjeldahl method (Bao, 2000). The grain and straw N contents were measured to determine the N uptake.

Nitrogen-use efficiency (NUE, %) and nitrogen partial factor productivity (PFPN, kg kg^{-1}) of each treatment were calculated using the following equations (Zhang et al., 2022):

$$\text{NUE} = (\text{N uptake in fertilizer treatment - N uptake in the control})/\ \text{N total input (maize and intercrop)} \times 100\% \tag{1}$$

$$\text{PFPN} = \text{yield/N application total amount (maize and intercrop)} \quad (2)$$

2.3. Determination of ammonia volatilization

The gas samples used to determine ammonia volatilization were collected by the ventilation method on the second day after fertilization and harvest of maize (April 29, May 12, May 17, May 26, June 30, and August 2) in 2021 (Jiang et al., 2018; Liu et al., 2020b). The ammonia volatile gas samples were collected within 15 days of N fertilization. Samples of ammonia volatilization were collected once every day for the first six days and once every three days for the last nine days. Ammonia volatilization was also collected after maize harvest, and the number of collection days depended on the actual ammonia volatilization. Sampling was done using a rigid PVC plastic pipe device with an inner diameter of 0.15 m and a height of 0.15 m. A rain cover was installed above the plastic pipe, with a bracket in between for communication between the internal and external air. Two sponges with a thickness of 0.20 m and a diameter of 0.16 m were evenly soaked in 5 mL of glycerol phosphate solution (50 mL of phosphoric acid plus 40 mL of glycerol; total volume of 1000 mL) and placed in the plastic pipe, with the sponge on the lower layer 5 cm away from the bottom of the pipe and the sponge on the upper layer flushed with the top of the pipe (Liu et al., 2020b). The next day after applying N fertilizer to crops, the gas collection device was placed on the area between maize and interplanting crops at 8:00 a.m. and sampling was done 24 h after placing the device. The sponge on the lower layer of the gas collection device was taken out, quickly placed in a dense bag, and sealed; this sponge was replaced with another one soaked in glycerol phosphate. The upper sponge was replaced once every 3–7 days depending on the condition (dry and wet). The replaced sponges were placed in 500 mL plastic bottles to which 300 mL of 2 M KCl solution was added to soak the sponges completely and shaken for 1 h. The ammonium N concentration in the leaching solution was measured with an automatic intermittent chemical analyzer (Smartchem 200, AMS Alliance, Italy). The cumulative amount of ammonia volatilization was normalized by total amount of N fertilizer in developing all the inter relationship with N amount (Zhang et al., 2022).

The ammonia volatilization rate was calculated as follows:

$$F = \frac{M}{\pi r^2 t} \times 10^{-2} \quad (3)$$

$$M = cvf \quad (4)$$

where F is the ammonia volatilization rate (kg ha^{-1} d^{-1}), M is the amount of ammonia N absorbed in a single ammonia volatilization collection device (mg), r is the radius of the device (m), t is the absorption time (day), 10^{-2} is the conversion coefficient, c is the measured ammonia N concentration (mg L^{-1}), v is the volume of leaching solution (L), and f is the dilution ratio.

The cumulative amount of ammonia volatilization was calculated as follows:

$$W = \sum_{1}^{n} tF_{(i)} \quad (5)$$

where W is the cumulative amount of ammonia volatilization (kg ha^{-1}), F(i) is the i^{th} ammonia volatilization rate, and n is the total number of days measured.

2.4. Determination of nitrogen runoff loss

In 2021, the N runoff due to rainfall was determined following the volume method, which measured the change in the hydrological scale in the runoff collection pools of each treatment; the water in a collection pool (1.5 m length × 0.6 m width × 0.7 m height) was evenly stirred with tools before measurement. The bottom of the pond was provided with a water outlet and drainage valve, and the top cover of the pond was covered with iron sheet. A portion of the water sample were collected in 500 mL plastic bottles, fixed in acid and chloroform, and stored at 4 °C. These water samples were taken back to the laboratory to analyze total N, dissolved N, NH_4^+-N, and NO_3^--N within 24 h.

The total N concentration of the water samples was measured by alkaline potassium persulfate-ultraviolet spectrophotometry (Zhang et al., 2021). When measuring the dissolved N concentration, the water sample was first passed through a 0.45 μm microporous membrane and then the filter liquor was determined by the same method as the total N (Zhang et al., 2021). The N cumulative losses in different forms were calculated by multiplying the concentration of each variable with the runoff volume. The cumulative loss amounts of total N, dissolved N, NH_4^+-N, and NO_3^--N were normalized by total amount of N fertilizer in developing all the inter relationship with N application rates.

2.4.1. Determination of soil physicochemical properties

At the seedling, elongation, flowering, and mature stages of maize in 2021, five soil cores (0–0.2 m layer depth) were collected from each plot from the middle position between maize and the intercrops and mixed into one composite sample. These samples were sieved through 2.0 mm mesh to remove plant debris and rock. Each sample was then divided into two parts: one part was stored at 4 °C for physicochemical property analysis, and the other part was stored at − 20 °C for biological property analysis.

Soil properties were analysed as previously described (Bao, 2000). Soil pH was determined using a soil-water (1:2.5, w/v) slurry with a compound electrode (PE-10; Sartorius, Germany) (Luo et al., 2017). Soil organic carbon (C) content was determined by the potassium dichromate volumetric method (Bao, 2000). Soil total N content was determined by the Kjeldahl method (Bao, 2000). Soil NH_4^+-N and NO_3^--N content were extracted by 2 M KCl solution, and then measured by a colorimetric method using an automatic intermittent chemical analyzer (Smartchem 200, AMS Alliance, Italy). Soil microbial biomass C (MBC) and microbial biomass N (MBN) were determined following the chloroform fumigation extraction method (Vance et al., 1987).

The soil leucine aminopeptidase (LAP) and β-N-acetylglucosaminidase (NAG) activities were measured using the MUB-linked model substrate method (Deforest, 2009). Briefly, soil suspensions were prepared by homogenizing 1.0 g of fresh soil with 100 mL of acetate buffer (50 mM). The soil suspensions, acetate buffer, 10 μM references and 200 μM MUB-labeled substrates were dispensed into the wells of a black 96-well microplate. After the plates were incubated in the dark at 25 °C for 4 h, 10 μl of 1.0 M NaOH was added to each well to stop the reaction. Finally, fluorescence intensity was quantified using a microplate fluorometer with 365 nm excitation and 450 nm emission filters. Soil urease activity was measured using a spectrophotometer (610 nm) with urea as the substrate (Ge et al., 2018).

2.5. Data analysis

Microsoft Office Excel 2010 (Microsoft Corporation, Washington, USA) was used for data processing. Origin 2018 (OriginLab Corporation, Northampton, MA, USA) and Adobe Illustrator CC2021 (version 25.0; Adobe Corporation, SAN Jose, USA) were used for image rendering. Unless otherwise stated, significant differences in the data were analyzed via ANOVA and the Duncan's method was used to compare the means for each variable ($P < 0.05$) based on the IBM SPSS Statistics (version 26; IBM Corporation, New York, NY, USA). All datas were found to follow normal distribution based on the coefficient of skewness and kurtosis and visualization by Q-Q plot tests. Pearson correlations between plant productivity, N losses, and soil properties were assessed by modeling a matrix based on percent identity using the package 'corrgram' in R software (version 4.0.5).

3. Results

3.1. Maize yield, nitrogen use efficiency, and nitrogen partial factor productivity

The average maize yield of intercropping treatments (M-G, M-P, M-S, and M-SP) was higher than that of M-M (Fig. 1A). Among them, the average yield of M-G, M-P, M-S, and M-SP was 8%, 22%, 29%, and 17% higher than the M-M, respectively (Fig. 1D). The average NUE of the intercropping treatments was also higher than that of M-M (Fig. 1B). The average NUE of M-G, M-P, M-S, and M-SP treatments was 28%, 40%, 49%, and 36% higher than M-M, respectively,(Fig. 1E). The average PFPN of the intercropping treatments was also higher than that of M-M (Fig. 1C). The average PFPN of the M-S, M-P, M-G, and M-SP increased by 36%, 71%, 80%, and 20%, respectively, compared with M-M (Fig. 1F).

3.2. Maize plant nitrogen accumulation

The aboveground N accumulation under all treatments increased with maize development in 2021. Under intercropping treatments, the aboveground N uptake was significantly higher than that under M-M during the elongation, flowering, and mature stages (Fig. 2A). The N accumulation increased by 8–18%, 13–81%, 19–107%, and 12–39% in M-G, M-P, M-S, and M-SP treatments, respectively, compared with M-M at the three stages mentioned above (Fig. 2A). The average increase in the maize aboveground N content under the M-G, M-P, M-S, and M-SP were − 19–5%, 2–21%, 1–15%, and 2–22%, respectively, at the four growth stages (Fig. S3A). The root N content of M-SP at the seedling stage was significantly higher than that of other treatments (Fig. 2B). During flowering, the root N content of all intercropping treatments was higher than the M-M (Fig. 2B). The root N content of the M-G was 15.% lower than the M-M, and that of the M-P, M-S, and M-SP treatments was 3%, 7%, and 23% higher than the M-M, respectively, at the mature stage (Fig. 2B). The intercropping treatment and plant development independently and via interaction explained the variations in plant N accumulation; plant development (3–9%; $P < 0.001$) had a greater impact on N accumulation than intercropping treatment (28–79%; $P < 0.001$).

3.3. Nitrogen loss by ammonia volatilization

The ammonia volatilization rate under the intercropping treatments dynamically changed after N fertilization (3 times) and maize harvest (Fig. 3). The ammonia volatilization rate under all treatments after fertilization reached a maximum on the third day, and after using the seedling fertilizer, reached the maximum on the fourth day; further, the rate gradually decreased and flattened. After harvest, the volatilization rate of all treatments was low, which almost approached zero. The rate under M-G, M-P, M-S, and M-SP was significantly lower than that under M-M (Fig. 3A). The accumulated loss amount under M-G, M-P, M-S, and M-SP treatments reduced by 29%, 34%, 38%, and 19%, respectively, compared with M-M ($P < 0.05$; Fig. S4). Compared with the M-M, the M-G, M-P, M-S, and M-SP reduced the normalized accumulated loss amount through ammonia volatilization by 11.8%, 11.7%, 14.0%, and 18.5%, respectively (Fig. 3B).

3.4. Nitrogen runoff loss

The total N runoff loss of the M-SP on May 26 was slightly higher than that of M-M, and the total N loss of the M-G, M-P, M-S, and M-SP were lower than that of M-M in the other five runoff events (Fig. 4A). The M-G, M-P, M-S, and M-SP significantly reduced the cumulative N runoff losses by 29–60%; the cumulative N losses under the M-P and M-S were significantly lower than that under the M-G and M-SP (Fig. S5A). The M-G, M-P, M-S, and M-SP reduced the normalized cumulative losses of total N by 11%, 30%, 43%, and 31%, respectively (Fig. 4B). The reduction rates in total N accumulation loss under the M-P and M-S were 50% and 59%, respectively, while that in M-G and M-SP were 29% and 31%, respectively (Fig. S5A). The dissolved N losses of the five runoff

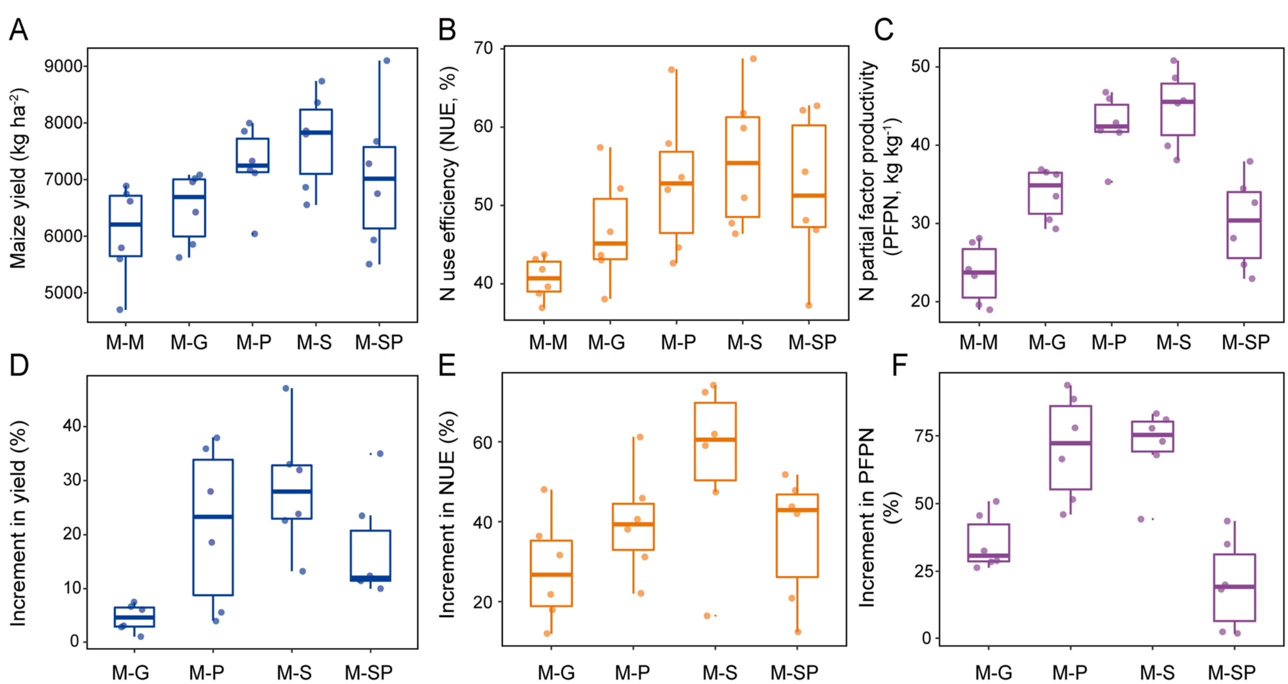

Fig. 1. The average maize yield (A), average nitrogen (N) use efficiency (NUE, B), and average N partial factor productivity (PFPN, C) of all treatments in 2013 and 2021, as well as the corresponding increment (D-F) of the three variables in intercropping treatments compared with the monoculture. The upper and lower boundaries of each box indicate the 75th and 25th percentiles, respectively. The dot inside the box represents the repetition of each treatment. Values followed by a different lowercase letter indicate significant differences according to Duncan's Duncan test ($P < 0.05$). M-M, maize monoculture; M-G, maize and gingelly intercropping; M-P, maize and peanut intercropping; M-S, maize and soybean intercropping; and M-SP, maize and sweet potato intercropping.

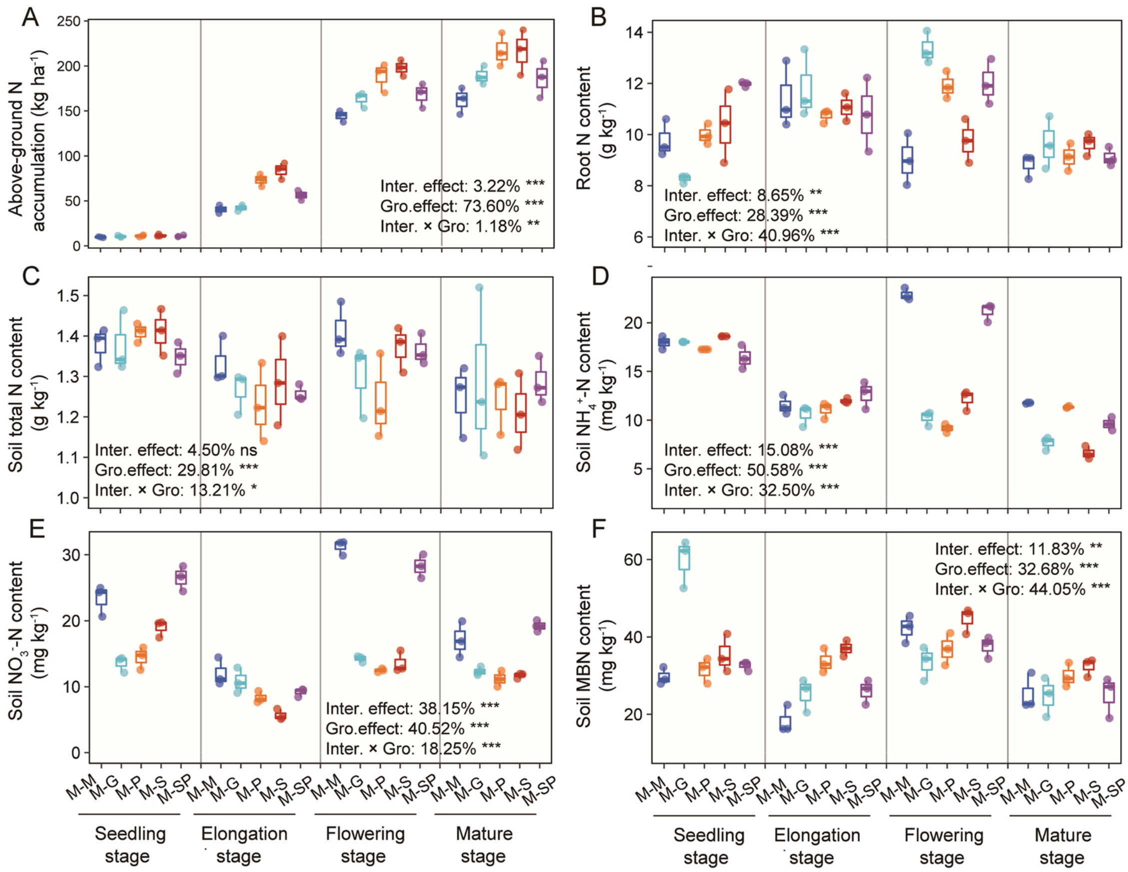

Fig. 2. The above-ground N accumulation (A), root N content (B), soil total N content (C), soil NH_4^+-N content (D), soil NO_3^--N content (E), and microbial biomass N (MBN, F) of all treatments across crop development in 2021. The upper and lower boundaries of each box indicate the 75th and 25th percentiles, respectively. Inter. effect and Gro. effect stand for the intercropping effect and maize growth effect on the variabes, respectively. M-M, maize monoculture; M-G, maize and gingelly intercropping; M-P, maize and peanut intercropping; M-S, maize and soybean intercropping; and M-SP, maize and sweet potato intercropping.

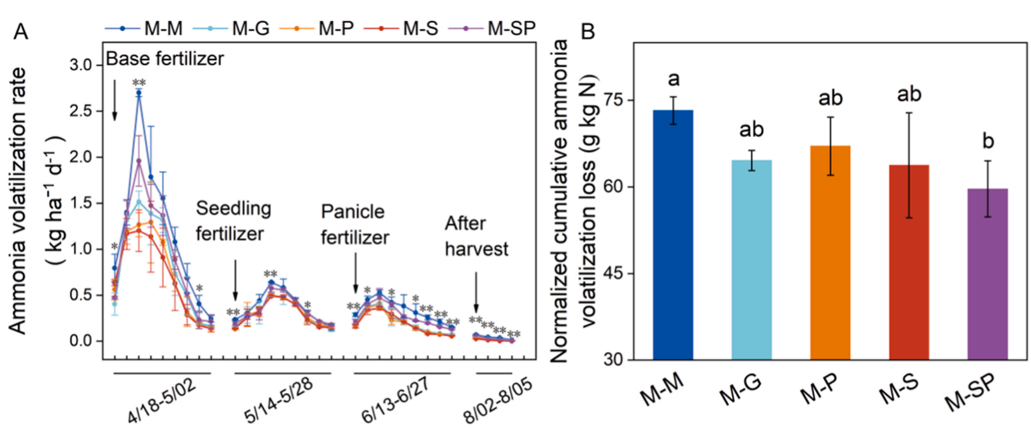

Fig. 3. The ammonia volatilization rate (A) and normalized ammonia volatilization accumulation (B) of all treatments in 2021. Vertical bars indicate the standard errors. Asterisks (* and **) indicate significant differences at $P < 0.05$ and $P < 0.01$ probability levels. Different letters indicate significant differences at $P < 0.05$. M-M, maize monoculture; M-G, maize and gingelly intercropping; M-P, maize and peanut intercropping; M-S, maize and soybean intercropping; and M-SP, maize and sweet potato intercropping.

events were lower than M-M, except that the dissolved N loss in M-G on May 26 was slightly higher than that in M-M (Fig. 4C). The M-G, M-P, M-S, and M-SP significantly reduced the cumulative loss of dissolved N by 38%, 46%, 56%, and 34%, respectively (Fig. S5B). The normalized dissolved N accumulation loss rates in M-G, M-P, M-S, and M-SP were 23%, 24%, 39%, and 34%, respectively (Fig. 4D).

A significant difference was detected in the NH_4^+-N runoff loss between the treatments during each runoff event (Fig. 4E). The cumulative NH_4^+-N loss amount under the M-G, M-P, M-S, and M-G decreased by 47%, 61%, 70%, and 33%, respectively, compared with the M-M (Fig. S5C). The M-G, M-P, M-S, and M-SP significantly reduced the normalized cumulative loss amount of NH_4^+-N by 34%, 45%, 57%, and 33%, respectively (Fig. 4F). The dynamic changes in NO_3^--N runoff loss were different from the other N forms across the treatments (Fig. 4G), but the general trend was similar. The cumulative NO_3^--N loss amounts under the M-G, M-P, M-S, and M-SP were 28.%, 37%, 43%, and 21%, respectively (Fig. S5D). The normalized cumulative amounts of runoff NO_3^--N in M-G, M-P, M-S, and the M-SP were 12%, 11%, 20%, and 21% lower than the M-M, respectively (Fig. 4H).

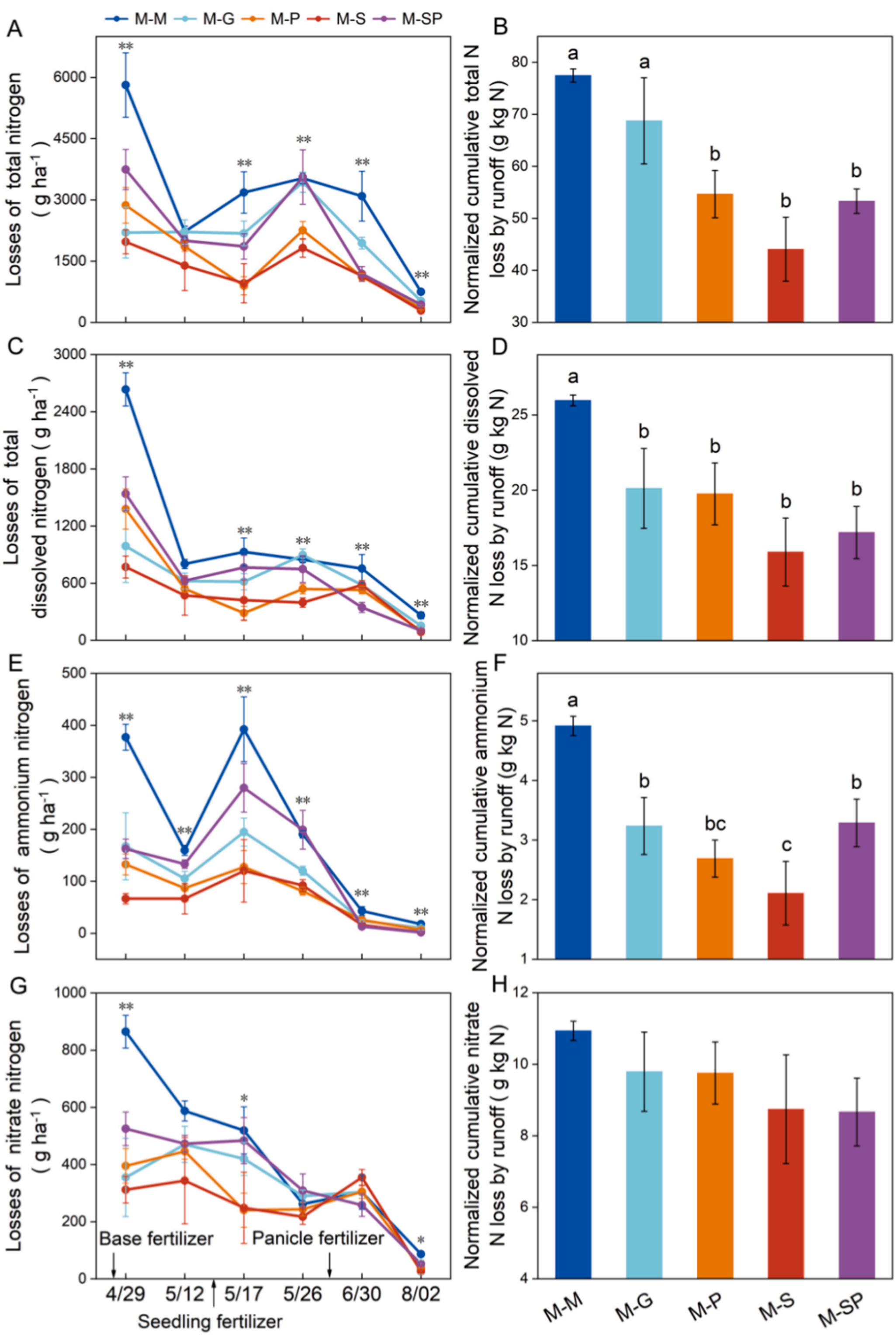

Fig. 4. The runoff loss and normalized cumulative runoff loss of total N (A and B), dissolved N (C and D), ammonium N (NH_4^+-N; E and F), and nitrate N (NO_3^--N; G and H) of all treatments in 2021. Vertical bars indicate the standard deviation. Asterisks (* and **) indicate significant differences at $P < 0.05$ and $P < 0.01$ probability levels. Different letters indicate significant differences at $P < 0.05$. M-M, maize monoculture; M-G, maize and gingelly intercropping; M-P, maize and peanut intercropping; M-S, maize and soybean intercropping; M-SP, and maize and sweet potato intercropping.

3.5. *Soil nitrogen pool*

The intercropping treatment and plant development independently or interactively explained the variations in soil total N, NH_4^+-N, NO_3^--N, and MBN content, in 2021 (Fig. 2C–F). The M-G, M-P, M-S, and M-SP reduced soil total N content at the elongation and flowering stages; the maximum decrease was under the M-P (8% and 12%, respectively; Fig. 2C). At seedling and mature stages, soil total N content showed no significant difference among the treatments. Soil NH_4^+-N content under the M-S and M-SP increased by 5% and 10%, respectively, at the elongation stage, and decreased by 10–47% and 8–18%, respectively, at the other stages (Fig. 2D). Soil NO_3^--N content under the M-G, M-P, and M-S decreased by 8–54%, 30–60%, and 19–56%, respectively. The soil NO_3^--N content under the M-SP increased at seedling and mature stages (14%) and decreased at elongation and flowering stages (9% and 22%; Fig. 2E). The M-G, M-P, M-S, and M-SP significantly decreased soil inorganic N content compared with the M-M (Fig. S3F).

Soil MBN content under the M-G, M-P, M-S, and M-SP increased by

102%, 7%, 20%, and 10%, respectively, at the seedling stage, and increased by 44%, 86%, 109%, and 47%, respectively, at elongation stage compared with M-M (Fig. 2F). At the flowering stage, soil MBN content under the M-G, M-P, and M-SP decreased by 20%, 12%, and 10%, respectively, and under M-S increased by 6% (Fig. 2F). At the mature stage, soil MBN content under M-P and M-S treatments increased by 21% and 32%, respectively (Fig. 2F). The M-G, M-P, M-S, and M-SP reduced soil MBC:MBN ratio at the seedling, elongation, and mature stages and increased the ratio at the flowering stage compared with the M-M (Fig. S3H).

3.6. Soil potential enzyme activity

The urease, LAP, and NAG activities per unit soil and SOC showed similar trends under all treatments across four growth stages. At the seedling stage, soil urease activity under M-G and M-SP was 14% and 11% higher than under the M-M (Fig. 5A). At the elongation stage, the urease activity under M-S and M-SP was 53% and 43% higher than that under the M-M ($P < 0.05$). At the flowering stage, the M-S, M-P, M-G, and M-SP increased urease activity by 26%, 59%, 34%, and 26%, respectively, compared with the M-M. At the mature stage, the M-P, M-S, and M-SP significantly decreased urease activity compared with the M-M (Fig. 5A).

At the seedling stage, soil LAP activity of the M-S, M-P, M-G, and M-SP increased by 19%, 32%, 47%, and 27% compared with the M-M, respectively (Fig. 5C). At the elongation stage, soil LAP activity of the M-S was significantly higher than that under M-M (18%). Soil LAP activity of the M-G, M-S, and M-SP was 16%, 49%, and 28% higher than that of M-M, respectively, in the flowering period. At the mature stage, LAP activity under M-G was 28% higher than the M-M (Fig. 5C).

At the seedling stage, soil NAG activity under M-SP was significantly lower (16%) than under M-M; the NAG activity was higher under M-S, M-P, and M-G treatments than that under M-M (Fig. 5E). Compared with the M-M, the M-S, M-P, M-G, and M-SP decreased soil NAG activity by 18–38% and 21–37% at the elongation and the flowering stage, respectively. Soil NAG activity under M-P and M-S at the mature stage decreased by 15% and 35%, respectively, while under M-G and M-SP increased by 2% and 6%, respectively (Fig. 5E).

3.7. Correlation between crop productivity and system nitrogen trade-off

We evaluated the correlation between crop productivity, plant N accumulation, soil N pool, and soil properties by modeling a network matrix (Fig. 6 and S6). Maize yield, PFPN, and NUE positively correlated with aboveground N accumulation ($R^2 = 0.66–0.92$; $P < 0.001$) and soil MBN content ($R^2 = 0.41–0.47$; $P < 0.01$). Maize yield, PFPN, and NUE negatively correlated with N loss amounts by NH_3 volatilization ($R^2 = 0.40–0.51$; $P < 0.01$) and runoff ($R^2 = 0.35–0.56$; $P < 0.05$), and soil NAG activity ($R^2 = 0.36–0.55$; $P < 0.05$) (Fig. S6). Nitrogen losses by NH_3 volatilization and runoff positively correlated with soil inorganic N content and NAG activity ($P < 0.05$; Fig. 6). Soil C:N ratio and MBC content negatively correlated with urease, LAP, and NAG activities ($P < 0.05$).

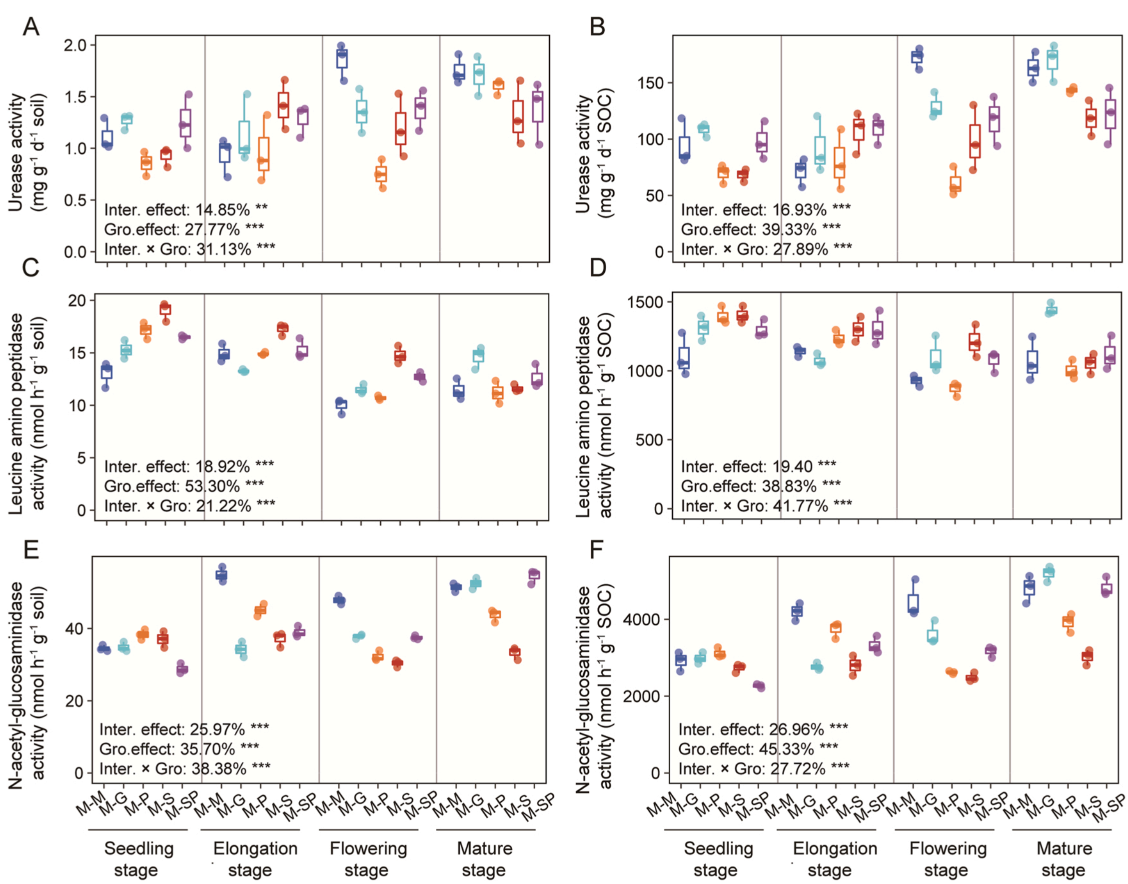

Fig. 5. The potential activity of soil urease (A and B), leucine (C and D), and N-acetyl-glucosaminidase (E and F) associated with N cycle in all treatments across crop development in 2021. The upper and lower boundaries of each box indicate the 75th and 25th percentiles, respectively. Inter. effect and Gro. effect stand for the intercropping effect and maize growth effect on the variabes, respectively. M-M, maize monoculture; M-G, maize and gingelly intercropping; M-P, maize and peanut intercropping; M-S, maize and soybean intercropping; and M-SP, maize and sweet potato intercropping.

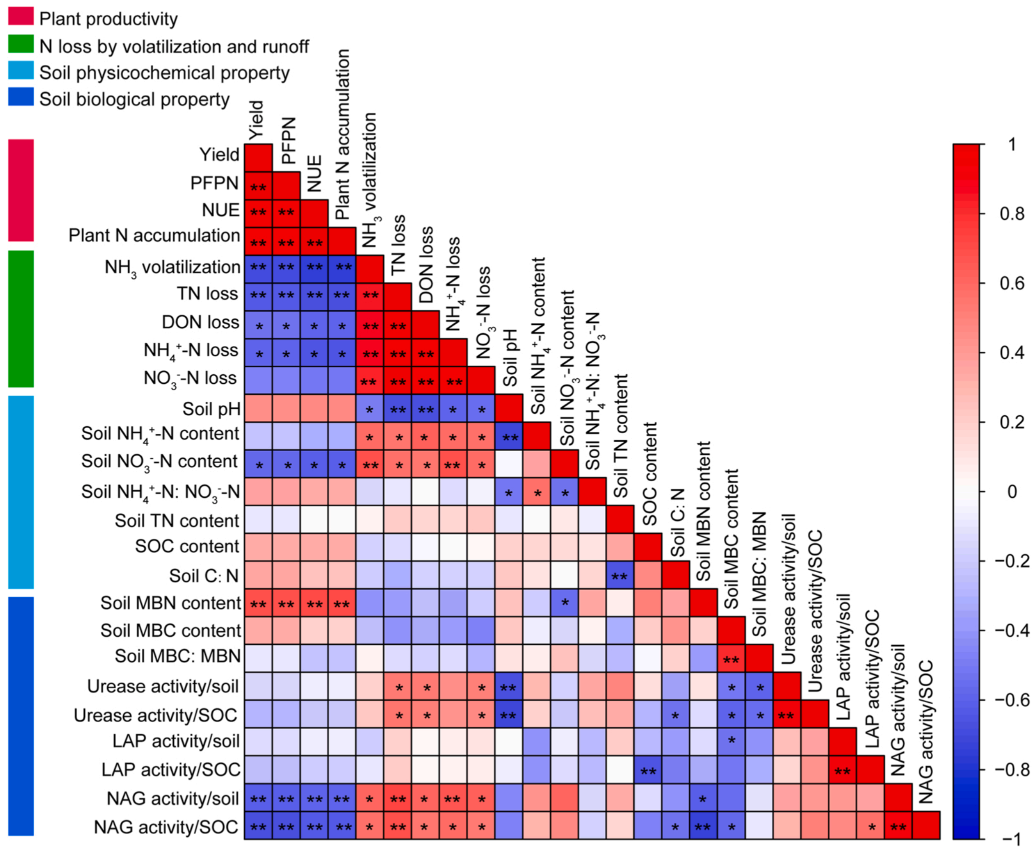

Fig. 6. A matrix showing the Pearson correlations among plant productivity, N losses, and soil properties based the data of the 2021. Asterisks denote significance at the P < 0.05 and P < 0.01 probability levels (* and **, respectively). Notes, we only tagged the significance level of correlations between variables in the figure.

4. Discussion

4.1. Intercropping improves maize productivity

Generally, the improved biomass and yield under the intercropping systems are mainly due to the effective use of available resources (Duchene et al., 2017; Raza et al., 2019). Consistent with previous studies, we also found that intercropping maize with legumes and non-legumes significantly improved maize biomass and yield compared with the monocropping (Figs. 1 and 7). Plant species can be

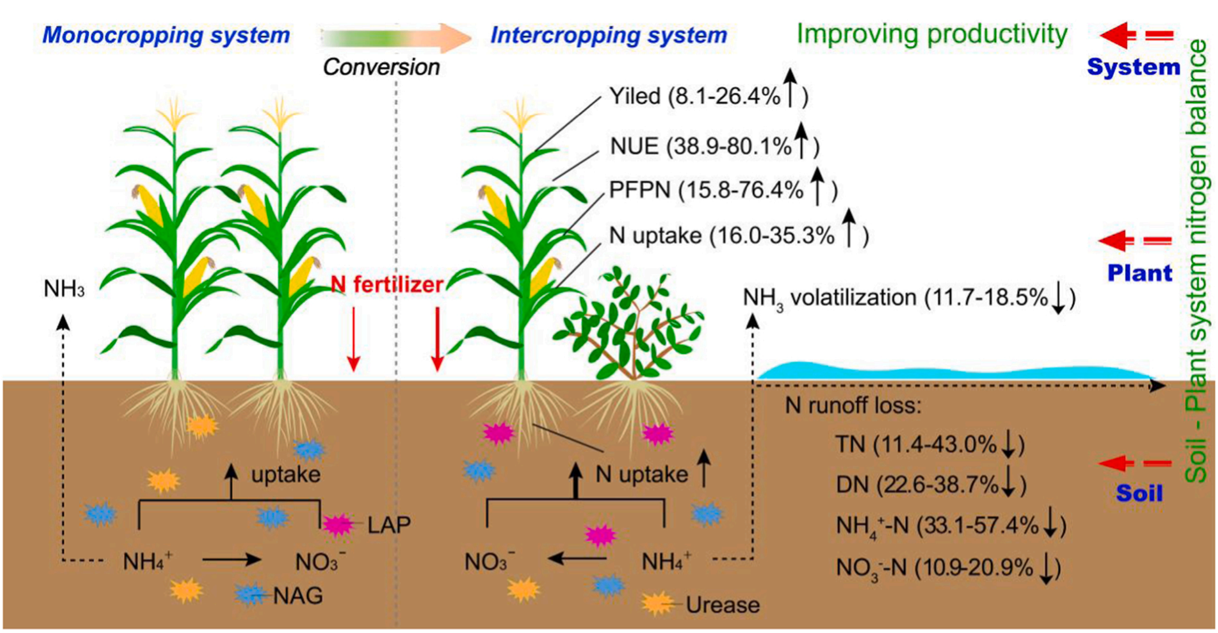

Fig. 7. Conceptual schema depicting the portfolio effects of intercropping pattern on maize planting productivity and plant-soil nitrogen balance. NUE, nitrogen use efficiency; PFPN, nitrogen partial factor productivity; TN, total nitrogen in runoff; DN, dissolved nitrogen in runoff； LAP, leucine aminopeptidase; and NAG, β-1,4-N-acetyl-glucosaminidase.

complementary when there is a significant time lag between their requirement (Duchene et al., 2017). Species with a similar spatial and/or temporal niche tend to compete intensively, which would reduce biomass and production of mono-crop system (Yang et al., 2014; Yu et al., 2016). Thus, above- and below-ground spatial and/or temporal stratification may influence maize N uptake and loss. Our previous study also found that intercropping improved the maize leaf chlorophyll content and photosynthetic characteristics (Wang et al., 2014). Improvement in physiological and photosynthetic characteristics could enhance root system's nutrient absorption ability (Zhang et al., 2014; Zheng et al., 2021). In the study, yield increment in maize/legumes system was higher than in maize/non-legumes (Fig. 1). Legumes preferentially absorb N inorganic form and fix atmospheric N only under limiting soil N conditions due to low availability or increased N competition in intercropping systems (Duchene et al., 2017). Thus, differences in yield increment among the maize/legumes and maize/non-legumes systems may be partly explained by differences in N fixing or compensation capacity of the intercrops. Our study confirms that legumes are highly suitable for intercropping since they can substitute one source of N for another under critical situations (Duchene et al., 2017; Xu et al., 2020).

Intercropping is a practical approach to reduce N fertilizer input while stabilizing or improving crop yield, as well as increasing NUE and PFPN (Figs. 1 and 7). In addition to N fixation, legumes effectively utilize the chemical N via interspecific N competition in intercropping systems (Duchene et al., 2017). The NUE and PFPN of maize intercropped with gingelly, peanut, soybean, and sweet potato increased by 28–49% and 20–80%, respectively; here, the maize/soybean system showed the highest increment under low N input (Fig. 1), consistent with previous reports (Chen et al., 2019; Fan et al., 2019). Intercrops absorb more N than sole crops, and N uptake by the intercropped cereal and legume is significantly greater than that by the sole crops (Xu et al., 2020; Hu et al., 2020). Our results demonstrated that intercropping could significantly increase maize plant N uptake, and the value was improved under the maize/legume system (Fig. 2). Plant N uptake depends mainly on soil N supply (Luo et al., 2018a), thus intercropping-driven increase in maize productivity (yield, NUE, and PFPN) is likely related to N trade-off.

5.2. Intercropping increases plant nitrogen uptake and maintains soil nitrogen pool

The balance between competition and complementarity constantly fluctuates in an intercropping system, depending on environmental changes or plant developmental stages. Our study found that intercropping and plant development independently or interactively explained the variations in plant N content and total N uptake (Fig. 2). Intercropping influenced the N content of soil and root across plant development, which contributes to plant N uptake and accumulation in different growth periods (Figs. 2 and 7). The increased plant N uptake in intercropping systems is predominantly due to root-soil interaction (Neugschwandtner and Kaul, 2015; Duchene et al., 2017). Thus, N's transfer into, within, and out of the soil likely affects N trade-offs between plant and soil.

Increase in plant N uptake is related to systemic N fixation and soil N activation under low N availability or increased N competition (Mahieu, 2009; Luo et al., 2018a). Our study found no difference in soil total N content between intercropping and monoculture systems in seedling and mature stages. Still, it decreased at the elongation and flowering stages (Fig. 2). Soil inorganic N content under intercropping was lower than monoculture at the various stages of plant (Fig. 2). Nitrogen fixing ability of the intercrops depends on soil N availability and is negatively correlated with soil inorganic N content (Mahieu, 2009). Thus, low N availability can stimulate N fixation in intercropping systems to meet N requirement during plant development (Du et al., 2020; Hu et al., 2020).

4.3. Intercropping influences soil nitrogen dynamics and losses

Considering N competition between plants and soil organisms, low availability of soil N may drive organic N mineralization by influencing soil microbiome. Intercropping influences soil microbial biomass and selecting functionally microbial populations that rely on C fluxes in the rhizosphere (Philippot et al., 2013). Our results indicated that soil MBN content varied considerably during maize growth stages, and the intercropping systems showed a greater content than the monoculture (Fig. 2). Cereal/legumes intercropping could increase soil microbial biomass (e.g. MBN) under field conditions (Tang et al., 2014; Lian et al., 2019). Soil microbial biomass acts as both a source and a sink for nutrients such as N, which become available through the turnover of soil microbes (Irshad et al., 2012). Soil microbial biomass facilitates essential soil functions, such as microbial community-mediated soil NUE (Mooshammer et al., 2014; Luo et al., 2018b). Present study found that the potential activity of soil urease and NAG in the intercropping systems, especially in maize/legume system, was lower than that under monoculture in the mid to late stages of plant development. Inversely, soil LAP activity under the intercropping was higher than that under monoculture (Fig. 5; Wang et al., 2021). These findings suggest that plant growth and intercropping regulate soil N-acquisition enzyme activity.

Maize intercropping with gingelly, peanut, soybean, and sweet potato all could reduce total N losses via ammonia volatilization and runoff (Figs. 3 and 4). Maize/soybean system had the lowest N runoff loss, followed by maize/peanut and maize/sweet potato (Fig. 4). The maize/legume system specifically showed a lower N loss than the maize/non-legume. Legume intercropping increases leaf area index as legumes exhibited rapid growth which enhanced canopy overlap thus covering the empty spaces in the inter-rows of crops (Nyawade et al., 2020). This reduces the raindrop hitting force and slows down the velocity of runoff, and increases the effective rain-receiving area which mitigates N runoff generation (Nyawade et al., 2020; Mei et al., 2021). Low N loss may be a main reason for high plant N uptake under intercropping, maintaining soil N retention under low N input. Low soil N availability and urease activity stimulate the fixation of atmospheric N by N-fixing microbes, and the fixed N may be absorbed by roots (Duchene et al., 2017; Hu et al., 2020). Soil pH, inorganic N content, and urease and NAG activities significantly affected the N losses via ammonia volatilization and runoff (Fig. 6), which was consistent with previous studies (Zhang et al., 2022). Swain (2016) found that intercropping improves soil water-holding capacity, reducing N runoff loss. These suggest that intercropping reduces N loss, improving plant N uptake under low N input, which is consistent with an earlier argument on intercropping as a method that mitigates N loss and environment (Rosolem et al., 2017).

4.4. Dependence of crop productivity on maize nitrogen trade-off

Our results demonstrated that maize productivity positively correlated with plant N uptake and soil MBN content while it negatively correlated with N loss amount, soil N availability, and soil NAG activity (Fig. 6). Thus, the N regulation and balance under intercropping may be the key factor for improving crop productivity (Duchene et al., 2017; Hu et al., 2020; Du et al., 2020). Increase in plant N uptake is largely affected by light use, alternation growth, and biological N fixation of the intercrops (Duchene et al., 2017). Li et al. (2021) found that intercropping configuration increases the light capture of maize by 29% compared with the light capture under sole crops. The light capture and photosynthesis of crops strongly depend on N absorption and plant biomass (Zhang et al., 2021). Thus, increased plant N uptake and biomass via improved light capture and photosynthesis likely contribute to yield improvement (Fig. 2; Honda et al., 2021).

Component crops' growth traits and N requirements vary greatly (Hu et al., 2016). In our experiment, reduced N input in intercropping systems was also beneficial for the biological N fixation of legumes (Du et al., 2020). Under low N input, increase in plant N uptake and biomass may be attributed to the preferential supply of soil N by fixing atmospheric N, mitigating N loss, and enhancing root N competitiveness (Figs. 2–5). Leguminous biological N fixation increases the mineral N of soil for maize, and then increasing the aboveground N accumulation (Xu et al., 2020). The continuous absorption of plants reduced available soil N, stimulating soil N mining via multiple pathways. Maize intercropped with legumes had lower N loss and higher productivity than maize intercropped with non-legumes (Figs. 1–4). Under maize/legume system, increased soil coverage reduces water and nutrient losses and promotes the nutrient absorption and root interaction effect (Hu et al., 2021). Most importantly, maize competition for N reduces the root N of legumes, which enhances N fixation efficiency (Du et al., 2020). Studies on cereal/legume have reported that the main process affecting N facilitation is changing root-driven pH through N fixation (Bargaz et al., 2015).

Thus, intercropping is gradually developing as an indispensable farming pattern, which guarantees the stability of maize production; this approach reduces N input and enhances NUE, reducing environmental pollution (Fig. 7). Intercropping is a powerful way to enable N complementary and facilitative relationships between crops by balancing soil N supply and plant absorption. The complementarity and balance for the acquisition of soil resources and the facilitation of processes mainly occur in rhizosphere via positive plant-soil-microbial interactions (Brussaard et al., 2007; Duchene et al., 2017). In the future, we will analyze the rhizosphere to decipher the plant-microbial interactive mechanisms in N trade-offs, and further demonstrate the climate-dependence of the effect of intercropping on maize productivity and N balance (Ofori and Stern, 1987; Hulugalle and Lal, 1986).

5. Conclusion

Our study demonstrated that intercropping with legumes and non-legumes significantly improved maize productivity (yield, NUE, PFPN, and plant N uptake) and mitigated N losses via ammonia volatilization and runoff. Maize/legume system showed greater maize productivity than the maize/non-legume system. Maize productivity was positively correlated with plant N uptake and soil MBN content, while it was negatively correlated with N loss amount, soil inorganic N, and NAG activity. These results confirmed that regulating the trade-offs between soil N supply and plant N requirement in an intercropping system under low N fertilization resulted in high productivity. Nitrogen balance under the intercropping system was associated with plant development.

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.

Data Availability

The authors do not have permission to share data.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.fcr.2022.108671.

References

Bao, S.D., 2000. Soil and Agro-Chemistry Analysis, third ed. China Agric. Press, Beijing.
Bargaz, A., Zaman-Allah, M., Farissi, M., Lazali, M., Drevon, J.J., Maougal, R.T., et al., 2015. Physiological and molecular aspects of tolerance to environmental constraints in grain and forage legumes. Int. J. Mol. Sci. 16, 18976–19008.
Brussaard, L., de Ruiter, P.C., Brown, G.G., 2007. Soil biodiversity for agricultural sustainability. Agric. Ecosyst. Environ. 121, 233–244.
Chen, P., Song, C., Liu, X.M., Zhou, L., Yang, H., Zhang, X.N., et al., 2019. Yield advantage and nitrogen fate in an additive maize-soybean relay intercropping system. Sci. Total Environ. 657, 987–999.
Cong, W.F., Hoffland, E., Li, L., Six, J., Sun, J.H., Bao, X.G., et al., 2015. Intercropping enhances soil carbon and nitrogen. Glob. Chang. Biol. 21 (4), 1715–1726.
Dang, K., Gong, X.W., Zhao, G., Wang, H.L., Ivanistau, A., Feng, B.L., 2020. Intercropping alters the soil microbial diversity and community to facilitate nitrogen assimilation: a potential mechanism for increasing proso millet grain yield. Front. Microbiol. 11, 601054.
Deforest, J.L., 2009. The influence of time, storage temperature, and substrate age on potential soil enzyme activity in acidic forest soils using MUB-linked substrates and ldopa. Soil Biol. Biochem. 41, 1180–1186.
Du, Q., Zhou, L., Chen, P., Liu, X.M., Song, C., Yang, F., et al., 2020. Relay-intercropping soybean with maize maintains soil fertility and increases nitrogen recovery efficiency by reducing nitrogen input. Crop J. 8 (1), 140–152.
Duchene, O., Vian, J.F., Celette, F., 2017. Intercropping with legume for agroecological cropping systems: complementarity and facilitation processes and the importance of soil microorganisms. A review. Agric. Ecosyst. Environ. 240, 148–161.
Fan, Z.L., Zhao, Y.H., Chai, Q., Zhao, C., Yu, A.Z., Coulter, J.A., et al., 2019. Synchrony of nitrogen supply and crop demand are driven via high maize density in maize/pea strip intercropping. Sci. Rep. 9, 10954.
Feng, C., Sun, Z., Zhang, L., Feng, L., Zheng, J., Bai, W., et al., 2021. Maize/peanut intercropping increases land productivity: a meta-analysis. Field Crop. Res. 270 (2), 108208.
Ge, Y.Y., Wang, Q.L., Wang, L., Liu, W.X., Liu, X.Y., Huang, Y.J., et al., 2018. Response of soil enzymes and microbial communities to root extracts of the alien Alternanthera philoxeroides. Arch. Agron. Soil Sci. 64 (5), 708–717.
Glaze-Corcoran, S., Hashemi, M., Sadeghpour, A., Jahanzad, E., Keshavarz Afshar, R., Liu, X., et al., 2020. Understanding intercropping to improve agricultural resiliency and environmental sustainability. Adv. Agron. 162, 199–256.
Honda, S., Ohkubo, S., Nan, S.S., Nakkasame, A., Adachi, S., 2021. Maintaining higher leaf photosynthesis after heading stage could promote biomass accumulation in rice. Sci. Rep. 11 (1), 7579.
Hu, F., Gan, Y., Chai, Q., Feng, F., Zhao, C., Yu, A., et al., 2016. Boosting system productivity through the improved coordination of interspecific competition in maize/pea strip intercropping. Field Crop. Res. 198, 50–60.
Hu, F., Tan, Y., Yu, A., Zhao, C., Fan, Z.L., Yin, W., et al., 2020. Optimizing the split of N fertilizer application over time increases grain yield of maize-pea intercropping in arid areas. Eur. J. Agron. 119, 126117.
Hu, X., Li, W., Liu, Q., Yin, C., 2021. Root physiological responses can explain the effects of short-term plant-plant interactions on growth of two subalpine coniferous species. Can. J. For. Res. 51 (11), 1595–1606.
Hulugalle, N.R., Lal, R., 1986. Soil water balance of intercropped maize and cowpea grown in a tropical hydromorphic soil in western Nigeria. Agron. J. 78, 86–90.
Irshad, U., Brauman, A., Villenave, C., Plassard, C., 2012. Phosphorus acquisition from phytate depends on efficient bacterial grazing, irrespective of the mycorrhizal status of Pinus pinaster. Plant Soil 358, 155–168.
Jiang, Y.Z., Liu, Q.L., Zhang, Y.G., Li, Z.H., Zou, Y., Zhu, J.W., et al., 2018. Effects of different tillage modes for ammonia volatilization emissions from flue-cured tobacco fields. Int. J. Agric. Biol. 20 (10), 2237–2242.
Kermah, M., Franke, A.C., Adjei-Nsiah, S., Ahiabor, B.D., Abaidoo, R.C., Giller, K.E., 2017. Maize-grain legume intercropping for enhanced resource use efficiency and crop productivity in the Guinea savanna of northern Ghana. Field Crop. Res. 213, 38–50.
Li, S., van Der Werf, W., Zhu, J., Guo, Y., Li, B., Ma, Y., et al., 2021. Estimating the contribution of plant traits to light partitioning in simultaneous maize/soybean intercropping. J. Exp. Bot. 72 (10), 3630–3646.
Lian, T.X., Mu, Y., Jin, J., Ma, Q., Nian, H., 2019. Impact of intercropping on the coupling between soil microbial community structure, activity, and nutrient-use efficiencies. PeerJ 1 (1), 14.
Liu, Y.X., Sun, J.H., Zhang, F.F., Li, L., 2020a. The plasticity of root distribution and nitrogen uptake contributes to recovery of maize growth at late growth stages in wheat/maize intercropping. Plant Soil 447 (1–2), 39–53.
Liu, X.D., Chen, L.Y., Hua, Z.L., Mei, S.C., Wang, P., Wang, S.W., 2020b. Comparing ammonia volatilization between conventional and slow-release nitrogen fertilizers in paddy fields in the Taihu Lake region. Environ. Sci. Pollut. Res. 27 (8), 8386–8394.
Liu, X.M., Yong, T.W., Liu, W.Y., Ben-Ying, S.U., Song, C., Yang, F., et al., 2014. Effect of reduced N application on soil N residue and N loss in maize-soybean relay strip intercropping system. Chin. J. Appl. Ecol. 25 (8), 2267–2274.
Luo, G., Ling, N., Nannipieri, P., Chen, H., Raza, W., Wang, M., et al., 2017. Long-term fertilisation regimes affect the composition of the alkaline phosphomonoesterase encoding microbial community of a vertisol and its derivative soil fractions. Biol. Fertil. Soils 53 (4), 375–388.
Luo, G.W., Friman, V.P., Chen, H., Liu, M.Q., Wang, M., Guo, S.W., et al., 2018a. Long-term fertilization regimes drive the abundance and composition of N-cycling-related prokaryotic groups via soil particle-size differentiation. Soil Biol. Biochem. 116, 213–223.

Luo, G.W., Li, L., Friman, V.P., Guo, J.J., Guo, S.W., Shen, Q.R., et al., 2018b. Organic amendments increase crop yields by improving microbe-mediated soil functioning of agroecosystems: a meta-analysis. Soil Biol. Biochem. 124, 105–115.

Mahieu, S., 2009. Assessment of the below ground contribution of field grown pea (Pisum sativum L.) to the soil N pool. Citeseer.

Marques, E., Kur, A., Bueno, E., Wettberg, E., 2020. Defining and improving the rotational and intercropping value of a crop using a plant-soil feedbacks approach. Crop Sci. 60 (5), 2195–2203.

Mei, P.P., Wang, P., Yang, H., Gui, L.G., Christie, P., Li, L., 2021. Maize/faba bean intercropping with rhizobial inoculation in a reclaimed desert soil enhances productivity and symbiotic N^2 fixation and reduces apparent N losses. Soil Tillage Res. 213, 105154.

Mooshammer, M., Wanek, W., Hämmerle, I., Fuchslueger, L., Hofhansl, F., Knoltsch, A., 2014. Adjustment of microbial nitrogen use efficiency to carbon: nitrogen imbalances regulates soil nitrogen cycling. Nat. Commun. 5, 3694.

Neugschwandtner, R.W., Kaul, H.P., 2015. Nitrogen uptake, use and utilization efficiency by oat–pea intercrops. Field Crop. Res. 179, 113–119.

Nyawade, S.O., Karanja, N.N., Gachene, C.K., Gitari, H.I., Schulte-Geldermann, E., et al., 2020. Optimizing soil nitrogen balance in a potato cropping system through legume intercropping. Nutr. Cycl. Agroecosyst. 117, 43–59.

Ofori, F., Stern, W.R., 1987. Cereal-legume intercropping systems. Adv. Agron. 41, 41–90.

Peel, M.C., Finlayson, B.L., McMahon, T.A., 2007. Updated world map of the Koppen-Geiger climate classification. Hydrol. Earth Syst. Sci. 11, 1633–1644.

Philippot, L., Raaijmakers, J.M., Lemanceau, P., van der Putten, W.H., 2013. Going back to the roots: the microbial ecology of the rhizosphere. Nat. Rev. Microbiol. 11 (11), 789–799.

Raza, M.A., Feng, L.Y., Iqbal, N., Ahmed, M., Chen, Y.K., Khalid, M.H., et al., 2019. Growth and development of soybean under changing light environments in relay intercropping system. PeerJ 7, e7262.

Renard, D., Tilman, D., 2019. National food production stabilized by crop diversity. Nature 571 (7764), 257–260.

Rosolem, C.A., Ritz, K., Cantarella, H., Galdos, M.V., Hawkesford, M.J., Whalley, W.R., et al., 2017. Enhanced plant rooting and crop system management for improved N use efficiency. Adv. Agron. 146, 205–239.

Sanginga, N., 2003. Role of biological nitrogen fixation in legume based cropping systems; a case study of West Africa farming systems. Plant Soil 252 (1), 25–39.

Schwerdtner, U., Spohn, M., 2021. Interspecific root interactions increase maize yields in intercropping with different companion crops. J. Plant Nutr. Soil Sc. 184 (5), 596–606.

Stern, W.R., 1993. Nitrogen fixation and transfer in intercrop systems. Field Crop. Res. 34, 335–356.

Swain, S.C., 2016. Influence of intercropping systems on soil health, productivity and quality of guava (*Psidium guajava l.*) in Eastern India. J. Plant Nutr. 39 (14), 2037–2046.

Tang, Q.X., Haile, T., Liu, H.B., Ren, T.Z., Jiang, P.A., Zhai, L.M., et al., 2018. Nitrogen uptake and transfer in broad bean and garlic strip intercropping systems. J. Integr. Agric. 17 (1), 220–230.

Tang, X., Bernard, L., Brauman, A., Daufresne, T., Deleporte, P., Desclaux, D., et al., 2014. Increase in microbial biomass and phosphorus availability in the rhizosphere of intercropped cereal and legumes under field conditions. Soil Biol. Biochem. 75, 86–93.

Vance, E.D., Brookes, P.C., Jenkinson, D.S., 1987. An extraction method for measuring soil microbial biomass C. Soil Biol. Biochem. 19 (6), 703–707.

Wang, X.M., Yang, F., Yang, S.X., Chen, X.L., Yuan, Q., Ye, J.X., 2017. Study on non-point source nitrogen and phosphorus pollution and its law of accumulation in villages and towns. Agro Food Ind. Hi Tech 28 (3), 2005–2009.

Wang, X.X., Rong, X.M., Zhang, Y.P., Xie, Y., 2014. Effects of different intercropping on growth,nutrient accumulation and yield of maize. J. Anhui Agric. Sci. 42 (10), 2897–2899.

WRB, 2015. World Reference Base For Soil Resources 2014, Update 2015. International Soil Classification System For Naming Soils And Creating Legends For Soil Maps. World Soil Resources Reports No. 106. FAO, Rome.

Xiao, L., Huang, Y.M., Zeng, Q.C., Zhao, J.F., Zhou, J.Y., 2018. Soil enzyme activities and microbial biomass response to crop types on the terraces of the Loess Plateau, China. J. Soils Sediments 18 (5), 1971–1980.

Xu, Z., Li, C.J., Zhang, C.C., Yu, Y., Zhan, X., van der Werf, W., et al., 2020. Intercropping maize and soybean increases efficiency of land and fertilizer nitrogen use; a meta-analysis. Field Crop. Res. 246, 107661.

Yan, P., Tao, Z., Chen, Y., Zhang, X., Sui, P., 2017. Spring Maize Kernel number and assimilate supply responses to high-temperature stress under field conditions. Agron. J. 109 (4), 1433–1442.

Yang, F., Huang, S., Gao, R., Liu, W., Yong, T., Wang, X., et al., 2014. Growth of soybean seedlings in relay strip intercropping system in relation to light quantity and red: far-red ratio. Field Crop. Res. 155, 245–253.

Yang, W., Miao, J., Wang, X., Xu, J., Lu, M., Li, Z., 2018. Corn-soybean intercropping and nitrogen rates affected crop nitrogen and carbon uptake and C:N ratio in upland red soil. J. Plant Nutr. 41 (15), 1890–1902.

Yu, Y., Stomph, T.J., Makowski, D., Zhang, L.Z., van der Werf, W., 2016. A meta-analysis of relative crop yields in cereal/legume mixtures suggests options for management. Field Crop. Res. 198, 269–279.

Yun, Z., Pengbing, L., Jianping, K., Xiangwen, X., Tiansheng, Y., Liang, Z., et al., 2020. Effects of topdressing nitrogen fertilizer at different growth stages on growth dynamics and quality of beer barley. Xinjiang Agric. Sci. 57 (12), 2176–2185.

Zhang, X.Q., Huang, G.Q., Zhao, Q.G., 2014. Differences in maize physiological characteristics, nitrogen accumulation, and yield under different cropping patterns and nitrogen levels. Chil. J. Agric. Res. 74 (3), 326–332.

Zhang, Y., Zhao, H., Hu, W., Wang, Y., Zhang, H., 2022. Understanding how reed-biochar application mitigates nitrogen losses in paddy soil: Insight into microbially-driven nitrogen dynamics. Chemosphere 295, 133904.

Zhang, Y.P., Yan, J., Rong, X.M., Han, Y.L., Yang, Z.Y., Hou, K., et al., 2021. Responses of maize yield, nitrogen and phosphorus runoff losses and soil properties to biochar and organic fertilizer application in a light-loamy fluvo-aquic soil. Agric. Ecosyst. Environ. 314, 107433.

Zheng, B.C., Zhang, X.N., Chen, P., Du, Q., Zhou, Y., Yang, H., et al., 2021. Improving maize's N uptake and N use efficiency by strengthening roots' absorption capacity when intercropped with legumes. PeerJ 9, e11658.