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RESEARCH ARTICLE

Crop rotation-induced soil aggregate restructuring enhances fertilizer nitrogen retention on the Loess Plateau of China

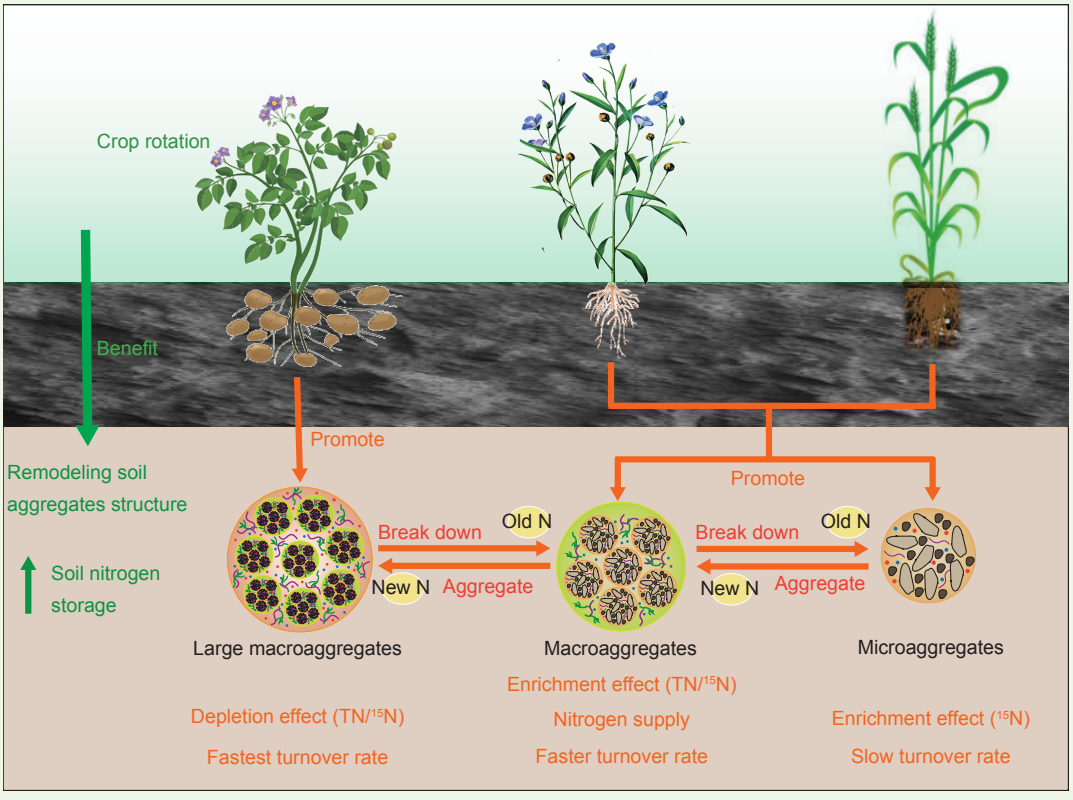
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Highlights

- Initial fertilizer N was preferentially distributed in macroaggregates.
- Subsequent annual fertilizer N was stabilized in microaggregates.
- Macroaggregates have dual functions of supplying N to plants and enriching new N.
- Crop rotations reshaped the soil aggregation structure.
- Crop rotations enhanced the long-term retention and stabilization of fertilizer N.

Graphical abstract



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Abstract

Soil aggregates highly regulate nitrogen (N) turnover, yet their functions in regulating N retention under long-term crop rotation remain unclear. This study used ^{15}N-labeled fertilizer N to investigate how different-sized soil aggregates regulate fertilizer N retention and redistribution under long-term crop rotation systems. The results revealed that large macroaggregates exhibited a more pronounced depletion of fertilizer N (enrichment factor, Ef: 0.73−0.95) than of total N (Ef: 0.93−1.00). In contrast, macroaggregates and microaggregates enriched fertilizer N (Ef: 1.00−1.16). Crucially, we found a temporal divergence: after harvest (with new ^{15}N-labeled fertilizer application), macroaggregates preferentially sequestered new N (current-season fertilizer N), whereas microaggregates dominated the stabilization of old N (previous-year fertilizer N) in the absence of ^{15}N-labeled fertilizer in 2024. This functional specialization is driven by aggregate turnover, whereby disintegrating macroaggregates release old N for stabilization in microaggregates, while reforming macroaggregates encapsulate new N. The accelerated release of fertilizer N from these macroaggregates during crop cultivation supplies N to crops, while their reformation concurrently enriches new N. This process underscores the dual functions of macroaggregates in both supplying N to crops and enriching new N. Ultimately, crop rotations reinforce this beneficial dynamic by restructuring soil aggregation, leading to a marked expansion of the soil N pool, with fertilizer N storage increasing by 27.11−111.68% and total N storage by 2.94−14.22% compared to continuous cropping. Our findings establish the functional heterogeneity of soil aggregates as a key mechanism for long-term fertilizer N retention and stabilization. This provides a mechanistic basis for optimizing N management under crop rotations.

Keywords: ^{15}N-labeled fertilizer, long-term crop rotation, soil aggregates, aggregates function, nitrogen turnover

1. Introduction

Nitrogen (N) fertilizer is essential for food production and security, so enhancing the efficiency of N utilization is critical for sustaining agricultural productivity and environmental security (Gao *et al.* 2020; Mi *et al*. 2025). Soil aggregates, as the basic structural units of soil, are key biochemical reactors in the soil N cycle and contribute to the long-term retention and supply of soil N (Egan *et al.* 2018; Bosilj *et al.* 2020). Soil aggregates of different sizes exhibit unique properties due to variations in their physicochemical characteristics, such as aeration, organic matter content, and the availability of ecological niches (Tian *et al.* 2022). The stratification effect of soil aggregates on soil nutrients and microbial functional diversity drives the differentiation of multifunctionality in soil aggregate ecosystems (Han *et al.* 2021).

Numerous studies have categorized bulk soil into distinct aggregate size fractions to characterize their functional attributes and ecological potentials. However, the role of different particle size aggregates in N retention is inconsistent with their contribution to the N pool in bulk soil. Research on maize has demonstrated that soil total nitrogen (TN) concentration decreases with decreasing aggregate size across various fertilizer regimes. Notably, macroaggregates constitute the primary reservoir for TN storage in bulk soil (Tian *et al.* 2022). In a 13-year study using ^{15}N tracer technology, the enhanced N retention under no-tillage combined with straw mulching in maize systems was attributed to promoted soil aggregation (Zhu *et al.* 2024). The initially applied N fertilizer remains stable in macroaggregates. Furthermore, during aggregate disintegration and reorganization, the "releasing the old and storing the new" effect facilitates substantial N retention in the silt and clay (SC) fraction, given the strong interaction between N and clay minerals (Zhu *et al.* 2024). In sandy loam soils, no-tillage and straw mulching promoted greater TN accumulation in the 0.053–2 mm aggregate size fraction across different cropping systems. During aggregate turnover, N from these aggregates was primarily lost as ^{14}N through microbial decomposition, mineralization, and denitrification, resulting in ^{15}N enrichment in microaggregates (Bhattacharyya *et al.* 2019). Moreover, the formation and stabilization mechanisms of soil aggregates differ significantly among different particle size classes. Specifically, the turnover rate of macroaggregates is faster than that of microaggregates driven by fungal hyphae and plant roots, as the cementing substances of macroaggregates are readily degradable. In contrast, microaggregates have stable bindings of chemically persistent organic components and oxides, which contribute to their slower turnover (Van Groenigen *et al*. 2002). Evidently, aggregates of varying particle sizes play distinct functions in the soil N cycle due to their divergent physicochemical properties. Additionally, these functions are modulated by soil types and agricultural management practices (Balabane *et al.* 1996; Bimüller *et al.* 2014; Murphy *et al.* 2016; Bhattacharyya *et al.* 2019).

Among various management practices, crop rotation is an essential component of sustainable agricultural practices that significantly enhances soil N accumulation (Chen *et al.* 2020; Li *et al.* 2023). It is a complex system encompassing crop species selection, stubble management, tillage practices, and fertilizer application strategies (Viaud *et al.* 2018). Research has demonstrated that the combination of crop rotation and no-tillage significantly enhances soil TN storage by increasing the proportion of macroaggregates (>0.25 mm) (Zou *et al.* 2015). A 39-year rotation experiment further revealed that long-term fertilization accelerates macroaggregate turnover, which in turn increases organic matter inputs, improves soil structure, and enhances N sequestration (Zhang *et al.* 2021). Typically, crops utilize a portion of current-season fertilizer N, while residual N replenishes the soil N pool for subsequent crops and microorganisms (Yan *et al.* 2020). This process is coordinated by aggregates of various particle sizes, whose formation and stabilization depend on multiple factors (Xie

et al. 2024). Existing research has demonstrated that crop rotation exerts significant regulatory effects on nitrogen distribution among aggregate particle sizes (Chen *et al*. 2020).

However, there is currently limited information regarding the effects of complex crop rotation systems on fertilizer N turnover. The roles of different aggregate particle sizes in the fertilizer N turnover process remain unexplored. Furthermore, the long-term impact of different rotation systems on the dynamic distribution of both fertilizer N and TN, as mediated by their regulation of soil aggregate structure and function, remains to be elucidated. A 12-year long-term crop rotation experiment was conducted. This study employed ^{15}N tracing to investigate the dynamics of fertilizer N and soil N within soil aggregates across different years and seasons under various crop rotation systems. We hypothesized that: (1) fertilizer N turnover within soil aggregates is time-dependent through aggregate dynamics; (2) the function of specific aggregate sizes to retain fertilizer N is generally conserved across crop rotation systems; (3) crop rotation regulates N retention by altering aggregate distribution.

2. Materials and methods

2.1. Experimental site

A field experiment employing ^{15}N-labeled fertilizer was conducted from 2023 to 2024. This experiment was conducted based on a long-term fixed crop rotation experiment initiated in 2013 at the Dingxi Academy of Agricultural Science (34.26°N, 103.52°E, and altitude 2,040 m), Gansu Province, China. The site is representative of the agricultural production and climate conditions of the Loess Plateau in China. The region has a temperate continental climate, with a frost-free period of 140 days. The annual average sunshine duration is 2,476.6 h, with an average annual temperature of 6.43°C and average annual solar radiation of 594.7 kJ cm^{-2}. The average annual precipitation is 390.9 mm. The experimental site is located in a typical rain-fed agricultural area. Prior to the initiation of this field experiment, the surface soil (0–30 cm) is classified as loess soil, with a pH of 8.3. The initial soil properties (0–30 cm) were as follows: 17.51 g kg^{-1} organic matter, 1.00 g kg^{-1} of TN, 56.50 mg kg^{-1} of available N, 0.85 g kg^{-1} of total phosphorus, and 26.43 mg kg^{-1} of available phosphorus.

2.2. Experimental design and crops management

This experiment incorporated the local staple crops wheat (*Triticum aestivum* L.) and potato (*Solanum tuberosum* L.), along with the characteristic oil crop oilseed flax (*Linum usitatissimum* L.), into the rotation systems. Crop selection was predicated on three key attributes: (1) These species exhibit ecological adaptability to the local temperate semi-arid climate; (2) their complementary root configurations enable optimized resource partitioning; (3) they fulfill critical economic roles, with wheat and potatoes securing food supply, and oilseed flax providing high-value edible oil. The experiment included four treatments (Table 1), consisting of three crop rotation systems and a continuous cropping of oilseed flax (FFFF). Each rotation cycle spanned four years, and a total of three complete rotation cycles were concluded between 2013 and 2024. The experiment adopted a randomized complete block design, with each treatment replicated three times. Each crop-fertilizer combination was treated as an integrated agronomic unit subject to crop sequence-specific legacy effects. Crop varieties, fertilizer application rates, sowing dates, and harvest dates for all crop rotation systems are provided in Table 2. For oilseed flax and wheat, aboveground biomass was harvested at maturity, with residual stubble retained about 8 cm height to simulate standard agronomic practices. After grain threshing, the retained stubble was incorporated into the soil during post-harvest tillage, whereas all other aboveground residues were removed from the field. For potato, aboveground biomass (stems and leaves) and belowground roots were completely removed from the plots after tuber harvest, consistent with regional practices to minimize pest and disease carryover. This differential residue management aligns with local agricultural practices and was standardized across all treatments to ensure consistency.

A micro-plot of 1 m^2 (1 m×1 m) was established in each random plot. Each micro-plot was bounded by stainless steel plates to prevent lateral migration of ^{15}N-labeled fertilizer. Before sowing, phosphorus fertilizer was broadcast on the soil surface and incorporated by plowing to a depth of 20 cm. Phosphorus application rates were tailored to local

Table 1 Description of crop rotation systems

Crop rotation[1)]	Crop year			
	2013/2017/2021	2014/2018/2022	2015/2019/2023	2016/2020/2024
FFFF	Oilseed flax	Oilseed flax	Oilseed flax	Oilseed flax
FWPF	Oilseed flax	Wheat	Potato	Oilseed flax
WFPF	Wheat	Oilseed flax	Potato	Oilseed flax
WPWF	Wheat	Potato	Wheat	Oilseed flax

[1)] FFFF, flax→flax→flax→flax; FWPF, flax→wheat→potato→flax, WFPF, wheat→flax→potato→flax; WPWF, wheat→potato→wheat→flax.

Table 2 Planting and harvesting information of oilseed flax, wheat, potato in the rotation systems

Crop	Variety	Fertilizer (kg ha^{-1})		Planting date		Harvest date	
		N	P_2O_5	2023	2024	2023	2024
Oilseed flax	Longya 10	112.5	75.0	2 April	7 April	8 August	30 July
Potato	Xindaping	225.0	150.0	1 May	–	2 Oct	–
Wheat	Ganchun 27	150.0	112.5	22 Mar	–	4 Aug	–

optimal requirements of each crop (Table 2). No potassium fertilizer was applied, as soil potassium levels were sufficient (She *et al.* 2010). In 2023, ^{15}N-labeled urea (10% atom excess) was applied as an aqueous solution within the micro-plots. Within 24 h of sowing (after sunset), ^{15}N-labeled urea solution was uniformly applied to the entire micro-plot surface, followed immediately by water spraying to facilitate infiltration to the target 20 cm soil depth. The application date of ^{15}N-labeled fertilizer coincided precisely with the crop sowing dates listed in Table 2, and the application rates were consistent with the N rates specified therein. Specifically, the application rate of ^{15}N-labeled fertilizer per micro-plot (1 m^2) was 11.25 g for oilseed flax, 22.5 g for potato, and 15 g for wheat. The ^{15}N-labeled fertilizer was applied once per growing season. Before sowing in 2024, each micro-plot was evenly divided into two equal sub-plots by inserting another stainless steel plate that extends 10 cm above the ground and 90 cm into the soil. One sub-plot received ^{15}N-labeled urea (10% atom excess), while the other received conventional urea. The micro-plot design is schematically illustrated in Fig. 1.

2.3. Soil sampling

Soil samples were collected from five randomly selected points between crop rows at the 0–30 cm depth using a 4-cm diameter auger before sowing and after harvest in 2023 and 2024, respectively. The collected cores were thoroughly mixed to create a single composite soil sample for each micro-plot. To minimize damage to soil structure, the samples were stored in hard containers during transportation to the laboratory.

2.4. Soil aggregate fractionation

Fresh soil samples were split two subsamples after removing all visible small stones, roots, and other debris. One subsample was designated for bulk soil analysis, while the other was used for aggregate fractionation *via* the "optimal moisture screening method" (at approximately 15% soil water content). The soil water content in the 0–30 cm layer was determined before sampling, which satisfied the conditions for the "optimal moisture screening method", thereby eliminating the need for sample pre-treatment. For each micro-plot, approximately 500 g of soil was transferred into a stacked sieve set consisting of 2 and 0.25 mm sieves. The sieves were gently shaken for 2 min, allowing soil particles to fall through each sieve. Soil that did not pass through the 2 mm sieve was collected as large macroaggregates (>2 mm). The soil that passed through the 2 mm sieve but was retained on the 0.25 mm sieve was collected as macroaggregates (0.25–2 mm). Finally, soil that passed through the 0.25 mm sieve was collected as microaggregates (<0.25 mm). After sieving, each aggregate size fraction was weighed, air-dried, and stored for subsequent analysis of soil TN and ^{15}N abundance.

2.5. Determination of soil sample indicators

The concentration of soil total nitrogen was determined using the standard Kjeldahl method. The abundance of ^{15}N in aggregates of various particle sizes was analyzed with an isotope ratio mass spectrometer (IRMS) (Isoprime 100, Isoprime, UK). For bulk soil and aggregates, the concentration of fertilizer N was calculated according to the following equation:

$$\text{Fertilizer N}=(AT_e-AT_c)/(AT_f-AT_c)\times TN \quad (1)$$

where Fertilizer N (mg kg^{-1}) and TN (mg kg^{-1}) represent fertilizer N concentration and total N concentration in aggregates with various particle sizes and bulk soil, respectively. AT_e is ^{15}N atom percent (%) for the soil sample, AT_c is ^{15}N atom percent (%) of the identical sample taken before the addition of ^{15}N-labeled urea, and AT_f signifies the ^{15}N atom percent (%) of the ^{15}N-labeled fertilizer (10 atom% excess).

The enrichment factor (Ef) was calculated as the ratio of TN concentration or fertilizer N concentration in the individual aggregate particle size to that in the bulk soil. When Ef is greater than 1, it indicates that TN or fertilizer N is relatively enriched in this particle size compared to bulk soil. Conversely, when Ef is less than 1, it suggests a relative depletion in this particle size compared to bulk soil. The formula for calculation is as follows:

$$Ef=C_{agg}/C_{bulk} \quad (2)$$

where C_{agg} represents the concentration of TN (g kg^{-1}) or fertilizer N (mg kg^{-1}) in the individual aggregate particle size,

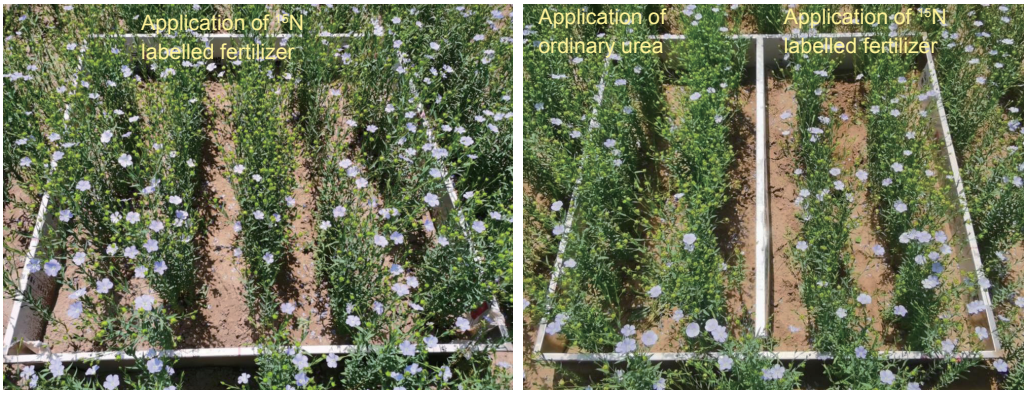


Fig. 1 Schematic diagram of ^{15}N-labeled fertilizer application in 2023 and 2024 in micro-plots.

and C_{bulk} represents the concentration of TN or fertilizer N in the bulk soil.

The storage (S_f, kg ha^{-1}) of TN or fertilizer N in the individual aggregate particle size was calculated as follows:

$$S_f=C_f\times H\times BD\times P_a/10 \quad (3)$$

where C_f (g kg^{-1}) represents the TN concentration or fertilizer N concentration in the individual aggregate particle size, H is soil layer height (cm), BD is bulk density (g cm^{-3}), and P_a (%) is the proportion of specific aggregate size fraction in bulk soil.

To characterize the temporal dynamics of fertilizer N retention in soil aggregates, two complementary metrics were calculated:

The cumulative reduction proportion (%), which quantifies the total percentage loss of fertilizer N from the initial post-application period to the final sampling point, reflects long-term retention efficiency across the entire rotation cycle. The calculation formula is as follows:

$$\text{Cumulative reduction proportion}=(FN_L-FN_1)/FN_1\times100 \quad (4)$$

where FN_L (mg kg^{-1}) signifies the fertilizer N concentration of the last sampled soil sample; FN_1 (mg kg^{-1}) represents the fertilizer N concentration in the soil after harvest of ^{15}N-labeled fertilizer in the first year.

Phased reduction proportion (%), which measures the percentage loss of fertilizer N between consecutive sampling events, captures short-term dynamics during distinct rotation phases (e.g., crop planting period and fallow period). The calculation formula is as follows:

$$\text{Phased reduction proportion}=(FN_j-FN_i)/FN_i\times100 \quad (5)$$

where FN_i (mg kg^{-1}) and FN_j (mg kg^{-1}) represent the fertilizer N concentration in the *i*th and *j*th soil samples, respectively.

2.6. Statistical analyses

The normality of the data was tested using the Kolmogorov-Smirnov test prior to analysis. The data were statistically analyzed using the Statistical Package for the Social Sciences software (version 26.0; IBM's Statistical Product and Service Solutions). A linear mixed-effect model was established to test the main and interactive effects of crop rotation systems, aggregate particle sizes, and sampling time. One-way analysis of variance (ANOVA) was employed to evaluate differences in individual indicators among crop rotation systems within each aggregate size fraction and sampling time. The least significant difference test was used for post-hoc comparison at a 5% probability level. Figures were plotted using Origin 2021 (Systat Software Inc., San Jose, CA, USA).

3. Results

3.1. Aggregate size distribution: Physical foundation for N retention

The distribution of soil aggregates was significantly influenced by crop rotation systems (Fig. 2), exhibiting variation over time and with crop species. Before sowing in 2023, the soil aggregate distribution was similar across all treatments,

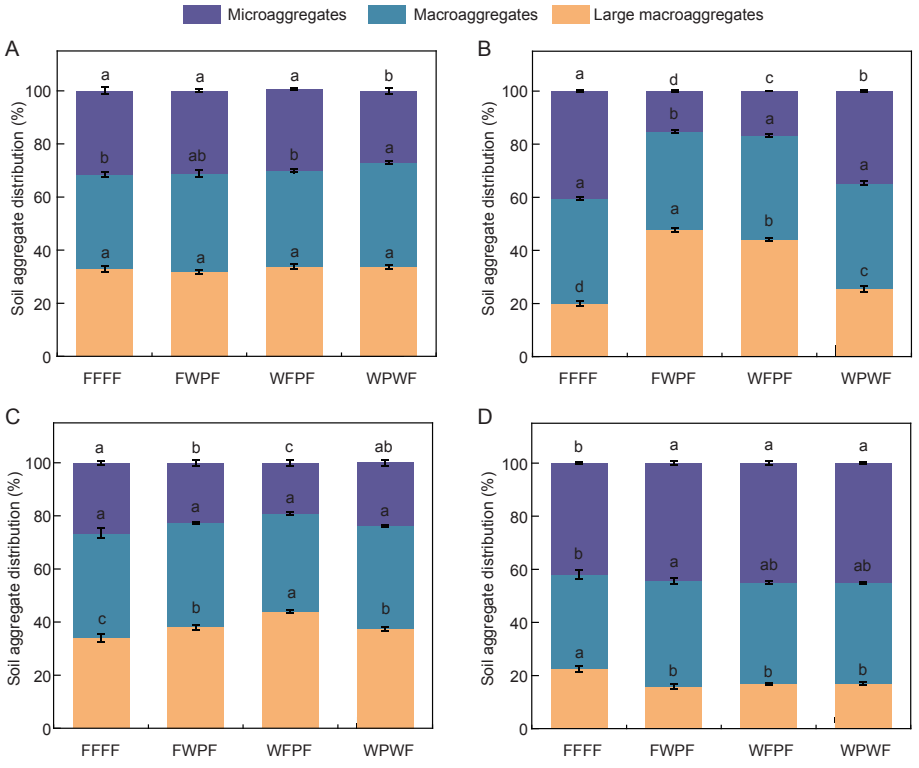


Fig. 2 Changes in distribution characteristics of soil aggregates under crop rotation systems. A and B, distribution characteristics of soil aggregates before sowing (A) and after harvest (B) in 2023. C and D, distribution characteristics of soil aggregates before sowing (C) and after harvest (D) in 2024. Treatment codes represent different rotation sequences: FFFF (flax→flax→flax→flax), FWPF (flax→wheat→potato→flax), WFPF (wheat→flax→potato→flax), and WPWF (wheat→potato→wheat→flax). Different lowercase letters above bars indicate significant differences between treatments (P<0.05). Error bars indicate the standard error of the means (n=3).

with the proportion of aggregates ranked as follows: macroaggregates>large macroaggregates>microaggregates (Fig. 2-A). However, after harvest, the distribution characteristics of aggregates changed depending on the crop species planted that season and the specific crop rotation systems used. Among these factors, crop species was identified as the primary factor influencing aggregate distribution patterns. After the 2023 harvest, potato cultivation promoted the formation of large macroaggregates, while microaggregates dominated wheat fields (Fig. 2-B). Oilseed flax fields comprised the smallest proportion of large macroaggregates, whereas macroaggregates and micro-aggregates constituted larger proportion. Notably, under the FFFF treatment, the proportion of micro-aggregates was 16.43−165.55% higher than other treatments. Following several months of fallow, the soil before sowing in 2024 was dominated by large macroaggregates (33.89−43.97%) and macroaggregates (36.92−39.51%) (Fig. 2-C). After the 2024 harvest, all treatments showed a consistent soil aggregate hierarchy: large macroaggregates<macroaggregates<microaggregates (Fig. 2-D). Among these, crop rotation systems demonstrated a significantly higher proportion of microaggregates compared to the FFFF treatment. In contrast, large macroaggregates showed an opposite trend, exhibiting a significant reduction of 25.34−29.10% compared to the FFFF. This phenomenon can be attributed to the fact that all crop rotation systems planted oilseed flax in 2024, whose distinctive root architecture particularly favors microaggregate formation.

3.2. Macroaggregates are persistent enrichment hotspots of TN in the crop rotation systems

Crop rotation systems significantly affected the TN concentration in various soil aggregate particle sizes (Fig. 3-A and B). Across all treatments, macroaggregates consistently exhibited the highest TN concentrations (0.98−1.24 g kg^{-1}) among all size classes, driving TN enrichment (Ef>1) in this fraction. Conversely, large macroaggregates showed Ef<1 (except for the WPWF treatment before sowing and the FFFF treatment after harvest in 2023) (Fig. 3-C and D), indicating size-dependent heterogeneity in TN enrichment capacity. This confirms that macroaggregates function as key hotspots for TN enrichment within these crop rotation systems. In the FFFF treatment, TN concentration in aggregates of various particle sizes decreased by 18.33−24.56% during the fallow period between the 2023 harvest and the 2024 sowing. In 2024, TN concentration in aggregates of different particle sizes under crop rotation systems remained significantly higher than that under the FFFF treatment, both before sowing and after harvest. Throughout the two-year study, the WPWF treatment maintained consistently higher TN concentration across aggregate fractions compared to other treatments. This is likely attributable to the higher cumulative nitrogen input associated with the WPWF rotation.

In summary, aggregate size governs soil TN distribution in these rotation systems, with different size fractions exhibiting

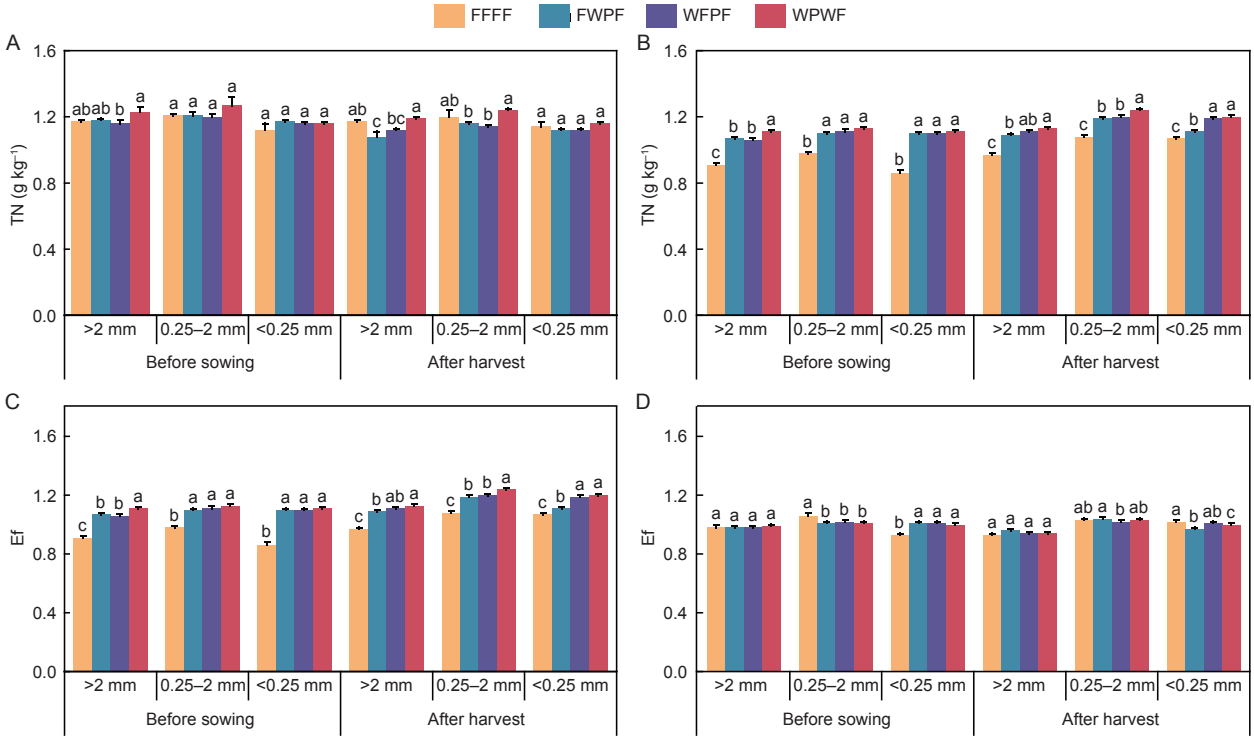


Fig. 3 The concentration and enrichment factor (Ef) of soil total nitrogen (TN) in soil aggregates in 2023 (A and C) and 2024 (B and D). Treatment codes represent different rotation sequences: FFFF (flax→flax →flax→flax), FWPF (flax→wheat→potato→flax), WFPF (wheat→flax→potato→flax), and WPWF (wheat→potato→wheat→flax). >2 mm, 0.25−2 mm and <0.25 mm represent large macroaggregates, macroaggregates and microaggregates, respectively. Different lowercase letters indicate that individual particle sizes varied significantly between crop rotation systems (P<0.05). Error bars indicate the standard error of the means (n=3).

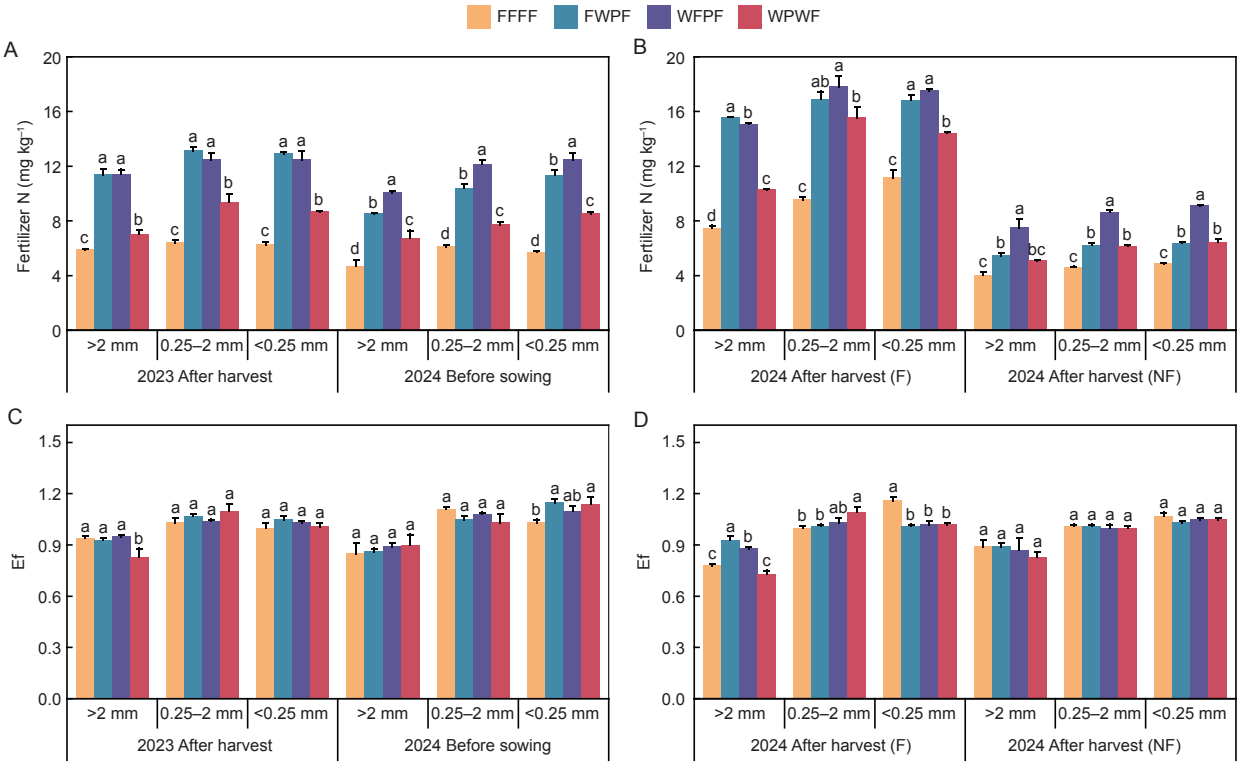


Fig. 4 The concentration and enrichment factor (Ef) of fertilizer N (^{15}N) in soil aggregates. Treatment codes represent different rotation sequences: FFFF (flax→flax→flax→flax), FWPF (flax→wheat→potato→flax), WFPF (wheat→flax→potato→flax), and WPWF (wheat→potato→wheat→flax). F indicates that ^{15}N-labeled fertilizer is applied in the current season; NF represents that ^{15}N-labeled fertilizer is not applied in the current season. >2 mm, 0.25−2 mm and <0.25 mm represent large macroaggregates, macroaggregates and microaggregates, respectively. Different lowercase letters indicate that individual particle sizes varied significantly between crop rotation systems (P<0.05). Error bars indicate the standard error of the means (n=3).

functional heterogeneity in their TN enrichment capacity. Crucially, macroaggregates consistently function as TN enrichment hotspots.

3.3. Fertilizer N retention and redistribution in aggregates under crop rotation systems

The dynamics of fertilizer N within soil aggregates exhibited distinct temporal patterns and crop rotation-specific trends (Table 3; Fig. 4). Temporally, after the harvests in 2023 and 2024 (^{15}N-labeled fertilizer application, except the FFFF treatment), fertilizer N concentrations ranked: macroaggregates>microaggregates>large macroaggregates (Fig. 4-A and B). In contrast, before sowing (except the FFFF treatment) and after harvest without ^{15}N-labeled fertilizer application in 2024, this hierarchy shifted, with microaggregates becoming the dominant reservoir, followed by macroaggregates. This shift was consistent with the Ef patterns, where both macroaggregates and microaggregates consistently showed Ef>1 (Fig. 4-C and D), indicating preferential retention of fertilizer N relative to the bulk soil. Regardless of sampling time and treatment, the Ef of TN in large macroaggregates was higher than that of fertilizer N, whereas the opposite trend was observed in microaggregates. Crop rotation systems significantly affected fertilizer N concentrations in aggregates of different particle sizes (Table 3). After the harvest in 2023, the FWPF and

Table 3 Test of a linear mixed effect model for the effects of crop rotation systems (R), time effect (T), aggregate particle size (A), and their interactions on fertilizer N concentration

Value	T	R	A	T×R	T×A	R×A	T×R×A
F-value	456.94	562.35	84.52	39.54	3.92	1.95	1.39
P-value	<0.01	<0.01	<0.01	<0.01	0.01	0.08	0.19

P<0.05 represents statistically significant difference; *P*<0.01 indicates a highly significant difference.

WFPF treatments (both including potato) had significantly higher fertilizer N concentrations in all aggregates than other treatments, consistent with the higher N input rate for potato cultivation. Over time, all treatments showed declining fertilizer N concentrations before sowing and after harvest in 2024 (without ^{15}N-labeled fertilizer application). However, the WFPF treatment maintained elevated levels, likely attributed to the residual effects of the higher initial N supply from potato. After harvest in 2024 (with ^{15}N-labeled fertilizer application), fertilizer N supplementation led to increased fertilizer N concentrations in aggregates of different particle sizes across all treatments.

Notably, potato-cropped treatments (FWPF and WFPF) exhibited significantly elevated fertilizer N concentrations across all aggregate size fractions during the current season. This legacy effect persisted through successive sampling events preceding and following oilseed flax cultivation. The observed difference was attributable to potato receiving the

highest N application rate (225 kg N ha^{-1}) among the three crops, which was 50.00% and 100.00% greater than that of wheat (150 kg N ha^{-1}) and oilseed flax (112.5 kg N ha^{-1}), respectively. Similarly, wheat-cropped treatments (WPWF) maintained 19.33−62.72% higher fertilizer N concentrations across all aggregate size fractions both in-season and during the subsequent growing year compared to oilseed flax monoculture (FFFF). This above-described causal cascade demonstrates that the legacy effects of preceding crops fundamentally restructure N partitioning within soil aggregates.

The reduction proportion of fertilizer N was higher during crop cultivation than during soil fallow (Fig. 5-A and B). Therefore, the cumulative reduction proportion of fertilizer N showed dynamics closely aligned with the reduction proportion specifically measured during the crop cultivation (Fig. 5-D). During soil fallow periods, the reduction proportion of fertilizer N in large macroaggregates was greater than that in macroaggregates, while microaggregates exhibited the lowest reduction proportion. This indicates that microaggregates had the strongest capacity to enrich fertilizer N during fallow. Conversely, the reduction proportion of fertilizer N during crop cultivation was highest in macroaggregates, suggesting that the Ef in macroaggregates at this time was lower compared to other soil sampling periods.

3.4. Diversified crop rotations increase TN and fertilizer N storages

Crop rotation systems exhibited significant effects on the storages of both soil TN and fertilizer N (Fig. 6). The soil TN storages were consistently higher under the crop rotation systems than under the FFFF treatment (Fig. 6-A and B). Specifically, compared to the FFFF treatment, crop rotations significantly increased TN storage by 13.04–14.20% before sowing and by 5.90–8.97% after harvest in 2024. Similarly, fertilizer N storages in the rotation system were significantly higher than those in the FFFF treatment, and they remained higher under FWPF and WFPF treatments (Fig. 6-C and D).

4. Discussion

4.1. Dynamic distribution of soil aggregates and fertilizer N on time scale in crop rotation systems

The distribution of soil aggregates and fertilizer N over time is dynamic and depends on the crop rotation systems. Crop rotation enhances soil aggregate stability by promoting a diversity of soil structures and avoiding monotonous soil structures (Chen *et al.* 2020). A higher proportion of >0.25 mm aggregates was consistently observed before sowing in both years. This is attributed to plowing after harvest, which was uniformly applied across all treatments to simulate conventional farming practices. Conversely, the aggregates size distribution after harvest during the two-year period varied with the specific crop species and rotation systems. These variations in aggregate structure are primarily driven by differences in root architecture and growth patterns among crop species (Tisdall and Oades 1982). For instance, potato cultivation led to the highest proportion of large macroaggregates (Zhang *et al.* 2022; Yan *et al.* 2025). This aligns with our observation that potato fields after harvest had a higher proportion of large

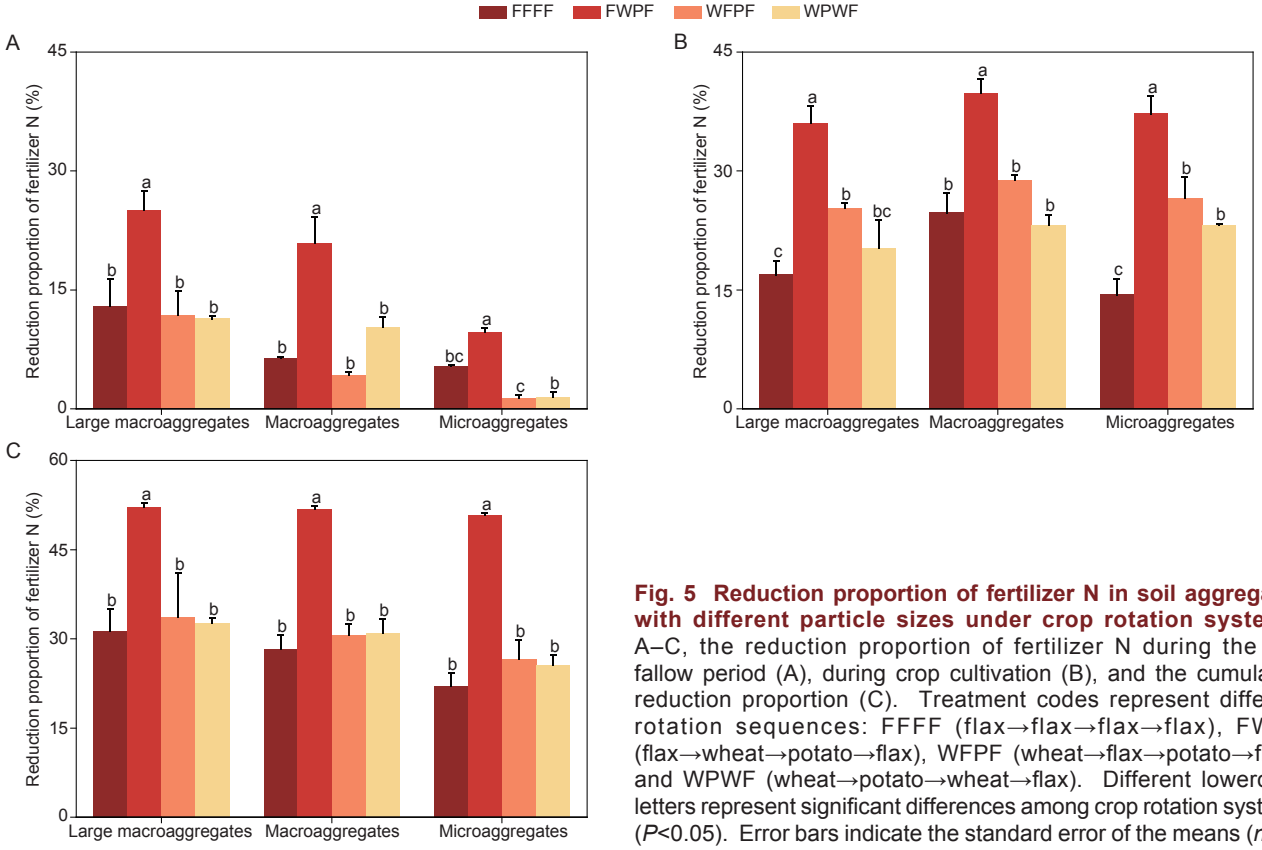


Fig. 5 Reduction proportion of fertilizer N in soil aggregates with different particle sizes under crop rotation systems. A–C, the reduction proportion of fertilizer N during the soil fallow period (A), during crop cultivation (B), and the cumulative reduction proportion (C). Treatment codes represent different rotation sequences: FFFF (flax→flax→flax→flax), FWPF (flax→wheat→potato→flax), WFPF (wheat→flax→potato→flax), and WPWF (wheat→potato→wheat→flax). Different lowercase letters represent significant differences among crop rotation systems (P<0.05). Error bars indicate the standard error of the means (n=3).

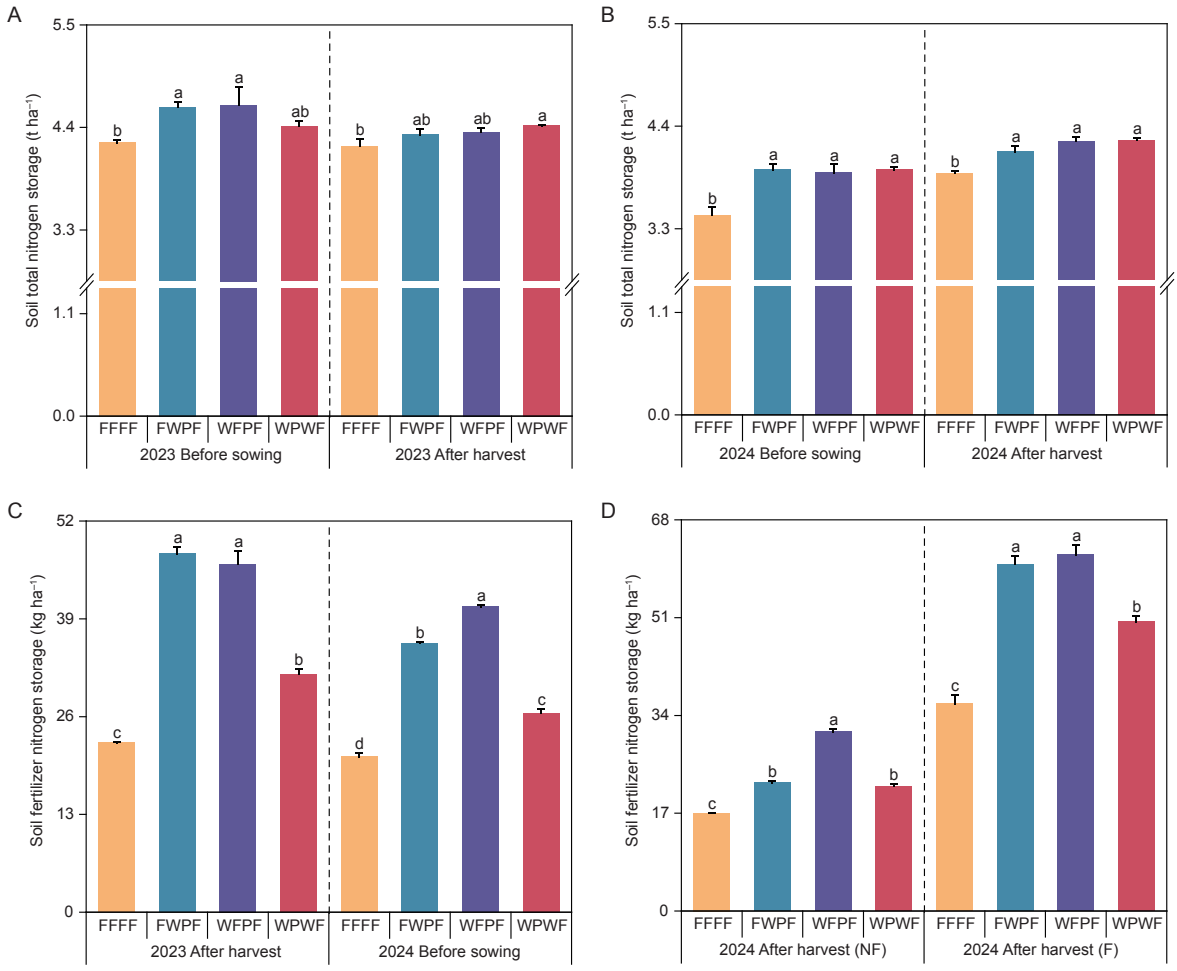


Fig. 6 The storages of soil total nitrogen (TN) and fertilizer N in bulk soil under crop rotation systems. A and B, TN storages of bulk soil in 2023 (A) and 2024 (B). C and D, fertilizer N storages of bulk soil. Treatment codes represent different rotation sequences: FFFF (flax→flax→flax→flax), FWPF (flax→wheat→potato→flax), WFPF (wheat→flax→potato→flax), and WPWF (wheat→potato→wheat→flax). NF represents that ^{15}N-labeled fertilizer is not applied in the current season; F represents that ^{15}N-labeled fertilizer is applied in the current season. Different lowercase letters indicate significant differences among crop rotation systems (P<0.05). Error bars indicate the standard error of the means (n=3).

macroaggregates than wheat and oilseed flax fields after harvest. This structural divergence can be explained by three key mechanisms associated with the potato root system. First, potato roots excrete greater quantities of polysaccharides and organic acids, which act as binding agents to promote the formation of large macroaggregates (Lu *et al.* 2023). Second, their greater root length density and biomass form more extensive rhizosphere networks, which physically enmesh smaller aggregates (Wang and Wang 2005). Third, their wider root diameter generates stronger radial pressures during growth, and the squeezing of surrounding particles promotes the formation of large aggregates (Hu *et al.* 2015; Lu *et al.* 2023). In contrast, the finer root systems of wheat and oilseed flax, which allow for greater soil penetration, tend to promote the formation and stabilization of smaller aggregates. While some short-term (three-year) studies reported non-significant effects of diversified rotation on aggregates (Canalli *et al.* 2020), our 12-year experiment demonstrates cumulative benefits. The short-term variability observed in our study, such as the weak differences before sowing in 2023 (2023BS), underscores the role of environmental constraints. Notably, a significant drought occurred prior to the 2023 sowing season. Specifically, annual precipitation in 2022 was only 246.80 mm, representing a 36.86% reduction from the long-term mean (390.90 mm). This severe moisture deficit slowed microbial decomposition of crop residues (Mi 2018), thereby attenuating differences in soil aggregates formation and nutrient release among treatments. Consequently, treatment differences in aggregate structure and TN concentration, which are closely linked to residue turnover, were temporarily muted before sowing in 2023. As precipitation rebounded to 313.40 mm in 2023 (predominantly from April to October) and exceeded 400 mm in 2024, the previously drought-constrained biological processes were reactivated, thereby unmasking the legacy effects of crop rotation. This phenomenon illustrates that the benefits of rotation persist over the long term but can be transiently masked by annual climate variability. In particular, precipitation acts as a key short-term modulation of the cumulative benefits conferred by diversified cropping systems.

Crop rotation plays a significant role in reshaping the

microstructure of soil and enhancing the retention of N fertilizer within soil aggregates. This improvement is likely correlated with enhanced microbial immobilization, driven by increased carbon availability from the greater quantity and diversity of organic matter returned to the soil in crop rotations (Van Groenigen *et al.* 2002). The crop rotation system for planting oilseed flax in the 2024 season resulted in the formation of smaller aggregates, with the highest proportion of microaggregates, followed by macroaggregates. The proportions of both these fractions were higher in the crop rotation systems than in the continuous cropping of oilseed flax (FFFF). This phenomenon can be explained by two synergistic mechanisms. On the one hand, complete crop rotation systems received greater total nitrogen fertilizer inputs than the FFFF treatment. On the other hand, a significantly larger pool of residual N accumulated in the soils under crop rotation systems. This residual N, combined with current-season fertilization, promoted oilseed flax root development, leading to increased polysaccharide secretion that stimulated microaggregate formation. These results demonstrate that crop rotation enhances the protective capacity of soil aggregates for long-term N storage. Previous studies have concluded that soil aggregation structure and TN concentration remain unchanged by N application. However, these characteristics mainly depend on crop rotation systems and other agronomic practices (Chen *et al.* 2020). Our findings indicate that TN concentrations across aggregate fractions under crop rotation systems were significantly higher than in the FFFF treatment in 2024. Notably, the WPWF treatment exhibited the highest TN concentration, likely attributable to greater N return from crop residues.

From a practical perspective, functional complementarity in root traits drives aggregate-mediated N stewardship. Strategic inclusion of crops with contrasting root architectures creates a self-perpetuating aggregate hierarchy. This architecture simultaneously optimizes short-term N retention and long-term stabilization.

4.2. Functional heterogeneity of aggregates on turnover and retention of soil N and fertilizer N

Regardless of changes in time scales and crop rotation systems, the Efs of soil TN and fertilizer N were greater than or equal to 1 in the macroaggregates. This consistency underscores the unique physicochemical characteristics and ecological function of the macroaggregate fraction. This observed enrichment is attributed to the physical protection offered by aggregates, which encapsulate N. Furthermore, macroaggregates serve as hotspots for soil microorganisms, facilitating microbial-mediated N retention and stabilization (Duan *et al.* 2021). In contrast, large macroaggregates showed depletion of both fertilizer N and TN, which can be attributed to their faster N turnover rate compared to more stable smaller aggregates (Six *et al.* 2000; Van Groenigen *et al.* 2002; Bhattacharyya *et al.* 2019). Moreover, N migrated to the smaller aggregates as the larger aggregates broke down (Zhu *et al.* 2024). The Ef of TN in large macroaggregates was greater than that of fertilizer N, indicating a stronger depletion effect on fertilizer N.

The temporal effect of aggregate protection and the effect of N retention control were variable. The function of aggregates on soil TN and fertilizer N demonstrated fluctuations. Although the enrichment or depletion of soil TN by microaggregates displayed uncertainty, the Ef of macroaggregates was greater than those of microaggregates. The enrichment of fertilizer N by aggregates was highly time-dependent. Following crop harvest (^{15}N was applied before sowing) in both years, the concentration and Ef of fertilizer N in macroaggregates exceeded those in microaggregates. However, before sowing and after harvest in 2024 without fertilizer N application, this pattern was reversed. This suggests that new N is preferentially allocated to macroaggregates, a finding that contrasts with some earlier studies suggesting rapid sequestration of new N in microaggregates (Balabane 1996). Our study reveals that old N was stabilized in microaggregates, which can be explained by the following points. First, microorganisms may enhance nitrogen fixation, as microbial biomass and abundance are correlated with the particle size of the aggregates (Tisdall and Oades 1982; Nie *et al.* 2014). Microbial biomass and abundance in smaller aggregates tend to be higher than in larger aggregates (Trivedi *et al.* 2015; Zhang *et al.* 2016; Tian *et al.* 2022). Second, the binding agents in larger aggregates are more readily degraded, leading to their disintegration and the release of protected microaggregates. In contrast, stability of microaggregates relies on ionic bond bridges, which strongly to retain N (Six *et al.* 2000; Van Groenigen *et al.* 2002). In addition, macroaggregates have a faster turnover rate than microaggregates due to the presence of additional organic carbon (Puget *et al.* 1995). Over time, nutrients are transferred from macroaggregates to microaggregates as microaggregates form within macroaggregates (Oades 1984; Angers *et al.* 1997).

Another explanation involves the theory of aggregate formation (Tisdall and Oades 1982), which suggests that soil mineral particles combine with polysaccharides and fungal hyphae to create microaggregates, while macroaggregates rely on organic matter as a cementing agent (Six *et al.* 2000). Organic matter inputs from crop residues (dominated by ^{14}N) dilute ^{15}N within macroaggregates (Mendonça *et al.* 2010). As aggregates turn over, they break down into microaggregates, with ^{14}N preferentially lost through mineralization and denitrification (Bhattacharyya *et al.* 2019). This leads to the relative enrichment of ^{15}N in the resulting, more stable microaggregates. This process, coupled with lower stability and higher turnover rates of larger aggregates (Kong *et al.* 2007), explains the greater fertilizer N losses in larger aggregates and more stable ^{15}N retention in microaggregates.

The fertilizer N concentrations within soil aggregates scaled predictably with application rates (e.g., the highest in potato, and 19.33−62.72% higher in wheat *vs*. flax treatments). However, the Ef revealed retention hierarchies that were independent of input levels: newly applied fertilizer N was preferentially enriched in macroaggregates shortly after application, whereas old fertilizer N stabilized in microaggregates during subsequent legacy phases. This decoupling of Ef patterns from input levels confirms that aggregate-mediated nitrogen retention and redistribution

mechanisms operate consistently across different crop-fertilizer regimes. The Ef thereby effectively isolates these intrinsic processes from the confounding influence of variable N supply.

Macroaggregates perform a dual function in supplying N to crops and enriching new N. Specifically, during crop cultivation (without application of ^{15}N in the current season), macroaggregates were the primary source of released fertilizer N. This aligns with their recognized role as a primary source of plant-available N (Van Groenigen *et al.* 2002). However, when new ^{15}N is applied, macroaggregates rapidly enrich this fresh N. This functional duality highlights their role as both active N suppliers and short-term reservoirs of N. In contrast, microaggregates act as long-term stabilizers. Their strong stability and low turnover rates reduce ^{15}N loss, making them critical for the extended retention of fertilizer N. Crop rotation enhances these dynamics by promoting soil aggregation, thereby reducing N losses from macroaggregates while preserving the stabilizing capacity of microaggregates.

In summary, our findings indicate that smaller aggregates are more effective at retaining and stabilizing fertilizer N due to their stronger adsorption and stability. Particularly, smaller aggregates exhibit a strong enrichment effect on new N, while microaggregates are more conducive to the long-term retention and stability of fertilizer N in the soil.

Notably, the FFFF treatment exhibited significant TN depletion across all aggregate fractions during the fallow period between the 2023 harvest and the 2024 sowing. This observation revealed two synergistic degradation mechanisms characteristic of continuous cropping systems. First, continuous cropping-induced elevated soil pH promotes substantial gaseous N losses through enhanced NH_4^+ conversion to NH_3 and stimulated N_2O emissions (Shan *et al.* 2015; Jia *et al.* 2016; Zhu *et al.* 2019). These losses are particularly pronounced during the non-growing season, when residual mineral N is not immobilized by plant uptake. Second, prolonged continuous cropping progressively impairs microbial N immobilization capacity through recalcitrant residue accumulation and suppression of diazotrophic bacteria (Kunito *et al.* 2022; Wang *et al.* 2024). This reduced capacity further disrupts the critical pathway for N retention in soil. In contrast, diversified crop rotations mitigate N loss through dual regulation of maintaining a stable soil pH and promoting microbial N immobilization.

These findings provide a scientific basis for policy frameworks aimed at sustainable agricultural intensification. Aligning with China's "Zero Fertilizer Growth Initiative", policies could establish targeted subsidies for farmers who adopt diversified crop rotations and residue retention practices. These subsidies aim to incentivize practices that stabilize soil pH and enhance microbial N immobilization, thereby directly curbing N losses.

4.3. Crop rotation systems increased the storages of TN and fertilizer N in bulk soil

Our results indicated that crop rotation systems increased the storage of both TN and fertilizer N in the bulk soil. Within these systems, the quantity of organic input was a critical factor. The higher organic matter input in crop rotations promotes aggregate stabilization, whereas low-input systems (e.g., continuous cropping) accelerate aggregate turnover, resulting in greater N losses (Kong *et al.* 2007). This explains why continuous cropping depletes the soil N pool, while crop rotations exhibit positive effects on N retention (Chen *et al.* 2020). Long-term fertilization is known to promote N accumulation in bulk soil and aggregates (Tripathi *et al.* 2014). However, the distribution of N is governed by rotation-induced shifts in the aggregate size distribution (Chen *et al.* 2020). These two complementary mechanisms are consistent with our findings. In our study, the higher cumulative fertilizer N input in rotational systems serves as the primary driver for enhancing both TN storage and fertilizer N retention. Furthermore, crop rotation systems facilitate the maintenance and stability of N by promoting soil aggregation and fostering the formation of smaller size aggregates.

In summary, this study demonstrates that macroaggregates function as transient nitrogen reservoirs for short-term N supply and initial enrichment, whereas microaggregates act as persistent N sinks for long-term stabilization. Future research should focus on rhizosphere-mediated aggregate formation dynamics during crop growth periods. Furthermore, synchronizing topdressing with aggregate turnover dynamics and optimizing N application timing/splitting ratios present promising strategies for enhancing N use efficiency. Moreover, the nitrogen retention capacity of rotation systems validates their potential for mitigating agricultural non-point source pollution through cropping system optimization. Collectively, these findings provide a theoretical framework for designing and implementing sustainable cropping systems at a regional scale. They also offer evidence-based support for relevant policies, including "fertilizer reduction and efficiency improvement" and "farmland quality conservation".

5. Conclusion

Regulating fertilizer N retention by aggregates of various particle sizes over time in crop rotation systems was investigated through a 12-year rotational experiment using ^{15}N tracer technology. Initially, applied fertilizer N was enriched in macroaggregates. During the growing season, macroaggregates served as the primary source of N for plant uptake. As aggregates turned over, a "release old, store new" mechanism was observed. Fertilizer N was transferred into microaggregates due to the breakdown of larger aggregates. The microaggregates, with its higher physicochemical stability and slower turnover rate, was identified as the key site for the long-term stabilization of fertilizer N. The superior N retention in crop rotations is therefore attributed to this aggregate-mediated physical protection, which is enhanced under crop rotation. Crop rotation systems maintain the long-term retention and stability of soil N by promoting soil aggregation.

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Declaration of competing interest

The authors declare that they have no conflict of interest.

Declaration of generative AI and AI-assisted technologies in the writing process

The authors declare that they did not use AI in the preparation and writing of this manuscript.

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