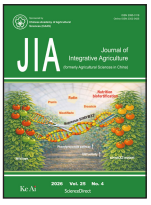
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RESEARCH ARTICLE

Straw returning and night-warming improve grain yield and nitrogen use efficiency of winter wheat under rice–wheat rotation

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Highlights

- More nitrogen (N) distribution in leaves boosts post-anthesis dry matter accumulation to improve grain yield.
- The enhancement of pre-anthesis N translocation ability is a key factor contributing to the improved N use efficiency.
- More root distribution within the topsoil layer and improved soil N-supply capacity enhance plant N uptake.

Abstract

Global climate warming is characterized by diurnal and seasonal asymmetry, with greater increases at nighttime and in winter and spring. Growing evidence has recognized that night-warming in winter and spring significantly impacts winter wheat production. Pre-crop straw returning is the principal method for straw utilization, but the interactions between straw returning and night-warming on wheat yield and N use efficiency (NUE) remain unclear. Here, a consecutive three-year field experiment with two straw treatments (S0, straw removal; S1, straw returning) and two warming treatments (W0, no warming control; W1, night-warming) found that both S1 and W1 improved wheat grain yield and NUE, with W1 exhibiting more pronounced improvements. Notably, the interaction between S1 and W1 (S1W1) further enhanced yield and NUE by 13.0 and 16.5%, respectively, compared to S0W0 through increasing grain number and 1,000-grain weight (three-year average). Additionally, root growth and topsoil inorganic N content decreased in S1 before jointing, thereby reducing plant dry matter and N accumulation. However, W1 exhibited an opposite trend, thereby mitigating these negative effects. Simultaneously, under S1W1, increased N translocation to grain and post-anthesis dry matter accumulation, driven by greater N distribution to leaves and higher N metabolism enzyme activity, enhanced both yield and NUE. This improvement was supported by better root morphology and biomass, particularly in the 0–40 cm soil layer, boosting plant N absorption. Additionally, elevated soil N-acquiring enzyme activity after jointing increased the net N mineralization rate and microbial biomass N, enhancing soil N-supply capacity. As a result, post-jointing inorganic N content rose in the 0–20 cm layer while decreasing at 20–60 cm, thus reducing the apparent N surplus. Collectively, straw returning, night-warming, and their interactions enhanced root distribution and N-supply capacity after jointing in the topsoil layer, thereby increasing plant N uptake and its translocation to grains, along with post-anthesis dry matter accumulation, ultimately improving grain yield and NUE.

Keywords: wheat, straw returning, night-warming, nitrogen use efficiency, root growth, soil nitrogen-supply capacity

1. Introduction

As one of the most important food crops worldwide, wheat plays a critical role in supporting global food security. Meeting the increasing food demand in the coming years will likely necessitate continued high nitrogen (N) fertilizer inputs to ensure food security (Hou *et al.* 2023). While increasing yield is crucial for food supply and economic growth, enhancing N use efficiency (NUE) can reduce environmental burdens and resource waste (Zhang *et al.* 2021; Schulte-Uebbing *et al.* 2022). Therefore, simultaneously increasing NUE

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and ensuring wheat yield is essential for sustainable wheat development both in China and globally (Bai *et al.* 2022).

Straw, often considered agricultural waste, poses a significant challenge in terms of its rational utilization, not only in China but globally (Ren *et al.* 2019). Straw returning stands out as the most scientifically sound method of straw utilization, playing a critical role in promoting sustainable agricultural development (Xu *et al.* 2018; Yu *et al.* 2024). In the North China Plain, Ling *et al.* (2024) reported that straw returning improved the average wheat productivity by 9.6−10.7% through enhancing the soil quality of the 0−40 cm layer in a maize–wheat cropping system. Similarly, a long-term study by Yang *et al.* (2023) revealed that upland soil water storage and inorganic N were increased under maize straw returning, thus causing a yield increase. So, the positive effects of straw on upland soil fertility (Latifmanesh *et al.* 2020) and crop yield (Zhang *et al.* 2022) have also been well-documented. Firstly, it serves as a valuable carbon source for microorganisms, leading to increased microbial N and organic N mineralization in the soil's tillage layer, ultimately improving soil N availability (Gai *et al.* 2019; Ren *et al.* 2023; Ling *et al.* 2024). Secondly, straw returning fosters root growth and enhances N uptake, consequently improving NUE and favoring high crop production (Wang Z *et al.* 2021; Gao *et al.* 2022). However, two common crop rotation patterns involving wheat are maize–wheat and rice–wheat, and the latter is predominant in the Yangtze River Basin and is also widely practiced in East and South Asia, providing a reliable food source for over 20% of the global population (Tian Z *et al.* 2024b). Unlike the maize–wheat rotation, where the soil tends to remain dry, the soil under the rice–wheat rotation undergoes constant cycles of wetting and drying (Ding *et al.* 2021). Jin *et al.* (2020) reported that the decomposition of rice straw is a slow and complex process influenced by climate and various other factors due to its high C/N ratio. This slow decomposition process can reduce soil N supply in the early stage of straw returning due to soil microbial N fixation, ultimately inhibiting the growth of wheat roots and shoots (Tian *et al.* 2019). Nonetheless, previous research has largely overlooked the effects of rice straw returning at different wheat growth stages in paddy soils; addressing this gap helps inform future scientifically grounded straw returning strategies.

Climate change, characterized by rising temperatures, is significantly impacting wheat production, posing a new challenge to food security (Abramoff *et al.* 2023). According to estimates, the global surface temperature is expected to rise by 1.5°C or more over the next 20 years (Seneviratne *et al.* 2018). Additionally, global warming exhibits noticeable asymmetries in diurnal and seasonal warming patterns, with greater temperature increases in winter and spring than in summer and autumn, and higher nighttime temperature rises than daytime ones (Giménez *et al.* 2021). Wheat is a warm- and cool-season crop, and these night-warming patterns are bound to have profound effects on wheat growth (Fan *et al.* 2024). The impact of night-warming on winter wheat production has already garnered significant research attention. Mamrutha *et al.* (2020) showed that increasing night temperatures before tillering reduced wheat biomass and tiller numbers, with no yield penalty. However, a study by Fan *et al.* (2024) found that night-warming enhanced grain yield by reducing frost damage and improving the development of young spikes and florets. Our previous research has also shown that pre-anthesis leaf growth and pro-anthesis photosynthetic capacity of flag leaves were facilitated under winter and spring night-warming, resulting in increased wheat grain yield (Fan *et al.* 2015; Hu *et al.* 2018). In addition, warming significantly improved root morphology, increased root biomass and root N concentration, and ultimately promoted root N uptake, thereby enhancing N utilization (Wang J *et al.* 2021; Xu *et al.* 2022). Thus, warming could regulate various transformations of N in the soil and supply to roots (Cai *et al.* 2023). For example, Hu *et al.* (2018) observed that night-warming increased the N uptake ability of wheat by improving root growth, ultimately increasing NUE. However, the focus has predominantly been on upland wheat (Fan *et al.* 2015; Hu *et al.* 2018), with limited understanding of the effects on winter wheat in paddy fields, especially within rice–wheat rotation systems.

Previous studies have shown that higher soil temperatures can accelerate straw decomposition by increasing the abundance of Actinobacteria and Firmicutes, thereby releasing more nutrients (Sain and Broadbent 1977; Zhou *et al.* 2016). A 10-year field experiment revealed that warming boosted soil organic carbon under chopped crop residue by accelerating fungal community turnover, an effect not observed with crop residue removal (Tian J *et al.* 2024). These findings suggested potential interactive effects between warming and straw management within the soil–crop system. For instance, in a two-year field experiment conducted on winter wheat–soybean rotation cropland, researchers observed that warming and straw application enhanced soil N turnover, leading to increased grain yield through augmented root biomass (Chen *et al.* 2021). Conversely, another study by Wu *et al.* (2022) in the North China Plain demonstrated that warming under straw returning inhibited root growth and post-anthesis dry matter transport, ultimately reducing wheat productivity. However, neither study considered the asymmetry in warming or the intricacies of straw return under the rice–wheat rotation. The primary objectives of this study were twofold: (1) to evaluate the impacts of straw returning and night-warming on wheat grain yield and NUE; and (2) to investigate the interaction effects on shoot N translocation, root growth, and soil N-supply capacity, all of which determine NUE. The outcomes of this research endeavor aim to offer a solid theoretical foundation for enhancing wheat yield and NUE simultaneously in the rice–wheat rotation system in China and, potentially, worldwide, particularly in the context of future climate change.

2. Materials and methods

2.1. Experimental site

A consecutive three-year wheat field experiment was conducted from 2020 to 2023 at the Research Farm of Nanjing Agricultural University, located in Liuhe, Nanjing, Jiangsu Province, China (32°23′N, 118°97′E). The experimental site falls within the Yangtze River Basin (YRB)

of China and has experienced long-term crop rotation with summer rice (from June to October) and winter wheat (from November to next May). This site is classified as having a subtropical monsoon climate, with an average annual precipitation of 1,243 mm and an average annual temperature of 16.5°C (Liu *et al.* 2016). The soil was identified as paddy soil, and the topsoil layer (0−20 cm) contained 1.10 g kg^{-1} of total N, 32.33 mg kg^{-1} of available phosphorus, 66.06 mg kg^{-1} of available potassium, and 23.97 g kg^{-1} of organic matter prior to sowing (three-year average). The daily average air temperature and precipitation during the three wheat seasons are shown in Fig. 1.

2.2. Experimental design

The winter wheat cultivar Yangmai 25 selected in this study is one of the most widely planted cultivars in YRB. Field experiments are divided into macro-plot experiments in 2020−2023 and micro-plot experiments in 2020−2021. The macro-plot experiment adopted a two-factorial design of two levels of straw treatment (S0, rice straw removal; S1, rice straw returning) and two levels of warming treatment (W0, no warming control; W1, night-warming), forming four treatments (S0W0, S0W1, S1W0, and S1W1). All treatments were arranged in a completely randomized block design with three replications, and the plot size was 2 m×4 m=8 m^2.

For rice straw returning, the amount of rice straw incorporated into the field was about 9,000 kg ha^{-1}. After the rice harvest, rice straw was first cut into 5−10 cm lengths and then tilled with a conventional tiller, in which the soil was tilled to a depth of about 25 cm and the straw incorporation was about 15−25 cm (Tian *et al.* 2019). For night-warming, we used a manually controlled movable plastic membrane based on passive night-warming technology. The setting and daily management of night-warming facilities are the same as those of Fan *et al.* (2015) and Hu *et al.* (2018). The tillering to booting stages of winter wheat mainly occurs in winter and spring (Hu *et al.* 2018), so we set up night-warming treatment during this period. In the night-warming treatment, a movable plastic film (approximately 0.01 mm thick) was used to cover the warming shed, which measures 4.2 m in length, 2.2 m in width, and 2 m in height. The plastic film was covered at sunset (18:00) and removed at sunrise (08:00) the next day. Each warming shed was equipped with fixed ventilation areas to minimize environmental differences between the inside and outside of the shed. To ensure that all plots receive the same amount of precipitation, the plastic film was uncovered during rainy and snowy nights. Canopy temperature and subsurface 5 cm soil temperature were monitored automatically every 10 min using a dual-channel LCD temperature instrument (NZ-LBR-F11, Nanjing Nengzhao Electronic Instrument Co., Ltd., China). During the consecutive three wheat seasons, the mean canopy temperature under night-warming was 1.46°C, 1.56°C, and 1.59°C higher than that of no-warming control, respectively (Fig. 1).

All macro-plot plots were fertilized with 240 kg N ha^{-1},

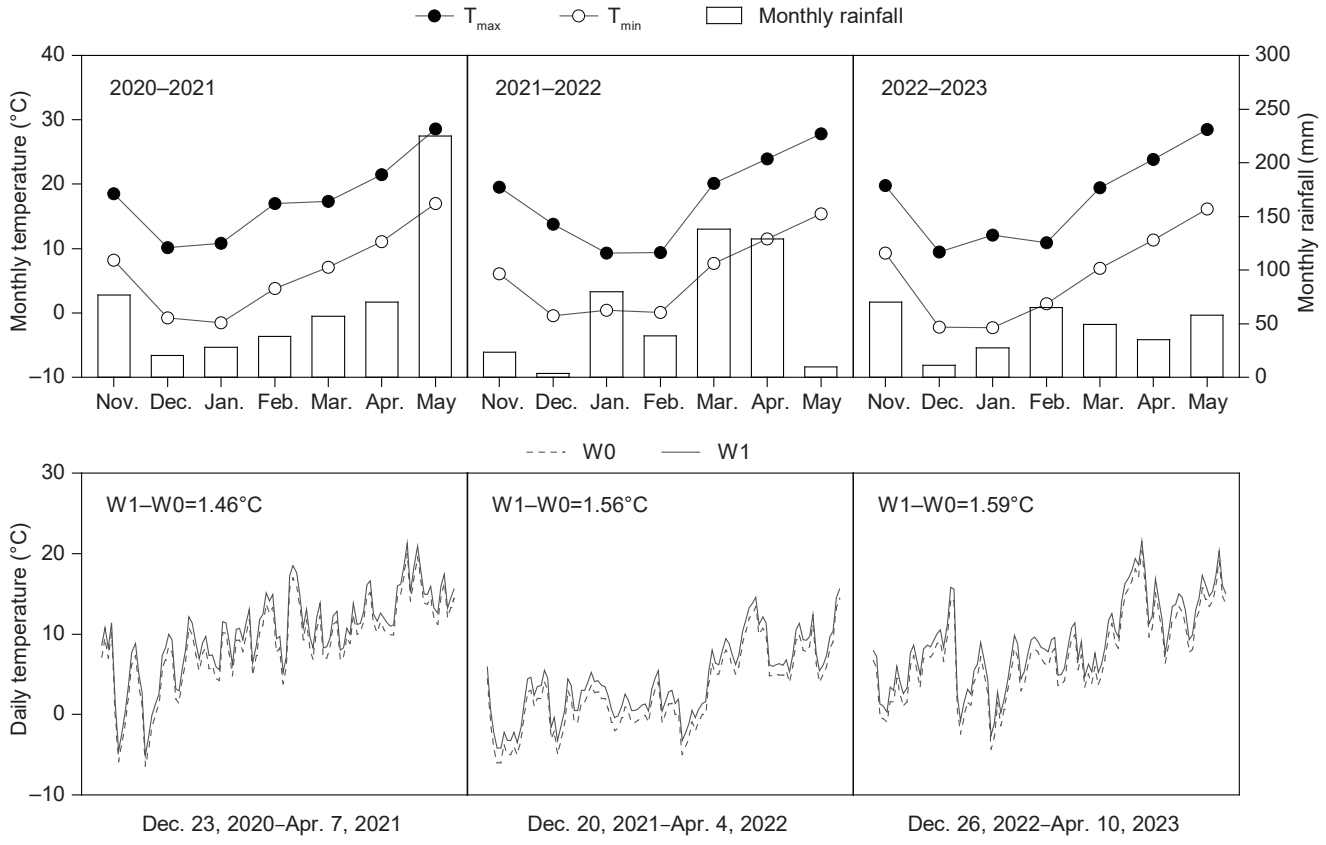


Fig. 1 Monthly mean temperature and monthly mean rainfall during the 2020−2023 wheat growing seasons in Nanjing, Jiangsu Province, China. T_{max} and T_{min}, maximum and minimum temperatures, respectively. W0, no warming control; W1, night-warming.

150 kg P_2O_5 ha^{-1}, and 150 kg K_2O ha^{-1} in the form of urea, superphosphate, and potassium chloride fertilizers, respectively. Half of N and all of P and K were applied as base fertilizer before sowing, and the other 30% of N and 20% of N were applied as top dressing before jointing and booting, respectively. A control plot receiving zero N was also included. Wheat sowing dates were Nov. 15, 2020, Nov. 13, 2021, and Nov. 7, 2022, respectively. The seeding density was 2.25 million seeds ha^{-1} with a spacing of 0.25 m between rows. Weeds, diseases, and pests were controlled consistent with Fan *et al.* (2023). Due to abundant rainfall in this region, all plots were irrigated by precipitation without additional irrigation, and drainage ditches were excavated around each plot to avoid later waterlogging at sowing. Other cultivation management measures are the same as those in the high-yield field. The experimental design of the micro-plot was the same as that of the macro-plot, and the experiment site distances were similar. Referring to the methods of Shi *et al.* (2012a), polyvinyl chloride (PVC) tubes with a diameter of 25 cm and a height of 105 cm were used to conduct micro-plots with the purpose of monitoring the growth of wheat roots and N fates at different growth stages. To ensure that soil conditions in the micro-plot experiment matached those of the macro-plot, the soil was excavated and backfilled in advance prior to wheat sowing (Hu *et al.* 2019).

2.3. Plant sampling methods and analysis

N accumulation At the jointing, anthesis, and maturity stages, 50 clums were sampled from each macro-plot, and the plants were separated into leaves, stems, chaffs, and grains (at maturity). The fresh samples were dried in a 105°C oven for 30 min to inactivate enzymes, and then dried at 70°C to a constant weight for dry weight determination. The dried samples were milled, and the total N content was determined by the semi-micro Kjeldahl method after H_2SO_4-H_2O_2 digestion. N accumulation amount (NAA) was calculated as follows (Tian Z *et al.* 2024a):

$$\text{NAA (kg ha}^{-1}\text{)}=\text{DMA}\times\text{NC} \quad (1)$$

where DMA is dry matter accumulation amount (kg ha^{-1}) and NC is N concentration (mg g^{-1} DM).

N translocation N translocation amount (NTA) and contribution rate of N translocation amount to grain (NTC) were calculated according to Tian *et al.* (2016):

$$\text{NTA (kg ha}^{-1}\text{)}=NAA_A-NAA_{MV} \quad (2)$$

$$\text{NTC (\%)}=\frac{\text{NTA}}{NAA_{MG}}\times 100 \quad (3)$$

where NAA_A (kg ha^{-1}) is NAA at anthesis, NAA_{MV} (kg ha^{-1}) is NAA of vegetative organs at maturity, and NAA_{MG} (kg ha^{-1}) is grain NAA at maturity.

Nitrate reductase (NR) and glutamine synthetase (GS) activity At the booting, anthesis, and grain-filling (14 days after anthesis) stages, fresh leaves were collected, rapidly frozen in liquid nitrogen, and stored at –40°C. A 0.3 g fresh sample was weighed, combined with an appropriate amount of quartz sand, and ground into a fine powder using a cryogenic grinder. Subsequently, 5 mL of extraction buffer (10 mmol L^{-1} cysteine, 1 mmol L^{-1} EDTA, 25 mmol L^{-1} phosphate buffer, pH 8.7) was added, and the mixture was homogenized thoroughly. Following centrifugation at 12,000×g and 4°C for 20 min, the supernatant was collected and designated as the crude enzyme extract. Nitrate reductase (NR) activity was assayed according to Baki *et al*. (2000). For this assay, 1 mL of the enzyme extract was mixed with 1.2 mL of 0.1 mol L^{-1} KNO3 and 0.4 mL of a 0.2% NADH solution. After thorough mixing, the reaction mixture was incubated at 25°C in a water bath for 1 h. A control was prepared by substituting the NADH solution with 0.4 mL of 0.1 mol L^{-1} phosphate buffer (pH 7.5). The enzymatic reaction was terminated by adding 1 mL of sulfanilamide solution, followed immediately by 1 mL of N-(1-naphthyl) ethylenediamine dihydrochloride solution. The mixture was allowed to develop color for 1 h and was then centrifuged at 4,000×g for 15 min; the absorbance of the resulting supernatant was measured at 540 nm. GS activity was determined following Zhang *et al*. (2000). A total of 1 mL of the enzyme extract was combined with 1 mL of reaction buffer (prepared by dissolving 12.323 g $MgSO_4$·$7H_2O$, 5.6133 g sodium glutamate monohydrate, 1.6535 g ATP-Na_2, 1.7019 g imidazole, and 6.949 g hydroxylamine hydrochloride in distilled water, with the final volume adjusted to 100 mL); for the control, distilled water was used in place of the reaction buffer. The mixture was incubated at 25°C for 20 min. The reaction was stopped by adding 1 mL of termination solution (prepared by dissolving 3.2976 g $FeCl_3$·$6H_2O$ and 8.17 g trichloroacetic acid in distilled water, with the final volume brought to 100 mL using 66.7 mL of 3 mol L^{-1} HCl solution). The terminated mixture was centrifuged at 10,000×g and 4°C for 10 min, and the absorbance of the supernatant was measured at 540 nm.

Root Root samples in microplots were collected at the jointing, anthesis, and maturity stages. Sampled roots were separated into 0−20, 20−40, 40−60, and 60−100 cm layers by washing off soil. Root length, root surface area, and root volume were measured digitally using a flatbed scanner (Epson, Jakarta, Indonesia) and analyzed using WinRhizo Pro 2013 software (Reagent Instruments, Inc., Canada). Then samples were placed in an oven at 105°C for 30 min and then dried at 70°C to a constant weight for root biomass. Root length density and root weight density were calculated for each soil layer according to Guo *et al.* (2019).

Grain yield and yield components In the macro-plot experiment, four rows of plants (1 m^2) were marked at the center of each plot, and these marked plants were not sampled before harvest. The plants were harvested at soil level by sickle at physiological maturity, and grain yield was determined assuming 14% moisture. Spikes m^{-2} were recorded in the marked area, and a total of 50 culms were sampled from the four central rows of each plot to determine grain number and grain weight.

NUE N recovery efficiency (NRE) and N agronomic efficiency (NAE) were calculated following previous studies (Tian *et al.* 2016):

$$\text{NRE (\%)}=\frac{NAA_M-NAA_{N0}}{\text{NAR}}\times 100 \quad (4)$$

$$\text{NAE (kg kg}^{-1}\text{)}=\frac{GY_N-GY_{N0}}{AN_S} \quad (5)$$

where NAA_M (kg N ha^{-1}) is NAA of N treatment at maturity,

NAA_{N0} (kg N ha^{-1}) is NAA of no N treatment at maturity, GY_N (kg grain ha^{-1}) is grain yield of N treatment, GY_{N0} (kg grain ha^{-1}) is grain yield of no N treatment, NAR (kg N ha^{-1}) is total N application rate, and AN_S (kg N ha^{-1}) is available N content of soil.

2.4. Soil sampling methods and analysis

Inorganic N content and apparent N surplus Soil samples were collected at five points in each plot using a soil auger to a depth of 60 cm (0−20, 20−40, and 40−60 cm) and thoroughly mixed to form a composite sample. The mixed soil was sealed in sterile bags by layer and immediately transported to the laboratory. After passing through a 2 mm sieve to remove debris such as straw, roots, and stones, the soil samples were stored in a 4°C refrigerator for further analysis. Soil NH_4^+-N and NO_3^--N contents were extracted with 0.5 mol L^{-1} K_2SO_4 and then measured by an automated continuous flow analyzer (Seal Autoanalyzer 3, Seal Analytical, Inc., Germany) (Hu *et al.* 2018). The sum of NH_4^+-N and NO_3^--N contents is the inorganic N content. Soil bulk density was determined using the cutting ring method, and soil water content was determined using the gravimetric method. The soil inorganic N accumulation (SNA) and soil apparent N surplus (SAN) were calculated as follows (Shi *et al.* 2012b; Hu *et al.* 2018):

$$\text{SNA (kg kg}^{-1}\text{)} = \frac{\text{ST}\times\text{BD}\times\text{SNC}}{10} \quad (6)$$

$$\text{SAN (kg ha}^{-1}\text{)} = \text{(Initial SNA+NAR)–(Residual SNA+NAA)} \quad (7)$$

where ST (cm) is soil thickness, BD (g cm^{-3}) is soil bulk density, SNC (mg kg^{-1}) is inorganic N content (NH_4^+-N and NO_3^--N), NAR (kg N ha^{-1}) is N application rate, and NAA (kg ha^{-1}) is N accumulation amount.

Net N mineralization rate (NMR) and microbial biomass N (MBN) The NMR was determined according to the methods of Zhang *et al.* (2019) with modifications. Fresh soil (10.0 g) was placed in a 100-mL plastic bottle with several small holes for ventilation. After adjusting the soil water content to 60% of the field capacity, the samples were placed in a 25°C incubator and incubated for 14 days. During the incubation period, the soil water content was adjusted every 2 days to maintain it at 60% of the field capacity. Soil NO_3^--N and NH_4^+-N contents were measured before and after incubation, and NMR was calculated based on the difference in NO_3^--N and NH_4^+-N contents before and after incubation. MBN was determined using the chloroform fumigation-K_2SO_4 extraction method, which was adapted from the method of Vance *et al.* (1987).

N-acquiring extracellular enzyme activity The determination of soil N-acquiring extracellular enzyme activity was conducted using fresh samples of 0−20 cm soil layer. β-1,4-acetylglucosaminidase (NAG) activity and leucine aminopeptidase (LAP) activity were determined according to the introduction of commercial colorimetric assay kits (Solarbio Science & Technology Co., Ltd., Beijing, China) (Shu *et al.* 2023; Xu *et al.* 2023). NAG catalyzed the decomposition of p-nitrophenyl-β-N-acetylglucosamine to p-nitrophenol, and p-nitrophenol exhibited a maximum absorption peak at 400 nm. The activity of NAG was then calculated by measuring the rate of change in absorbance using a UV-visible spectrophotometer (TU-1810, PRESEE, Beijing, China). LAP could catalyze the decomposition of L-leucine-pnitroanilide into p-nitroaniline, and p-nitroaniline has a maximum absorption peak at 405 nm. LAP activity was then calculated by measuring the rate of increase in absorbance with a UV-visible spectrophotometer.

2.5. Statistical analysis

For all data, the normal distribution and homogeneity of variances were determined by the Shapiro-Wilk test and Levene's test. All data were presented as means of three replicates. Statistical analysis was performed using SPSS version 24.0 (SPSS Inc., Chicago, IL, USA) with a two-way analysis of variance (ANOVA). Differences among treatments were compared using the least significant difference (LSD) test at a significance level of 5%. The graphics were generated using Origin Pro 2024.

3. Results

3.1. Grain yield and NUE

Grain yield, NAE, and NRE varied in response to the individual and combined effects of straw returning and warming (Fig. 2). Spike number was consistent across the four treatments, showing no significant variance. In contrast, grain number and 1,000-grain weight of S1 and W1 were enhanced relative to S0 and W0, respectively. Consequently, the grain yield of S1 and W1 increased 5.0–7.1% and 9.3–11.0% when compared to S0 and W0, respectively. Similarly, the NRE was enhanced by 4.9–7.9% under S1 and 9.3–10.6% under W1. And the NAE of S1 and W1 improved 6.1–12.0% and 15.6−19.3% relative to S0 and W0, respectively. A noteworthy interaction between straw and warming emerged, particularly in terms of grain yield, NAE, and NRE. Specifically, W1 improved yield by 6.0–8.5% under S0, whereas it increased by 12.0–13.4% under S1 compared to W0. The interaction effects further enhanced the NAE and NRE over three wheat growing seasons. These findings indicated that the benefits on yield and NUE were more pronounced for night-warming than for straw returning alone, and that the interaction between straw returning and night-warming further amplified the enhancements in grain yield and NUE.

3.2. Dry matter and N accumulation during different growth periods

Compared to S0, S1 reduced DMA and NAA from sowing to jointing, while it enhanced these metrics from jointing to anthesis and anthesis to maturity (Table 1). W1 improved the DAA and NAA compared to W0 before jointing, thus mitigating the negative impacts of S1. Moreover, the DAA increment of W1 (*vs.* W0) from anthesis to maturity (by 16.2%) was higher than that from jointing to anthesis (by 4.5%). However, the trend in NAA increment was entirely reversed. Additionally, the interaction between straw and warming significantly affected post-anthesis DMA, with W1 enhancing DMA by 10.0–13.2% under S0, and even more substantially, by 18.3–21.4% under S1. Meanwhile, NAA from jointing to anthesis

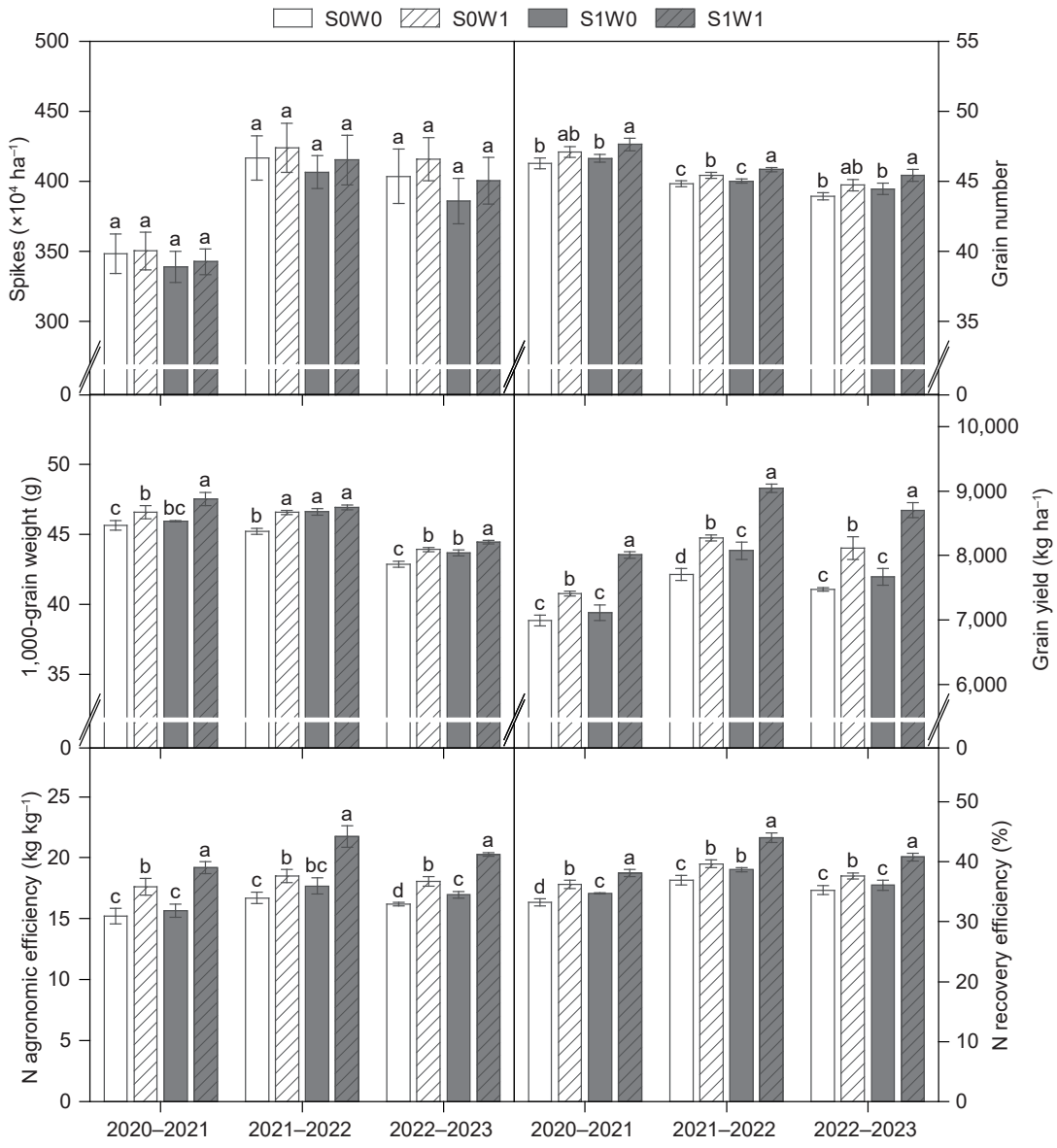


Fig. 2 Grain yield, yield components, N agronomic efficiency (NAE), and N recovery efficiency (NRE) affected by straw returning and night-warming during the 2020–2023 wheat growing seasons. S0, rice straw removal; S1, rice straw returning. W0, no warming control; W1, night-warming. Bars mean SE (n=3). Different lowercase letters indicate significant differences at P<0.05. The grain yield data presented in this figure were derived from a previous publication based on the same experiments (Hou *et al.* 2025).

and anthesis to maturity were affected by the interaction between straw returning and night-warming.

3.3. N translocation

The pre-anthesis N translocation amount of S1 and W1 improved by 9.1–13.0% and 21.6–23.2% when compared to S0 and W0, respectively (Fig. 3). And the interaction effects of straw and warming significantly impacted N translocation. Compared to W0, W1 improved the pre-anthesis N translocation amount by 14.6–17.3% under S0, and even more significantly, by 25.6–30.9% under S1. Therefore, the synergistic effect of straw returning and night-warming elevated the contribution rate of pre-anthesis N translocation amount to grain. Conversely, both S1 and W1 diminished the post-anthesis NAA compared to S0 and W0, respectively. The contribution rate of post-anthesis NAA to grain of S1 and W1 decreased by 10.6–14.2% and 18.7–23.5% compared to S0 and W0, respectively. These findings underscored the pivotal role of N translocation before anthesis in the accumulation amount of grain N.

3.4. N concentration and N distribution in different organs at anthesis

N concentration and distribution of leaf were affected, whereas those in the stem and spike remained unchanged (Table 2). Compared to S0, the leaf N concentration and distribution were increased by 3.5−6.1 and 8.3−8.5% in S1, respectively. Compared to W0, the leaf N concentration and distribution were enhanced 5.1−7.8 and 12.8−15.0% in W1, respectively. Notably, under S0, W1 led to a 2.47% increase

Table 1 Effects of straw returning and night-warming on dry matter and N accumulation during the 2020−2023 wheat growing seasons

Treatment[1)]	Dry matter accumulation (kg ha^{-1})[2)]			N accumulation (kg ha^{-1})[2)]		
	S−J	J−A	A−M	S−J	J−A	A−M
2020−2021						
S0W0	2,722 a	7,931 c	5,000 d	53.54 a	85.26 c	56.44 a
S0W1	2,770 a	8,221 b	5,505 b	54.87 a	103.0 b	53.66 a
S1W0	2,459 b	8,296 b	5,181 c	48.37 b	100.3 b	53.63 a
S1W1	2,765 a	8,740 a	6,292 a	54.48 a	124.9 a	45.24 b
2021−2022						
S0W0	2,986 b	8,878 c	5,657 d	58.96 b	102.9 c	61.21 a
S0W1	3,096 a	9,302 b	6,403 b	60.99 a	123.5 b	54.36 b
S1W0	2,764 c	9,556 b	6,029 c	52.23 c	114.8 b	58.97 ab
S1W1	3,045 ab	9,921 a	7,134 a	60.11 ab	149.0 a	47.17 c
2022−2023						
S0W0	2,874 b	8,575 b	5,416 d	64.70 b	91.49 c	60.18 a
S0W1	3,032 a	8,933 ab	6,085 b	68.04 a	106.9 b	57.30 a
S1W0	2,613 c	9,038 ab	5,657 c	59.02 c	102.1 bc	58.00 a
S1W1	2,998 a	9,494 a	6,852 a	67.27 a	131.1 a	49.93 b

[1)] S0, rice straw removal; S1, rice straw returning. W0, no warming control; W1, night-warming.
[2)] S, J, A, and M refer to the winter wheat growth periods of sowing, jointing, anthesis, and maturity, respectively.
Different lowercase letters following the date in the column indicate significant differences at P<0.05.

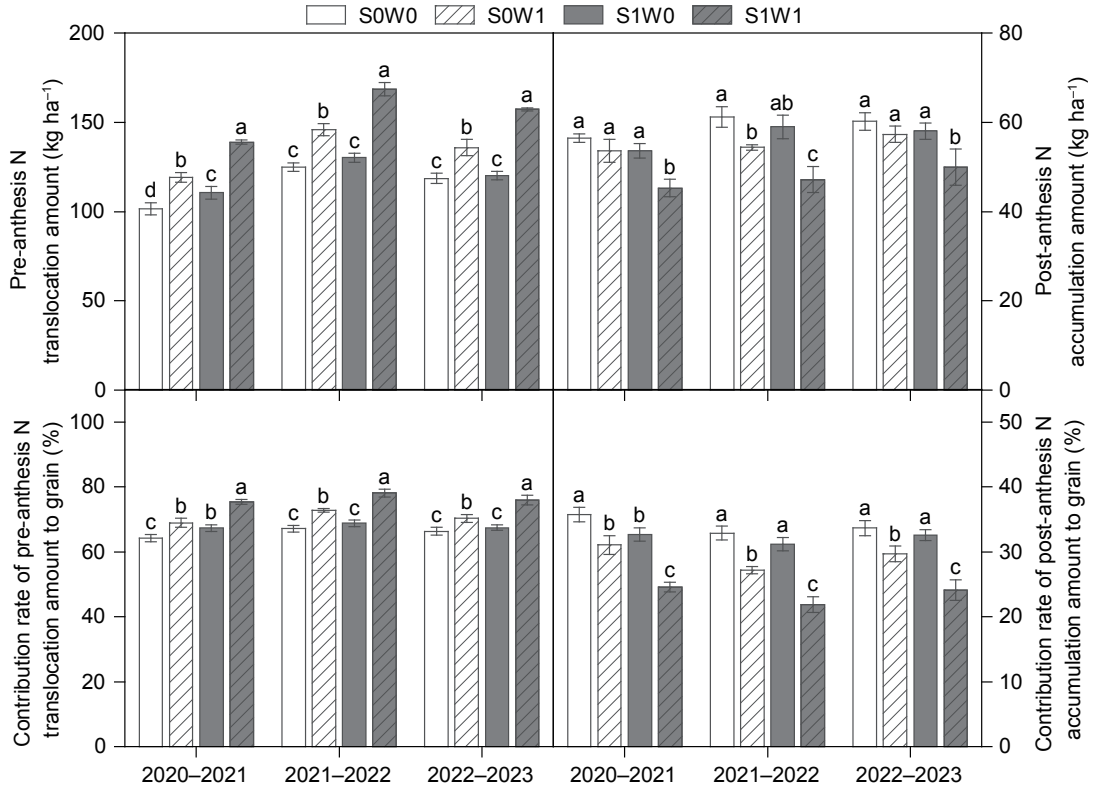


Fig. 3 N translocation affected by straw returning and night-warming during the 2020−2023 wheat growing seasons. S0, rice straw removal; S1, rice straw returning. W0, no warming control; W1, night-warming. Bars mean SE (n=3). Different lowercase letters indicate significant differences at P<0.05.

in leaf N concentration on average over two years, and a more substantial increase of 10.4% was observed under S1. Moreover, W1 enhanced leaf N distribution by 10.1–11.1% under S0 and by an even greater margin of 14.3–19.7% under S1. As previously mentioned, the enhancement of leaf N concentration and distribution at anthesis is crucial for facilitating post-anthesis N assimilation.

3.5. Enzyme activity of NR and GS

Both S1 and W1 were observed to enhance the activities of NR and GS compared to S0 and W0, respectively (Fig. 4). Meanwhile, under S0, W1 increased NR and GS activities by 11.7 and 9.5%, respectively, while under S1, these enhancements were more pronounced at 21.5% for NR and 18.0% for GS at the booting stage. Likewise, at anthesis, W1

led to a 15.0% increase in NR activity and a 20.0% increase in GS activity under S0, whereas under S1, the increases were 8.7% for NR and 15.9% for GS compared to W0, respectively. However, the same interaction effect as before was not observed at filling.

3.6. Root morphology, biomass, and distribution

At jointing, compared to S0, the root length, surface area, volume, and biomass were reduced by 5.5, 6.6, 5.2, and 7.2% in S1, respectively (Table 3). Conversely, W1 led to improvements in both root morphology and biomass at the jointing and anthesis stages when compared to W0. Specifically, at jointing, there were increases of 11.2% in length, 6.5% in surface area, 8.0% in volume, and 9.1% in biomass, and at anthesis, the increases were 11.0% in length, 15.3% in surface area, 11.4% in volume, and 12.3% in biomass. Furthermore, the interaction between straw and warming influenced root morphology and biomass at both stages, except for root volume. The spatial and temporal distribution of the root system, including root length density and weight density within the top 0−20 cm soil layer, showed significant variations across all treatments (Fig. 5). At jointing, root length density and weight density were lower under S1 than under S0, whereas both parameters were higher under W1 than under W0. However, both S1 and W1 enhanced root distribution in the top soil at the anthesis and maturity stages. Additionally, the root distribution within the 20–40 cm soil layer at anthesis

Table 2 Effects of straw returning and night-warming on N concentration and N distribution in different organs at anthesis during the 2020−2022 wheat growing seasons

Treatment[1)]	N concentration (g kg^{-1} DW)			N distribution (mg/culm)		
	Leaf	Stem	Spike	Leaf	Stem	Spike
2020−2021						
S0W0	30.92 c	10.07 a	16.48 a	16.17 c	13.71 a	8.53 b
S0W1	32.12 b	10.14 a	16.60 a	17.81 b	13.51 a	9.03 ab
S1W0	31.61 bc	10.22 a	16.50 a	16.77 c	13.30 a	8.62 b
S1W1	35.28 a	10.51 a	16.59 a	20.07 a	13.27 a	9.57 a
2021−2022						
S0W0	36.55 b	11.41 a	18.73 a	16.85 c	12.17 b	9.14 a
S0W1	36.94 b	11.53 a	18.51 a	18.73 b	12.95 a	9.18 a
S1W0	36.37 b	11.50 a	19.18 a	18.01 c	12.42 ab	9.59 a
S1W1	39.72 a	11.67 a	19.28 a	20.58 a	12.67 ab	9.72 a

[1)] S0, rice straw removal; S1, rice straw returning. W0, no warming control; W1, night-warming.
Different lowercase letters following the date in the column indicate significant differences at P<0.05.

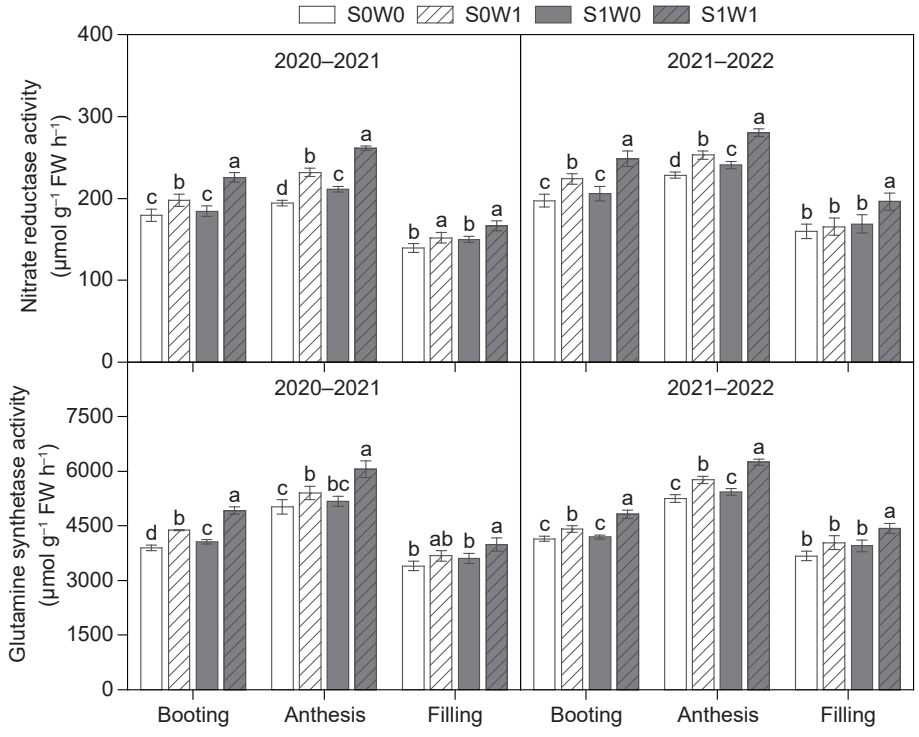


Fig. 4 Enzyme activity of nitrate reductase (NR) and glutamine synthetase (GS) of flag leaves affected by straw returning and night-warming during the 2020−2022 wheat growing seasons. S0, rice straw removal; S1, rice straw returning. W0, no warming control; W1, night-warming. Bars mean SE (n=3). Different lowercase letters indicate significant differences at P<0.05.

Table 3 Effects of straw returning and night-warming on root morphology and biomass in the 0−100 cm layer during the 2020−2021 wheat growing seasons

Treatment[1)]	Root length (m/pot)		Root surface area (cm^2/pot)		Root volume (cm^3/pot)		Root biomass (g/pot)	
	Jointing	Anthesis	Jointing	Anthesis	Jointing	Anthesis	Jointing	Anthesis
S0W0	116.1 b	244.3 c	1,715 b	4,219 d	10.54 b	30.35 c	7.73 bc	17.28 c
S0W1	122.9 a	265.6 b	1,909 a	4,790 b	11.56 a	33.34 b	8.73 a	18.32 b
S1W0	104.1 c	252.4 c	1,679 b	4,488 c	10.16 b	32.13 bc	7.45 c	17.69 c
S1W1	121.9 a	286.1 a	1,705 b	5,248 a	10.80 ab	36.27 a	7.83 b	20.96 a

[1)] S0, rice straw removal; S1, rice straw returning. W0, no warming control; W1, night-warming.
Different lowercase letters following the date in the column indicate significant differences at $P<0.05$.

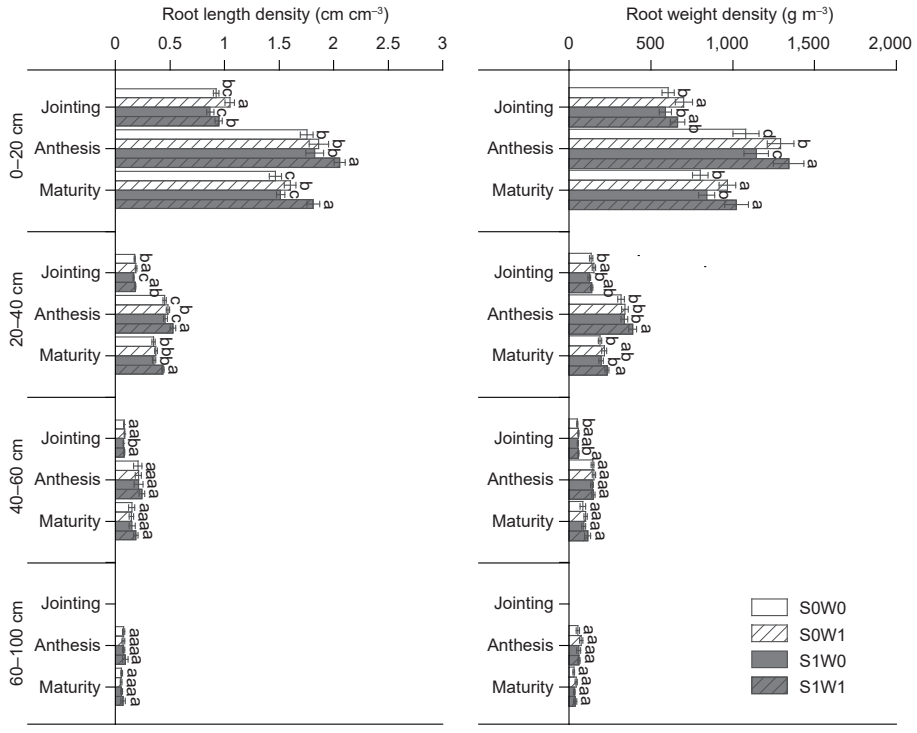


Fig. 5 Root length density and root weight density at jointing, anthesis, and maturity in the 0–100 cm layer affected by straw returning and night-warming during the 2020–2021 wheat growing seasons. S0, rice straw removal; S1, rice straw returning. W0, no warming control; W1, night-warming. Bars mean SE (n=3). Different lowercase letters indicate significant differences at $P<0.05$.

also showed improvements under both S1 and W1 compared to S0 and W0, respectively.

3.7. Soil NMR and MBN

The trends in NMR and MBN were consistent across different growth stages (Fig. 6). At overwintering, the NMR and MBN of S1 decreased 8.7 and 4.9% compared to S0. Inversely, S1 led to an increase in NMR by 7.7% at jointing and 12.0% at anthesis. Similarly, MBN saw increments of 5.0% at jointing and 12.2% at anthesis. Across all stages, W1 resulted in higher NMR and MBN compared to W0. Meanwhile, there were significant interactions between straw and warming on NMR and MBN.

3.8. Soil NAG activity and LAP activity

NAG and LAP activities were higher under S1 than under S0 at the jointing and anthesis stages, but not at the overwintering stage (Fig. 7). W1 consistently increased the NAG and LAP activity across various growth stages over two seasons. It was also noted that the activities of these two extracellular enzymes were affected by the combined effects of straw and warming.

3.9. Soil inorganic N content

The inorganic N content within the 0−60 cm soil depth exhibited variations across different seasons and growth stages over the two seasons (Fig. 8). Compared with S0, S1 led to a reduction in inorganic N content in the 0–20 cm layer from sowing to jointing (120 days after sowing (DAS)), but thereafter enhanced inorganic N content. The inorganic N content in the 0–20 cm depth was higher under W1 than under W0 from overwintering (60 DAS) to anthesis (160 DAS) across two wheat seasons. In contrast, at depths of 20–60 cm, the inorganic N content of S1 was consistently lower than under S0 at all stages. And W1 also decreased the inorganic N content from overwintering to anthesis relative to

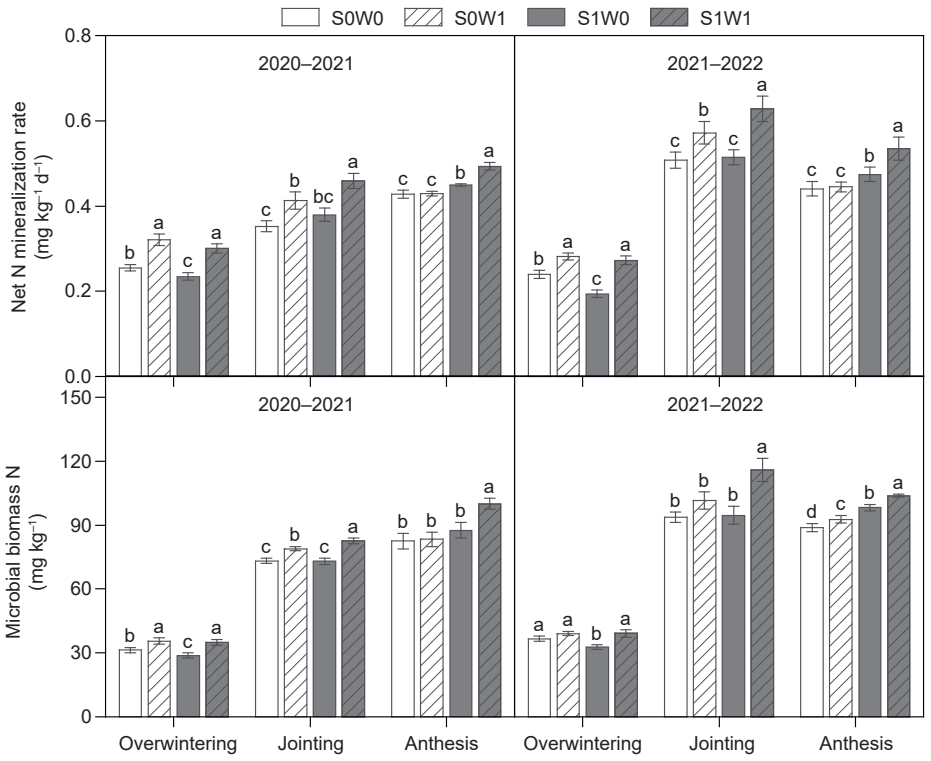


Fig. 6 Soil net N mineralization rate and microbial biomass N in the 0−20 cm layer affected by straw returning and night-warming during the 2020−2022 wheat growing seasons. S0, rice straw removal; S1, rice straw returning. W0, no warming control; W1, night-warming. Bars mean SE (n=3). Different lowercase letters indicate significant differences at P<0.05.

W0 in the 20–40 cm and 40–60 cm layers.

3.10. Apparent N surplus of soil–wheat system

In the soil–wheat system, the soil N balance was found to be in surplus from sowing to jointing and jointing to anthesis, while conversely, the soil N balance shifted to a deficit from anthesis to maturity (Table 4). The apparent N surplus from sowing to jointing of S1 increased 19.3% when compared to S0; however, S1 led to a reduction in the N surplus from jointing to anthesis and anthesis to maturity by 40.2 and 33.7%, respectively. Meanwhile, W1 reduced the soil N surplus from sowing to jointing and jointing to anthesis by 22.5 and 15.9%, respectively. A significant interaction effect for the N surplus between straw and warming was identified exclusively from sowing to jointing. Additionally, the interactions revealed noticeable differences in the apparent N surplus from sowing to maturity. W1 reduced the N surplus by 11.8–17.9% under S0, while under S1, the reduction was more pronounced, ranging from 32.1 to 37.8% relative to W0.

4. Discussion

4.1. Straw returning interacting with night-warming increased wheat yield

The temperature increase observed in this study fell between 1.46°C–1.59°C (Fig. 1), aligning closely with anticipated future climate warming scenarios under the 2015 Paris Agreement (Rose *et al.* 2017). Current studies on the effects of warming on wheat yields rarely consider the asymmetry of warming. Meanwhile, the impact of rice straw returning on wheat growth remains a contentious issue, likely due to regional variations in straw production, returning methods, and N application rates (Jin *et al.* 2020; Yu *et al.* 2024). In the present study, S1 and W1 enhanced yield caused by the improvement of grain number and grain weight when compared to S0 and W0, respectively (Fig. 2). Our recent study further supports the above view; Yu *et al.* (2024) reported that straw returning by ploughing could enhance wheat yield through an increase in grain number and 1,000-grain weight. Others have shown that straw return and night-warming could also increase grain number (Fan *et al.* 2022) and 1,000-grain weight (Li *et al.* 2020) by promoting the initiation of spikelets and florets. In addition, the degeneration of spikelets and florets was also related to soil inorganic N level; thus, S1 and W1 may enhance the soil mineral N at post-jointing to inhibit degradation. In contrast, Wu *et al.* (2022) found that warming reduced yield. This could be ascribed to the fact that whole-season warming can accelerate leaf senescence and inhibit post-anthesis photosynthetic capacity. Additionally, the formation of grain weight is predominantly attributed to the translocation of dry matter before anthesis and the accumulation of dry matter after anthesis, with the latter contributing to 60–80% of grain yield. Our findings further suggest that grain yield increased under the interactive effects of S1 and W1, primarily due to increases in grain number and grain weight. There was another reason that may explain the underlying mechanisms of this interaction. Enhancements in NAE are primarily attributed to improvements in grain yield (Ayadi *et al.* 2016).

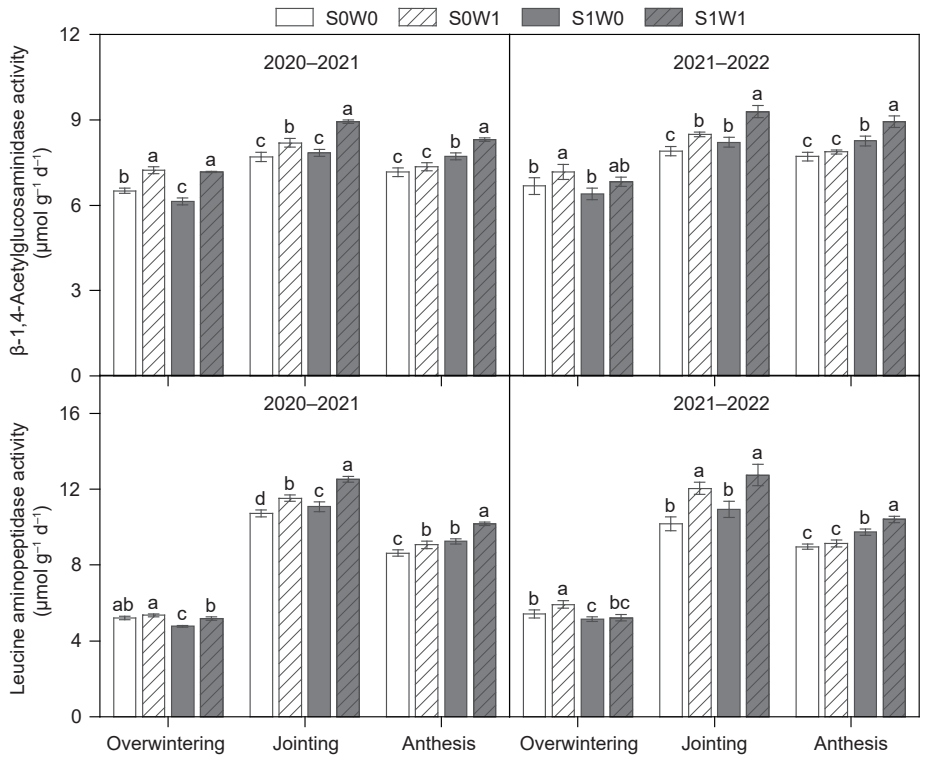


Fig. 7 Soil β-1,4-acetylglucosaminidase (NAG) activity and leucine aminopeptidase (LAP) activity in the 0–20 cm layer affected by straw returning and night-warming during the 2020−2022 wheat growing seasons. S0, rice straw removal; S1, rice straw returning. W0, no warming control; W1, night-warming. Bars mean SE (n=3). Different lowercase letters indicate significant differences at P<0.05.

Studies by Fan *et al.* (2015) and Hu *et al.* (2019) have shown that winter and spring night-warming improved DMA rate from jointing to anthesis and photosynthetic ability, thereby benefiting the NAE. In this study, the combined effect of S1 and W1 (S1W1) facilitated an increase in post-anthesis DMA (Table 1). Moreover, leaf N concentration, which is involved in photosynthesis, significantly influences photosynthetic carbon fixation and overall plant productivity (Tian *et al.* 2016; Lian *et al.* 2023; Hou *et al.* 2024). The increase in leaf N concentration under S1W1 at anthesis promoted N partitioning to the leaves, which is more favorable for photosynthesis (Table 2). Therefore, this enhanced leaf N distribution and accumulation of dry matter after anthesis under straw returning, combined with night-warming, provides a robust foundation for the efficient translocation of photosynthetically assimilated products, ultimately culminating in an increased yield.

4.2. Higher pre-anthesis N uptake and translocation capacity is key to improved N efficiency

The NRE of wheat crucially depends on its ability to accumulate, translocate, and distribute N effectively. Our results clearly demonstrated that the NRE of S1 and W1 was higher than S0 and W0, respectively (Fig. 2), which is similar to previous findings (Hu *et al.* 2019; Tian *et al.* 2019; Yu *et al.* 2024). And the combination of S1 and W1 further improved NRE (Fig. 2). There were several reasons that may explain the underlying mechanisms. Firstly, most studies have indicated that 70−90% of grain N in wheat originates from the remobilization of N stored in vegetative organs before anthesis (Kong *et al.* 2016). Thus, enhancing the pre-anthesis N accumulation in vegetative organs and N translocation ability are vital for boosting NRE (Ni *et al.* 2022). In our study, S1W1 significantly increased N accumulation from jointing to anthesis, thus establishing the groundwork for N translocation (Table 1). Moreover, we observed an increase in both the amount of N translocated and the contribution of pre-anthesis N translocation to grain N under S1W1 (Fig. 3). It is easy to understand this observation, Tian *et al.* (2016) also found that the increased absorption and translocation of N before anthesis in modern wheat cultivars are essential for ensuring high yield and N efficiency. Secondly, previous research has highlighted the crucial role of enzymes involved in N assimilation in crop N utilization (Thomsen *et al.* 2014). N is mainly carried out through the GS/GOGAT cycle pathway, and the increase of GS and NR can promote the absorption and utilization of N by plants (Xu *et al.* 2012). Notably, our findings indicated that S1W1 significantly increased NR and GS at the booting and anthesis stages (Fig. 4), thereby enhancing the assimilation ability of flag leaves to NO_3^--N and NH_4^+-N, which was beneficial to N absorption and utilization of winter wheat.

4.3. A fortified root system in the topsoil played a crucial role in augmenting plant N uptake

As the primary organ responsible for N uptake and utilization, the growth, morphology, and spatial distribution of the root play a crucial role in wheat yield and NUE (Xu *et al.* 2016; Yu *et al.* 2024). Previous studies have demonstrated that

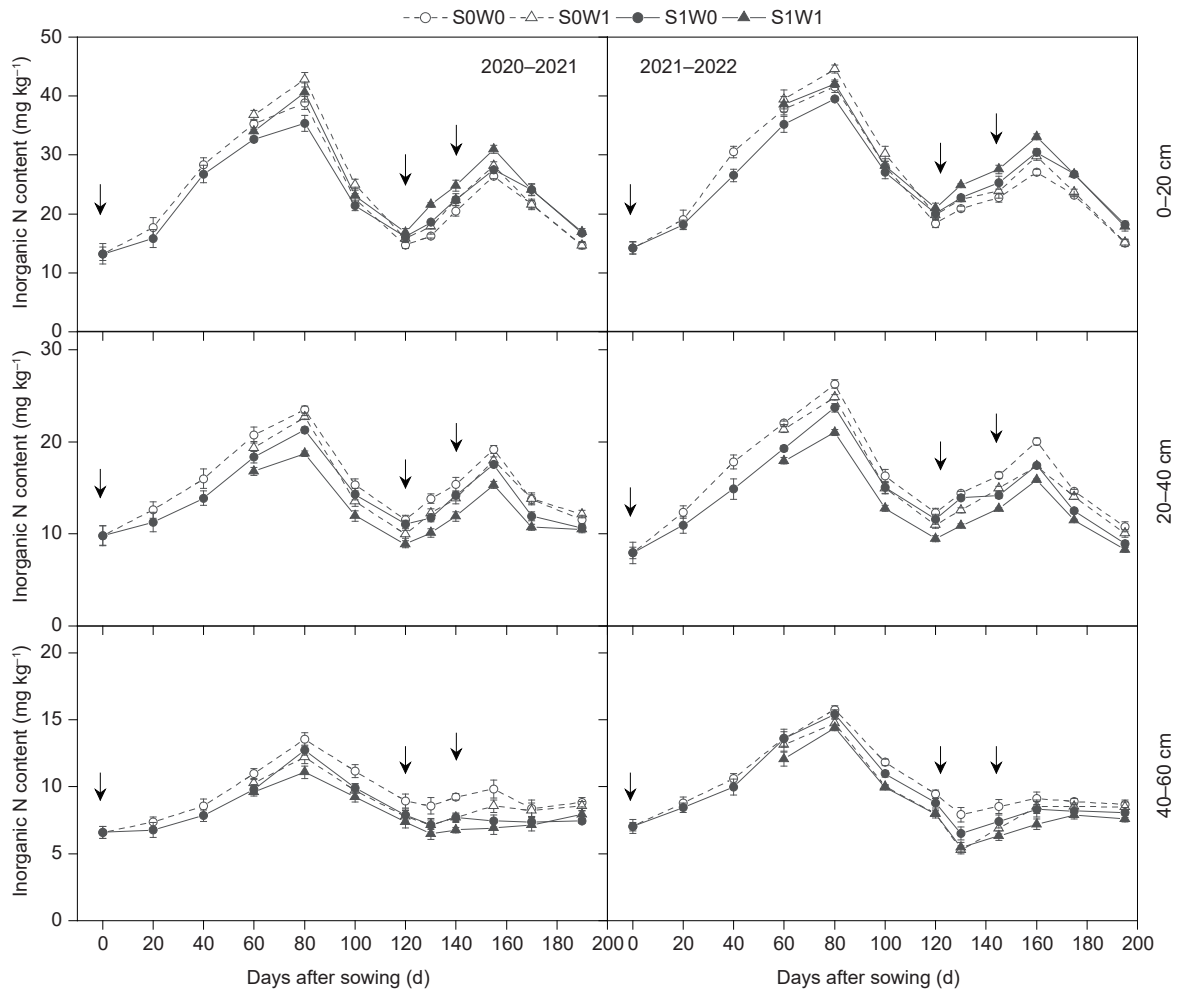


Fig. 8 Inorganic N content in the 0–20, 20–40, and 40–60 cm layers affected by straw returning and night-warming during the 2020–2022 wheat growing seasons. S0, rice straw removal; S1, rice straw returning. W0, no warming control; W1, night-warming. Arrows indicate basal fertilization and topdressing time. Bars mean SE (n=3).

Table 4 Effects of straw returning and night-warming on apparent N surplus (kg ha^{-1}) of soil–wheat system during the 2020−2022 wheat growing seasons

Treatment[1)]	2020–2021[2)]				2021–2022[2)]			
	S–J	J–A	A–M	S–M	S–J	J–A	A–M	S–M
S0W0	15.15 b	15.97 a	–6.22 b	24.90 a	13.11 b	14.55 a	–8.58 b	19.08 a
S0W1	13.25 d	14.66 a	–5.96 b	21.95 b	11.05 c	12.85 b	–8.24 b	15.66 b
S1W0	20.66 a	9.01 b	–3.25 a	26.42 a	16.13 a	10.70 c	–6.36 a	20.47 a
S1W1	14.37 c	7.03 c	–3.46 a	17.94 c	11.71 c	7.71 d	–6.68 a	12.74 c

[1)] S0, rice straw removal; S1, rice straw returning. W0, no warming control; W1, night-warming.
[2)] S, J, A, and M refer to the winter wheat growth periods of sowing, jointing, anthesis, and maturity, respectively.
Different lowercase letters following the date in the column indicate significant differences at P<0.05.

enhancing root morphology and optimizing its distribution across soil layers significantly enhanced N uptake capacity (Tian *et al.* 2018; Yu *et al.* 2024). Our research found that S1 before jointing inhibited root development, leading to marked declines in root morphology such as length, surface area, and volume (Table 3). This suppression could be attributed to the slow decomposition of rice straw during the initial phase of straw returning, which diminished the availability of inorganic N in the soil due to microbial immobilization (Tian *et al.* 2019). The root morphology of wheat at anthesis is an important factor determining the aboveground growth. We noted that root biomass and morphology of anthesis of S1 and W1 were higher than S0 and W0, respectively (Table 3). Additionally, we observed that their interaction (S1W1) further increased root biomass and morphology, thereby enhancing plant N uptake. These outcomes align with the findings of Yu *et al.* (2024) and Hu *et al.* (2019), who observed that both straw returning and night-warming fostered root system expansion, enhancing the recovery of ^{15}N-fertilizer and minimizing its losses. This

effect can be attributed to two main factors: firstly, this practice directly stimulated the root mycorrhizal colonization rate and soil respiration rate near the root system, thereby increasing the ability of the root system to absorb inorganic N (Heinemeyer *et al.* 2004). Secondly, S1W1 accelerated microbial metabolic activity, leading to a rise in inorganic N content (Fig. 8). The spatial and temporal distribution of wheat root systems plays a pivotal role in the plant's ability to access water and nutrients, directly influencing its growth, yield, and overall resilience to environmental stresses (Hu *et al.* 2020; Ober *et al.* 2021). Tian *et al.* (2020) reported that the middle and lower roots become more active than the upper roots as the growth process of wheat progresses. Additionally, the distribution of roots in deeper soil layers could delay root senescence by reducing the oxidation rate of the cell membrane and prolonging root vitality (Shi *et al.* 2012a; Xu *et al.* 2018; Li *et al.* 2022). However, our analysis of root spatiotemporal distribution revealed that S1W1 had a significant enhancement in the distribution of 0–40 cm layer roots at anthesis, with no variation in deep (40–100 cm) roots (Fig. 5). The variation in these results could be attributed to the following two reasons. On one hand, straw was returned to the soil at a depth of 15–25 cm in this study, and the paddy soil underwent continuous wet–dry cycles in YRB, thereby providing a stable environment for the middle to upper roots (Calleja-Cabrera *et al.* 2020; Ding *et al.* 2021). On the other hand, the typically shallow tillage layer of rice paddies may inhibit the downward growth of roots (Zheng *et al.* 2021; Liang *et al.* 2023). Guo *et al.* (2019) also discovered that an N-efficient wheat cultivar could allocate more photosynthates to the roots, thereby extending root distribution within the soil. In summary, a fortified root system in the topsoil at anthesis, by enhancing overall root morphology and biomass, plays a crucial role in augmenting plant N uptake, thereby contributing to heightened N efficiency.

4.4. Straw returning combined with night-warming decreased the apparent N surplus of the soil–wheat system

Xue *et al.* (2024) employed ^{15}N isotope-labeled fertilizer and discovered that 45–51% of the total N accumulation in wheat plants originated from ^{15}N fertilizer, while 49–55% was derived from soil N. Therefore, further stimulating the contribution of soil native N to plants could potentially enhance plant N efficiency. Soil N-supply capacity can be directly reflected by the inorganic N content, or indirectly measured by the NMR and microbial biomass N, which turn over rapidly and can more accurately characterize soil N availability (Hartmann *et al.* 2014; Li *et al.* 2019). In this study, S1W1 increased NMR, microbial biomass N, and N-acquiring extracellular enzyme activity at the jointing and anthesis stages (Figs. 6 and 7). This has also been confirmed by Peng and Wang (2016), the variability in soil extracellular enzyme activity was more effectively explained by edaphic abiotic factors than soil biotic factors. Furthermore, the inorganic N content in the 0−20 cm layer was enhanced under S1W1 after jointing (Fig. 8), which helped improve soil N supply. However, an increase in soil inorganic N content may elevate the risk of N leaching and gaseous N losses (ammonia and nitrous oxides), exacerbating N depletion while harming the ecological environment (Wu *et al.* 2021). Our study observed contrasting trends in inorganic N content between the 0–20 and 20−60 cm soil depths (Fig. 8). And S1W1 significantly reduced the inorganic N content at the overwintering stages and from jointing to anthesis (Fig. 8), indicating a marked reduction in inorganic N leaching losses, likely due to straw improving the interception of inorganic N. Nonetheless, the emission of gaseous N from the soil is an undeniable factor in N loss, especially in paddy fields (Chen *et al.* 2015). In terms of the soil apparent N surplus of the soil–wheat system, we observed a decrease in apparent N surplus throughout the growing season under S1W1 (Table 4). This may be because of the decrease in inorganic N content in the 20–60 cm layer and increased plant N accumulation. Similarly, Zhou *et al.* (2022) found that increased soil quality could bolster soil N supply ability and elevate plant N absorption, further decreasing the apparent N surplus. Our research indicated that rice straw returning primarily benefits the post-jointing growth of wheat, which may reduce the need for topdressing N fertilizer, allowing straw-derived N to partially substitute for N fertilizer in the future.

5. Conclusion

Our findings demonstrate that both straw returning and night-warming enhanced grain yield and NUE, with their combined application producing markedly greater enhancements than either treatment alone. This enhancement is underpinned by a broader root distribution at anthesis and an augmented post-jointing soil N-supply capacity in the topsoil layer, which collectively boosted the plant's N uptake capacity. The enhanced N uptake subsequently promoted post-anthesis DMA and pre-anthesis N translocation, thereby elevating yield and NUE. Furthermore, the combined influence of straw returning and night-warming reduced inorganic N content in the 20–60 cm soil, decreasing apparent N surplus of the soil–wheat system and ultimately minimizing N loss. Moving forward, straw returning stands out as the most rational and effective strategy for straw utilization under global climate warming, demonstrating evident benefits for enhancing grain yield and N efficiency in wheat under rice–wheat rotation.

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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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