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Effects of Straw Return with Nitrogen Fertilizer Reduction on Rice (*Oryza sativa* L.) Morphology, Photosynthetic Capacity, Yield and Water–Nitrogen Use Efficiency Traits under Different Water Regimes

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Abstract: The sustainability of rice (*Oryza sativa* L.) cultivation has been threatened by water deficit and nitrogen (N)-fertilizer abuse. Straw return combined with N-fertilizer reduction could be an effective agronomic practice to improve N-use efficiency in rice production, but the interaction with water-saving irrigation regimes remains largely unknown. Here, a 2-year paddy field experiment was conducted to elucidate the effects of irrigation regime (continuously flooded, CF; controlled irrigation and drainage, CID) and straw return with N reduction (conventional farmers' fertilization practice of 300 kg N ha^{-1} without straw return, N300; straw return with 25% N reduction, SN225; straw return with 50% N reduction, SN150) on rice growth dynamics, grain yield and water–nitrogen utilization. The results showed that CID significantly affected photosynthesis and fluorescence indicators, and increased grain yield and water productivity of rice. Straw return with N reduction reduced most rice growth traits, exhibiting lower plant height, tillers, leaf photosynthesis, chlorophyll fluorescence and dry matter accumulation, especially in vegetative growth under CF. In contrast, SN225 under CID showed compensatory effects on photosynthetic and fluorescence traits, thus improving N uptake during the reproductive growth stage. Despite a 6.6–7.1% yield reduction in SN225, 25% of N-fertilizer input was saved, with a corresponding increase in internal N-use efficiency and N-partial factor productivity. Overall, the present study indicates that straw return combined with moderate N deficiency might be a more eco-friendly and sustainable agronomic practice in water-saving irrigated rice fields.

Keywords: rice (*Oryza sativa* L.); water productivity; photosynthesis; chlorophyll fluorescence; dry matter; nitrogen uptake; alternate wetting and drying

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1. Introduction

Rice (*Oryza Sativa* L.) is a staple food for more than half of the world's population [1]. Approximately 75% of rice production comes from lowland rice systems under continuous flooding conditions [2,3], consuming one-third of the world's available freshwater for irrigation [4]. Water reserves are diminishing amid rapid urbanization and industrialization, and water scarcity under climate change further threatens the stability of rice production. It is estimated that, by 2030, global rice production will need to be increased by 70% to feed the growing world population [5], which will face a critical resource gap. Thus, water-saving irrigation (WSI) techniques have become an essential agronomic practice to reduce irrigation in rice paddies while guaranteeing high yield to food security [6]. On the other hand, for intensive farming systems, a sustained increase in nitrogen (N) fertilizer application is a traditional measure to improve yield stability. According to field surveys and literature statistics in China, 45% of paddy fields had amounts of N fertilizer applied that exceeded the environmental optimum [7–9]. High-cost N application patterns lead to soil acidification, loss of soil organic carbon due to mineralization, and imbalance in nutrient supply [10,11], which in turn further limits agricultural productivity.

Straw return (SR), as an important source of organic fertilizer, has been widely applied in the Yangtze River basin in southern China [12]. It is regarded as an efficient agronomic practice that not only preserves soil fertility but also diminishes fertilization investment [13]. A two-year field experiment with rice–wheat rotations suggested that SR with a 20% N reduction may be a dual-win approach that balances agricultural productivity with a low risk of cadmium contamination [7]. Moreover, SR significantly improves the distribution of assimilates and increases yield production, and this beneficial effect tends to increase progressively each year [14]. However, other studies have suggested that SR has neutral [15] or even negative [16] impacts on plant growth and yield formation. The high carbon-to-nitrogen ratio of straw decomposition stimulated microbial colonization and correspondingly depleted hydrolyzable N in soil, resulting in insufficient N availability during early rice growth [17,18], delaying the tillering stage and further affecting crop yield [19]. Several studies investigated the responses of canopy structure and physiological characters to changes in N-fertilizer [20], but few have quantified the effect of SR combined with N reduction.

Under conventional continuously flooded irrigation regimes, rice consumes 50–300 cm of field-input water, 50–80% of which is lost through runoff, percolation and seepage [21], and these water-transport processes are accompanied by 5.7–68.2% of N-fertilizer loss [22,23]. As the water crisis intensifies under climate change, WSI such as alternate wetting and drying (AWD) has been widely used in paddy fields [6,21]. Paddy soils under AWD are subject to alternating flooding and drying in contrast to continuously flooded conditions. The associated changes in alternating aerobic and anaerobic environments in paddy soil altered microbial nutrient cycling and N-supply processes [24]. It was reported that the greater photosynthetic rate and dry-matter accumulation was obtained by AWD due to active root metabolism ensuring sufficient nutrients and water entering the leaves [25,26]. In fact, the individual effects of AWD or SR on rice growth and yield have been well-documented by previous studies [27–30]. Zhang et al. [31] suggested that, under submerged anaerobic conditions, the rapid decomposition of straw may be accompanied by the derivation of substances harmful for rice, including H_2S, which could counteract the beneficial effects of SR and limit agronomic efficiency. The response of lowland rice applied with WSI to photosynthetic physiology and water–nitrogen utilization in the context of straw return with N reduction remains somewhat obscure.

As both water and N are essential factors affecting rice growth and photosynthetic products, how to optimize water consumption and mineral N-fertilizer input during rice cultivation and make full use of straw resources is one of the research goals in studying carbon sequestration and controling agricultural diffuse pollution [32,33]. In light of this, the objectives of this study were to: (1) investigate the effects of straw return with N reduction on rice growth under different water regimes; (2) explore the response and recovery of rice morphological and physiological indicators under different water and fertilizer management practices; and (3) quantify the individual and interactive effects of these factors on rice growth, yield, and water/N-use efficiency. Identifying the potential for N-fertilizer reduction under SR, while maintaining yields, will help ensure environmental sustainability and meet the challenges of feeding a growing population under resource scarcity.

2. Materials and Methods

2.1. Experiment Site

The field experiment was conducted in 2020 and 2021 at the Water Conservation Park (31°54′ N, 118°46′ E) in Jiangsu Province, China. The experiment site is a typical wheat–rice double-cropping area in the lower Yangtze River. The site has a subtropical and humid monsoon climate with the following climatic characteristics: mean annual temperature of 15.3 °C, mean evaporation of 900 mm, and mean rainfall of 1051.0 mm. Specific air temperature and rainfall values during the experiment were obtained from the meteorological station (AGWS100, TECHNO, Beijing, China) at the site, as illustrated in Figure 1. The initial topsoil (0–20 cm) was classified as loam according to the USDA Soil Classification System, with available N, P and K of 16.2, 9.9 and 20.4 mg kg^{-1}, respectively. The soil bulk density was 1.38 g cm^{-3} and the organic matter was 21.6 g kg^{-1}.

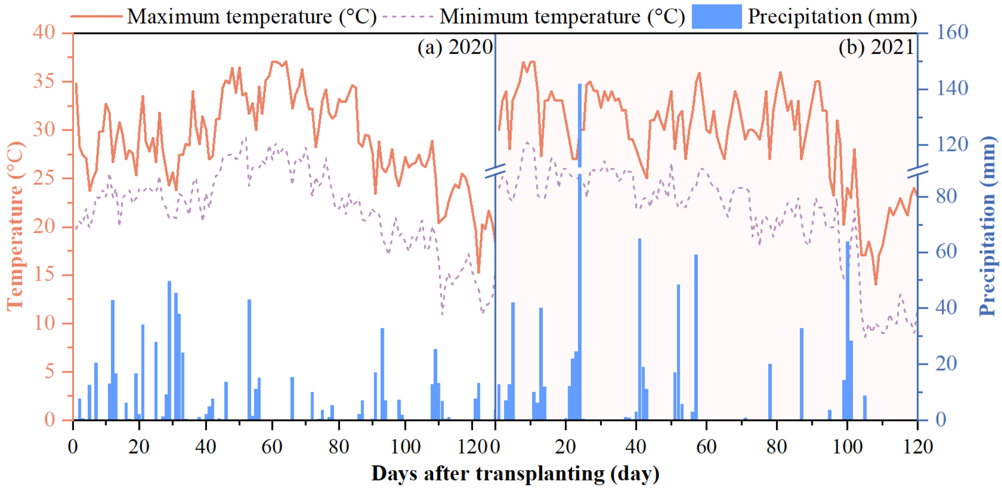

Figure 1. Dynamics of daily rainfall and air temperature during the rice-growing season in 2020 (**a**) and 2021 (**b**) at the experiment site.

2.2. Experimental Design

Japonica rice (*Oryza sativa* L.) Nanjing 9108 was transplanted with three seedlings on each hill at a spacing of 15.0 cm × 20.0 cm. The rice was transplanted on 17 June 2020 and 4 July 2021, and harvested on 2 November 2020 and 25 October 2021, respectively. The completely randomized design was adopted for the rice cultivation experiment, including the combination of two water regimes (continuously flooded and controlled irrigation and drainage, designated as CF and CID, respectively) and three straw-returned N reduction treatments (conventional farmers' fertilization of 300 kg N ha^{-1} without straw return; straw return with 25% N reduction at 225 kg N ha^{-1}; straw return with 50% N reduction at 150 kg N ha^{-1}; designated as N300, SN225 and SN150, respectively) with three replicates. Each field micro-plot with an area of 2.5 × 2 m^2 had a separate irrigation and drainage system, separated by a concrete and waterproof steel plate to prevent lateral water flow.

Controlled irrigation and drainage (CID) was designed to combine the advantages of both AWD and controlled drainage, and in particular, to capture more drainage during summer storms; paddy soils were not only frequently exposed to alternating dry/wet conditions, but also ponded more rainwater to reduce outflow rates and flows [34]. For the CID treatment, non-flooding was applied except for shallow ponding during the regreening stage. Apart from this, irrigation was applied only when the soil moisture reached the low thresholds (H_l) shown in Figure 2. In contrast, according to conventional tillage practices, the CF treatment maintained a flooding level of 1–5 cm in rice paddies until the yellow ripening stage [35], except for the drainage and dry set at the late tillering stage. Each micro-plot was irrigated individually using an electromagnetic flow meter (SM-10, Watergate, Nanjing, China) installed at the pipe outlet. During the experiment, field water level was monitored every morning at 9 am.

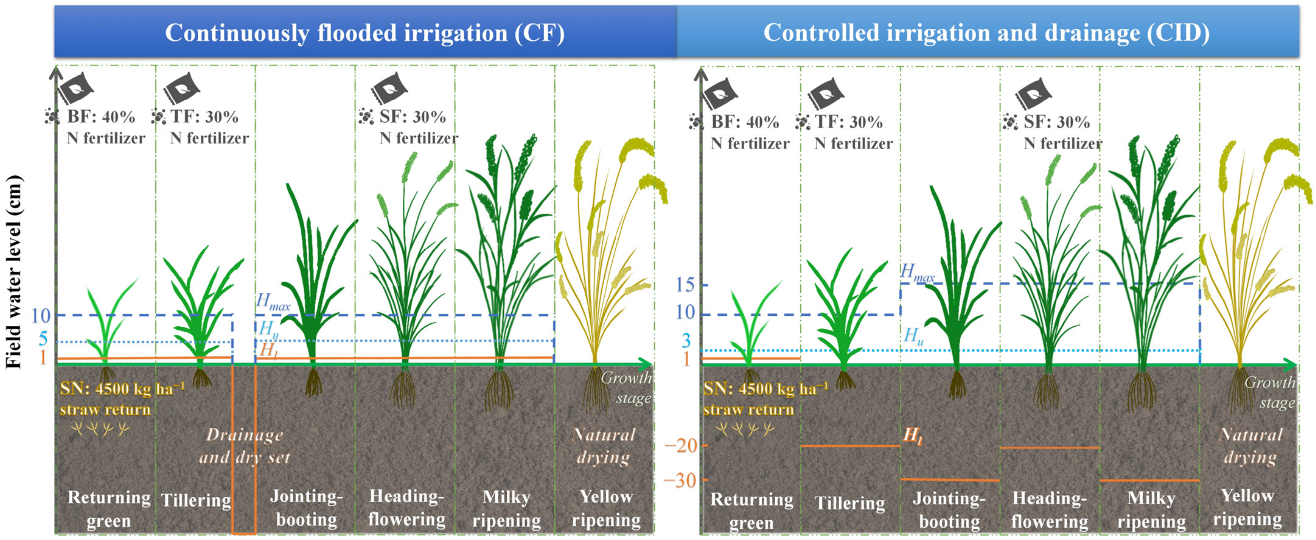

Figure 2. Schematic of fertilizer and water management for different treatments at various growth stages of rice. The soil surface is set as the zero point of the ordinate, so positive values indicate the ponding-water depth and negative values indicate the groundwater level. H_{max} represents the maximum ponding-water depth after rainstorm events; H_u represents the upper limit of irrigation; and H_l represents the lower threshold of irrigation when the field water level drops to it, respectively. N300 represents the local farmers' high fertilization level of 300 kg N ha^{-1} without straw return, while SN225 and SN150 represent straw return with 25% N and 50% N reduction, at 225 and 150 kg N ha^{-1}, respectively. BF, TF and SF denote the base, tillering, and spikelet-developing fertilizer, respectively.

Field management followed strictly the agronomic practices of local farmers, including those relating to pests, weeds, diseases and fertilization. For the N300 treatment, the application of mineral fertilizers was based on conventional high fertilization practices of using urea as an N fertilizer, superphosphate as a P fertilizer and potassium chloride as a K fertilizer at rates of 300 kg N ha^{-1}, 75 kg P_2O_5 ha^{-1} and 120 kg K_2O ha^{-1}, respectively. Urea was applied as base (BF), tillering (TF), and spikelet-developing fertilizer (SF) in the ratio of 4:3:3 (Figure 2). All treatments were fertilized with equal rates of P and K. One week before rice transplantation, air-dried straw from the previous wheat season was chopped into approximately 5-cm pieces using a straw grinder (9ZT-06, XD-Machinery, Xingyang, China), and then 4500 kg ha^{-1} of straw (437 g kg^{-1} of organic carbon) was mixed into the 0–20 cm topsoil of the SN225 and SN150 subplots. Both straw and basal fertilizer were plowed into topsoil during tillage and all other fertilizers were applied by surface application.

2.3. Measurements and Methods

2.3.1. Growth Dynamics

Six well-grown rice seedlings were randomly selected and tagged in each plot (avoiding selecting border rows) after entering the tillering stage. At the subsequent growth stages, the plant height and tiller number of the tagged plants were surveyed and averaged every five days. Plant height was measured from the surface of the rice field to the tip of each plant using a steel ruler. Tiller number was counted manually until maturity. In addition, the photosynthetic physiology of flag leaves was measured at 10 a.m. on a clear and cloudless day during the late tillering and heading–flowering stage, including the net photosynthetic rate (P_n, μmol CO_2/(m^2 s)), transpiration rate (T_r, mmol H_2O/(m^2 s)), and stomatal conductance (G_s, mmol H_2O/(m^2 s)). Analysis was performed using an LI-6800 photosynthesis system with photosynthetic active radiation of 1500 μmol/(m^2 s), a flow rate of 500 μmol s^{-1}, a CO_2 concentration of 400 μmol/mol, and a leaf chamber temperature of 30 °C, respectively. Likewise, the chlorophyll fluorescence of leaves was determined by a MINI-PAM-I fluorometer (WALZ, Germany), including the maximum efficiency of PSII photochemistry (F_v/F_m), actual quantum yield (Φ_{PSII}), photochemical extinction coefficient (qP) and non-photochemical extinction coefficient (NPQ) [36]. Three uppermost fully expanded flag leaves were randomly selected from each plot for photosynthesis measurements; the leaves were dark-adapted for 20 min for fluorescence analysis and then illuminated with light intensity of 1500 μmol/(m^2 s).

2.3.2. Nitrogen Uptake and Grain Yield

Three representative hills of rice from each micro-plot, without border plants, were collected from tillering to harvest to determine their above-ground dry-matter weight. Plant samples were dried at 80 °C to constant weight, weighed, ground and then sieved for subsequent analysis of total N content. The Kjeldahl apparatus (Kjeltec-8400, FOSS, Hillerød, Denmark) was used to measure N concentrations of the plant samples [37]. Total N uptake in rice plants was equal to dry matter multiplied by the N content of each organ. At maturity, rice from each plot was harvested separately by hand, threshed and impurities removed and weighed. Subsequently, the actual yield was calculated at a standard moisture content of 14%. Yield components, including panicles, spikelets per panicle, filled spikelets (%) and 1000-grain weight, were measured from six randomly selected hills of plants from each plot.

2.3.3. Water–Nitrogen Utilization

Various indicators of water–nitrogen use efficiency, including water productivity (WP, kg m^{-3}), harvest index (HI, kg kg^{-1}), internal N-use efficiency (IE, kg kg^{-1}), and N partial factor productivity (PFP, kg kg^{-1}) were calculated as follows, according to [2,38,39]:

$$WP = \frac{Y}{I + P} \tag{1}$$

$$HI = \frac{Y}{B} \tag{2}$$

$$IE = \frac{Y}{U} \tag{3}$$

$$PFP = \frac{Y}{F} \tag{4}$$

where Y and B are grain yield and above-ground biomass (kg ha^{-1}); P and I are the amount of rainfall and irrigation for each micro-plot (m^3 ha^{-1}); U represents N uptake in aboveground plants at harvest (kg ha^{-1}); and F represents N-fertilizer application rate (kg ha^{-1}).

2.4. Statistical Analysis

Data statistics and two-way analysis of variance were conducted using SPSS software. Means for each treatment were compared individually by the least significant difference test (LSD) at $p < 0.05$. Pearson's coefficients, which were the covariance of the two variables divided by the product of their standard deviations, were used to analyze correlations between morphological and physiological indicators, yield and water–nitrogen utilization in rice [40]. Both Pearson's analysis and graphical analysis were carried out by Origin software.

3. Results

3.1. Rice Morphological Traits

Plant height and tiller number, as the important indicators of rice growth, represent the ability of the crop canopy to extend longitudinally and laterally, respectively, and both are closely related to nutrient availability and yield formation [41]. As shown in Figure 3, the plant height exhibited variation between fertilizer treatments under the same water regime. Neither W nor N treatments significantly affected plant height, nor did their interaction (Table 1). The greatest plant height was obtained at N300 and SN225 for CF and CID, respectively. At the heading stage in both years, plant height under CF was in the order of

N300, SN225 and SN150, with no significant differences. The plant height under CF at the late tillering stage was 4.3% lower than for CID, and that of CF at the heading stage was 2.7% higher than for CID. Compared with the CF regime, rice undergoing alternating wet and dry was reported to have reduced plant height by ~10% but increased by two more tillers per hill [5], which facilitated the formation of a competitive canopy structure and reduced the risk of lodging [42].

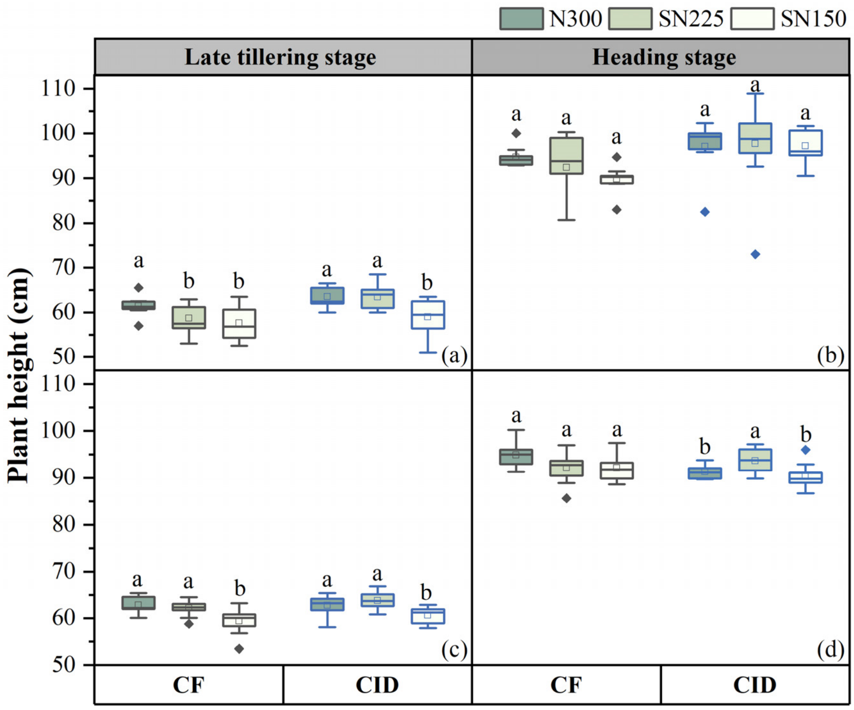

Figure 3. Plant height of Nanjing 9108 rice variety (*Oryza sativa* L.) under two water regimes (continuously flooded [CF] and controlled irrigation and drainage [CID]) and three fertilizer practices (conventional farmers' fertilization of 300 kg N ha^{-1} without straw return [N300], straw return with 225 kg N ha^{-1} fertilizer [SN225], and straw return with 150 kg N ha^{-1} fertilizer [SN150]) at the late tillering and heading stages during the 2020 (**a**,**b**) and 2021 (**c**,**d**) rice-growing seasons. The lines, squares, and diamonds in boxplots represent the medians, means and outliers, respectively. Different letters indicate significant differences at $p < 0.05$.

Table 1. Analysis of variance of water regime and N-fertilizer management and their interactions with morphological, photosynthetic and fluorescence indicators.

Source of Variation	Plant Height	Tiller Number	P_n	T_r	G_s	F_v/F_m	Φ_{PSII}	qP	NPQ
Water regime (W)	ns	*	*	*	*	*	**	*	**
N-Fertilizer management (N)	ns	*	*	ns	ns	ns	**	ns	**
W × N	ns	ns	ns	ns	ns	ns	ns	ns	ns

Note: Different symbols within each column represent significant differences based on the LSD test, where ns, * and ** represent nonsignificant, $p < 0.05$ and $p < 0.01$, respectively.

The tiller number of rice under various water regimes and N-fertilizer management practices is shown in Figure 4. The tiller number under CID was slightly higher than that under CF at the late tillering and heading stages of both seasons. In 2020, SN150 had significantly ($p < 0.05$) fewer tillers than SN225 or N300, while in 2021, there were no significant differences ($p > 0.05$) between the three N-fertilizer management practices. Upon entering the late tillering stage, the two water regimes experienced varying degrees of drought stress to suppress the generation of unproductive tillers (Figure 2). Both SN225 and SN150 had a greater proportion of productive tillers than N300 under CID, while N300 had the highest proportion of productive tillers under CF. CID showed more tillers than CF at each growth stage in the treatments of SN225 and N300 (Figure 4). Moreover, the CID regime promoted tillering in both years compared to CF; for example, CID had 17.3% and 3.2% more tillers than CF at the heading stage in 2020 and 2021, respectively. The analysis of variance showed that the tiller number was significantly affected ($p < 0.05$) by W and N, but their interaction was not significant ($p > 0.05$).

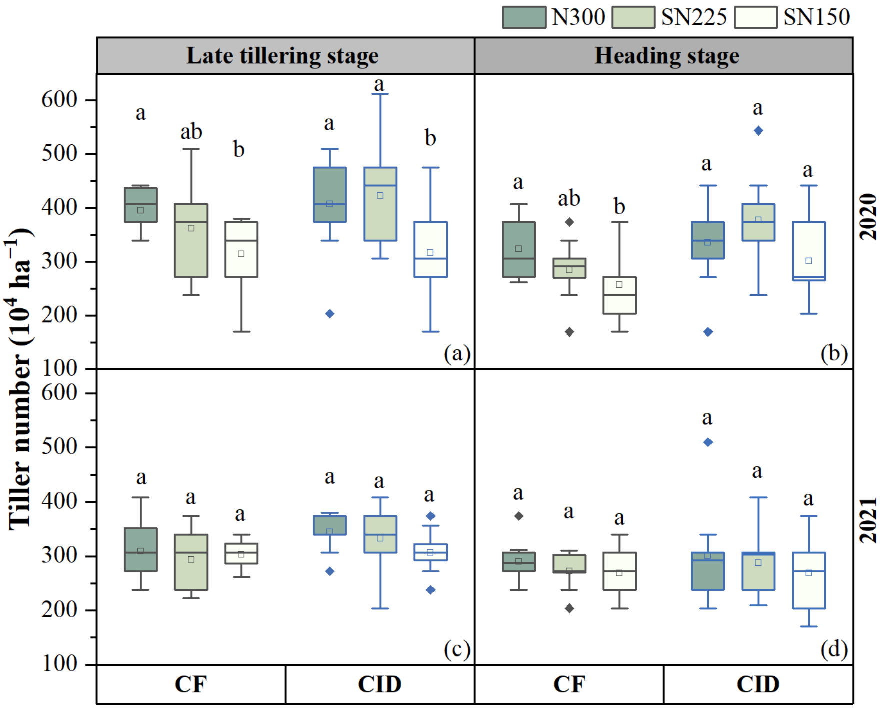

Figure 4. Tiller number of Nanjing 9108 rice variety (*Oryza sativa* L.) under two water regimes (continuously flooded [CF] and controlled irrigation and drainage [CID]) and three fertilizer practices (conventional farmers' fertilization of 300 kg N ha^{-1} without straw return [N300], straw return with 225 kg N ha^{-1} fertilizer [SN225], and straw return with 150 kg N ha^{-1} fertilizer [SN150]) at the late tillering and heading stages in the 2020 (**a**,**b**) and 2021 (**c**,**d**) rice-growing seasons. The squares, lines, and diamonds in boxplots represent the means, medians and outliers, respectively. Different letters indicate significant differences at $p < 0.05$.

3.2. *Leaf Chlorophyll Fluorescence and Photosynthetic Physiology*

The process of production, accumulation and distribution of biomass primarily depends on leaf photosynthesis and CO_2 assimilation capacity [43]. The response of photosynthesis rate (P_n) to water regime and N-fertilizer management was significant, and water regime significantly affected the transpiration rate (T_r) and stomatal conductance (G_s); however, no significant interaction effect on the photosynthesis indicators was observed between W and N (Table 1). Overall, leaf physiological traits of P_n and T_r increased gradually as rice progressed from nutritional to reproductive growth (Figure 5). Under the CF regime, the P_n and T_r of flag leaves generally increased with the increase of the application level of mineral N. In contrast, straw addition as base fertilizer promoted photosynthesis under CID, which could offset the negative effects of reduced N fertilization. SN225 improved P_n and T_r over N300 and SN150 under CID. Specifically, P_n increased by 3.8% and 3.7% and T_r increased by 2.8% and 2.2% at the late tillering and heading stages, respectively, for SN225 compared to N300 under CID. Both P_n and T_r at the heading stage were higher under CID than those under CF, but the pattern was reversed for G_s. Moreover, the G_s of flag leaves generally increased with increasing N fertilizer, and the differences were not significant ($p > 0.05$) under the CID regime.

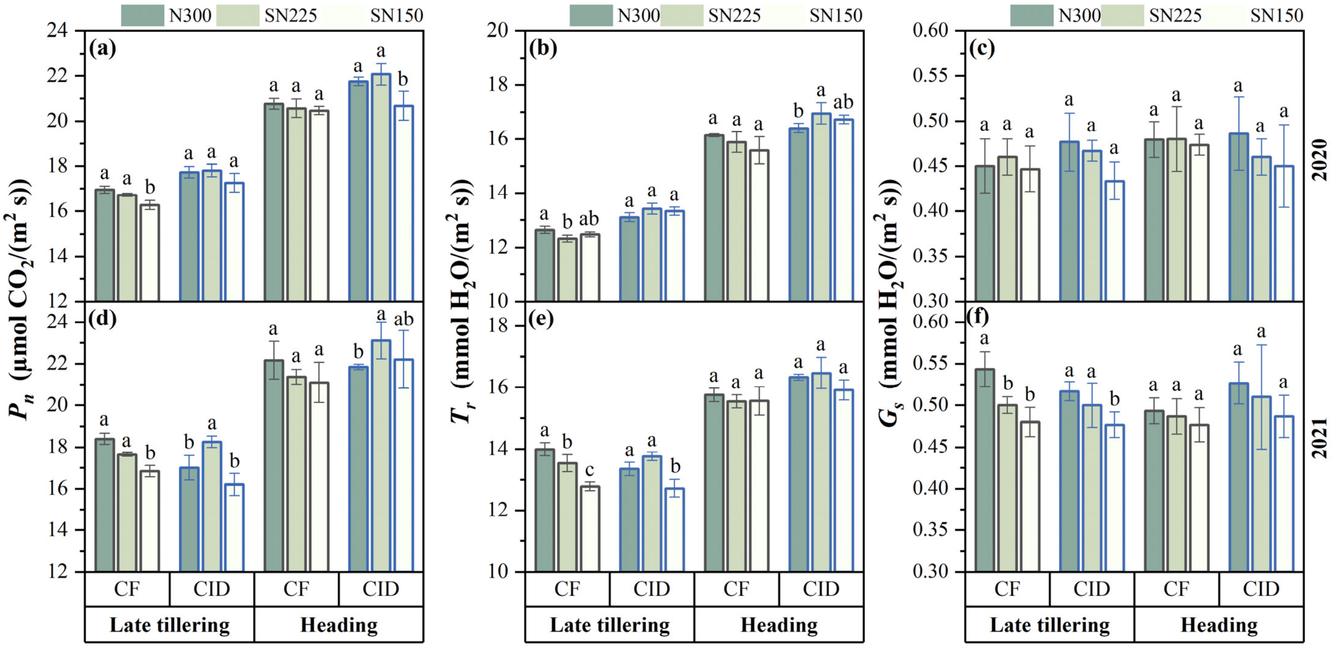

Figure 5. Dynamics of photosynthesis rate (P_n), stomatal conductance (G_s) and transpiration rate (T_r) at late tillering and heading stages of rice for various water and fertilizer treatment combinations in 2020 (**a**–**c**) and 2021 (**d**–**f**) seasons. CF and CID denote continuously flooded and controlled irrigation and drainage, respectively. N300 denotes conventional farmers' fertilization of 300 kg N ha^{-1} without straw addition, while SN225 and SN150 denote straw return with 225 and 150 kg N ha^{-1} fertilizer, respectively. Different letters indicate significant differences at $p < 0.05$.

The effects of straw return with N reduction on chlorophyll fluorescence under different water regimes are presented in Table 2. The F_v/F_m, Φ_{PSII}, qP and NPQ values showed some variability across different growth stages and seasons. The F_v/F_m values were higher in 2020 than in 2021, and the same occurred for Φ_{PSII} and qP. Furthermore, F_v/F_m, Φ_{PSII} and qP showed a significant upward trend as rice grew, whereas the pattern was not evident for NPQ. Generally, under the CF regime, higher F_v/F_m, Φ_{PSII}, qP values were observed with higher N-application rates. In both seasons, the leaf fluorescence indicators of CF were higher than CID at the late tillering stage, while the pattern was the opposite at the heading stage. The highest values of F_v/F_m, Φ_{PSII}, qP and NPQ under CID were observed when straw return was combined with 225 kg N ha^{-1}, followed by N300 and SN150, while the compensation effect of straw returning on chlorophyll fluorescence of rice under flooded irrigation was negligible. The individual effects of water regime on F_v/F_m and qP were significant ($p < 0.05$), whereas Φ_{PSII} and NPQ were highly significantly ($p < 0.01$) affected by the individual effects of water as well as N-fertilizer management (Table 1).

Table 2. PSII photochemistry (Φ_{PSII}), maximum efficiency of PSII photochemistry (Fv/Fm), photochemical quenching coefficient (qP) and nonphotochemical quenching coefficient (NPQ) in the flag leaves of Nanjing9108 rice variety (*Oryza sativa* L.) under various water and fertilizer treatments.

Year	Water Regime	N Fertilizer Management	Late Tillering Stage				Heading Stage			
			F_v/F_m	Φ_{PSII}	qP	NPQ	F_v/F_m	Φ_{PSII}	qP	NPQ
2020	CF	N300	0.737 a	0.511 a	0.735 a	0.393 a	0.838 a	0.519 ab	0.722 a	0.302 b
		SN225	0.735 a	0.510 a	0.730 a	0.391 a	0.832 b	0.512 ab	0.717 a	0.295 bc
		SN150	0.731 a	0.505 ab	0.724 a	0.382 a	0.829 b	0.511 b	0.715 a	0.292 c
	CID	N300	0.734 a	0.494 b	0.705 b	0.365 b	0.850 a	0.525 a	0.726 a	0.316 a
		SN225	0.738 a	0.496 ab	0.706 b	0.366 b	0.856 a	0.529 a	0.727 a	0.323 a
		SN150	0.728 b	0.487 b	0.695 c	0.359 b	0.843 a	0.515 ab	0.714 a	0.308 ab
2021	CF	N300	0.734 a	0.512 a	0.719 a	0.383 a	0.824 ab	0.519 ab	0.714 b	0.309 ab
		SN225	0.730 a	0.507 a	0.715 a	0.379 a	0.818 ab	0.511 b	0.705 b	0.301 b
		SN150	0.727 b	0.503 ab	0.711 a	0.377 a	0.814 b	0.509 b	0.703 b	0.300 b
	CID	N300	0.724 b	0.493 ab	0.692 b	0.349 b	0.827 a	0.522 a	0.730 a	0.311 a
		SN225	0.724 b	0.495 ab	0.694 b	0.350 b	0.830 a	0.522 a	0.733 a	0.318 a
		SN150	0.716 c	0.488 b	0.686 b	0.345 b	0.826 ab	0.515 b	0.727 a	0.311 a

Note: CF and CID represent continuously flooded and controlled irrigation and drainage, respectively. N300 denotes conventional farmers' fertilization of 300 kg N ha^{-1} without straw return, while SN225 and SN150 denote straw return with 225 and 150 kg N ha^{-1} fertilizer, respectively. Different letters within each column represent significant differences based on the LSD test ($p < 0.05$).

3.3. Dry Matter, N Uptake and Grain Yield

Above-ground biomass accumulation under different water–fertilizer treatments increased gradually and consistently with rice growth (Figure 6). Furthermore, as expected, higher rates of N-fertilizer application generally resulted in higher biomass accumulation and N uptake, irrespective of straw addition. Biomass at the milky ripening stage was increased significantly, ranging from 8.01 to 9.22 Mg ha^{-1} when the N-application rate exceeded 150 kg N ha^{-1}. Compared to the corresponding treatments for CF, the CID regime increased N uptake at milky ripening by 1.7%, 4.9% and 5.9% for N300, SN225 and SN150, respectively, in both seasons. Similar increases were observed in biomass accumulation. Moreover, there were significant differences between N300 and SN225 in dry matter and N uptake at the tillering and jointing–booting stages, suggesting that SN225 treatment may have a certain degree of N stress in the early growth stage; otherwise the plant N status of straw-return treatments should have been sufficient. After entering the heading stage, the differences in N accumulation between N300 and SN225 under CID were not significant ($p > 0.05$).

In both years, the CID regime increased grain yield by 4.6% but had no significant effect on panicles, spikelets and 1000-grain weight compared to CF (Table 3). The higher the total mineral N application, the higher the values of panicles, filled spikelets and 1000-grain weight at harvest under the same water regime. In particular, the largest spikelets were observed at SN225. No significant effect of water on rice yield was observed, while N-fertilizer management significantly affected panicles, spikelets, filled spikelets and grain yield in both seasons. The panicles response to the CID regime was dependent on N fertilizer-management practices (as indicated by significant W $\times$ N interactions). Although SN225 and SN150 have a 25% and 50% N reduction compared to N300, yields decreased by 7.1% and 23.1% in 2020 and by 6.6% and 25.5% in 2021, respectively. Straw return with 25% N reduction did not result in a significant reduction in spikelets and 1000-grain weight. The supply of straw resources was conducive to promoting plant growth and ensuring nutrient availability and yield recovery.

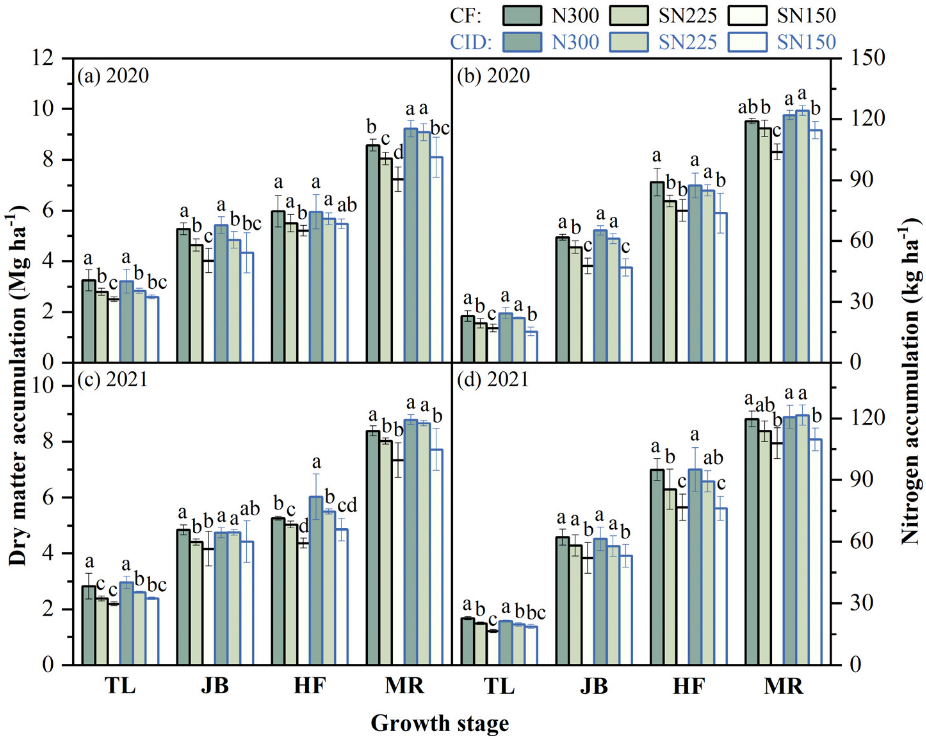

Figure 6. Dynamics of dry matter (**a**,**c**) and nitrogen (**b**,**d**) accumulation of above-ground plants of rice in the 2020 and 2021 seasons for various water and fertilizer treatment combinations. TL, JB, HF, and MR denote tillering, jointing–booting, heading–flowering, and milky ripening stages of rice. CF and CID represent continuously flooded and controlled irrigation and drainage, respectively. N300 denotes conventional farmers' fertilization of 300 kg N ha^{-1} without straw return; SN225 and SN150 denote straw return with 225 and 150 kg N ha^{-1} fertilizer, respectively. Different letters represent statistical significance ($p < 0.05$) based on the LSD test.

Table 3. Grain yield and yield components under various water and fertilizer treatments.

Year	Treatment	Panicles ($\times 10^4$ ha^{-1})	Spikelets (No. Panicle^{-1})	Filled Spikelets (%)	1000-Grain Weight (g)	Grain Yield (kg ha^{-1})
Water regime (W)						
2020	CF	296.3 a	142.3 a	83.7 a	24.8 a	8061.7 a
	CID	292.7 a	146.8 a	86.7 a	25.0 a	8306.4 a
2021	CF	289.8 a	148.4 a	83.8 a	24.8 a	7454.4 a
	CID	286.3 a	146.5 a	85.4 a	24.7 a	7919.1 a
N fertilizer management (N)						
2020	N300	315.2 a	147.3 a	88.8 a	24.9 a	8953.3 a
	SN225	296.3 b	158.3 a	85.0 b	24.6 a	8316.8 b
	SN150	272.1 c	150.6 a	81.8 c	24.2 a	6882.1 c
2021	N300	308.5 a	146.4 a	88.2 a	24.6 a	8533.2 a
	SN225	297.5 a	153.2 a	84.2 b	24.5 a	7966.1 b
	SN150	258.0 b	142.8 b	81.5 c	24.2 a	6360.9 c
Analysis of variance (ANOVA)						
2020	W	ns	ns	**	ns	ns
	N	**	*	**	ns	*
	W × N	*	ns	ns	ns	ns
2021	W	ns	ns	**	ns	ns
	N	**	*	**	*	**
	W × N	*	ns	ns	ns	ns

Note: CF and CID represent continuously flooded and controlled irrigation and drainage, respectively. N300 denotes conventional farmers' fertilization of 300 kg N ha^{-1} without straw return. SN225 and SN150 denote straw return with 225 and 150 kg N ha^{-1} fertilizer, respectively. Different letters within each column represent significant differences based on the LSD test, where ns, * and ** represent nonsignificant, $p < 0.05$ and $p < 0.01$, respectively.

3.4. Water–Nitrogen Utilization and Correlation Analysis

Water productivity (*WP*) varied significantly ($p < 0.05$) according to both water regime and N-fertilizer practice, but was not significantly ($p > 0.05$) affected by their interaction (Figure 7). The CID regime significantly reduced irrigation inputs under all N-fertilizer management practices with correspondingly higher *WP*. For the CID regime, *WP*s for N300, SN225 and SN150 were 1.075, 0.959 and 0.829 kg m^{-3} respectively, which was an increase of 6.5–12.4% over CF. *WP* increased with increasing N application, while *HI*, *IE* and *PFP* showed the opposite tendency. N-fertilizer management showed a significant effect on *HI*, *IE* and *PFP*, while W and W $\times$ N did not. *HI* was lower in 2021 than in 2020 with values of 0.464–0.526 and 0.507–0.562 kg kg^{-1}, respectively. Similar patterns were observed in *IE* and *PFP*. However, *IE* under CID was higher than CF in 2021 and vice versa in 2020. As more short-term intense rainstorms and greater total rainfall occurred in 2021 (Figure 1), there was more field drainage with a corresponding increase in N loss from paddy fields, which may have contributed to the reduced N-use efficiency. The average *PFP* for CID and CF was 36.25 and 34.61 kg kg^{-1}, respectively, in 2021, and 38.13 and 36.99 kg kg^{-1}, respectively, in 2020. An improvement in *PFP* was observed for the straw-returned treatments, with a significant increase of 24.2% and 51.5% for SN225 and SN150 compared to N300.

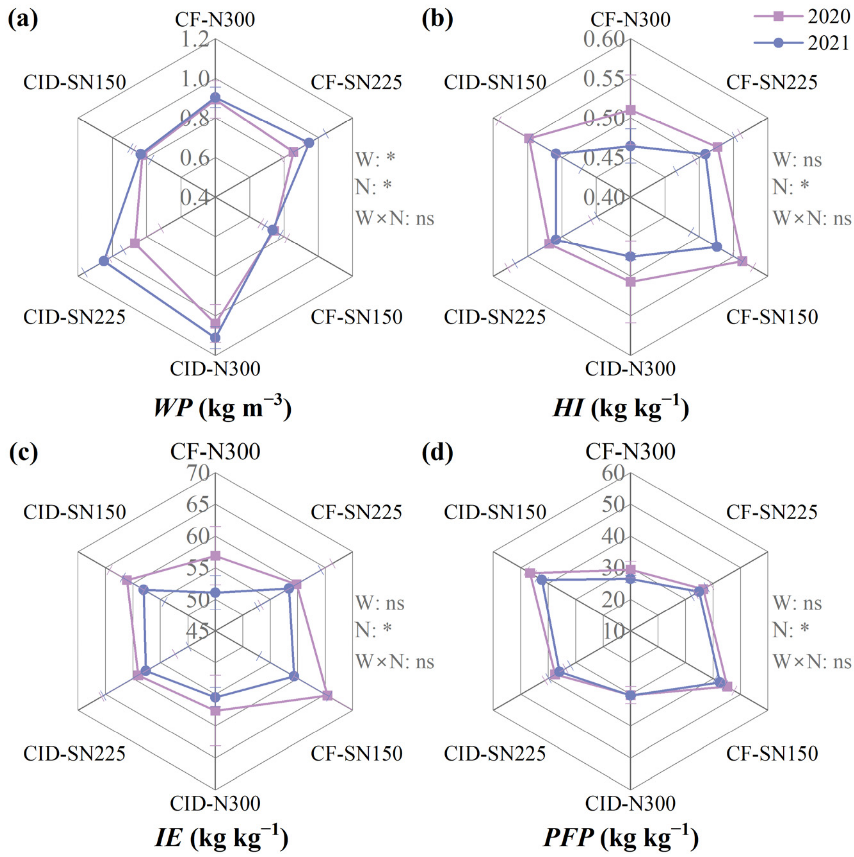

Figure 7. (**a**) Comparison of water productivity (*WP*), (**b**) harvest index (*HI*), (**c**) internal nitrogen-use efficiency (*IE*), and (**d**) partial factor productivity of nitrogen (*PFP*) for various water and fertilizer treatments. CF and CID represent continuously flooded and controlled irrigation and drainage, respectively. N300 denotes conventional farmers' fertilization of 300 kg N ha^{-1} without straw return. SN225 and SN150 denote straw return with 225 and 150 kg N ha^{-1} fertilizer, respectively. * and ns represent $p < 0.05$ and nonsignificant based on the LSD test, respectively.

The interrelationships between rice morphology, photosynthesis, chlorophyll fluorescence, dry matter and N accumulation, yield and efficiency indices were further investigated and the results are illustrated in Pearson's correlation matrix (Figure 8). Tiller number was positively correlated with T_r, F_v/F_m, Φ_{PSII}, NPQ, dry matter, N uptake and yield, with significant correlation coefficients of 0.36–0.51, while tiller number was negatively correlated with *PFP* with a correlation coefficient of −0.41. P_n and T_r positively correlated with N uptake and biomass accumulation, indicating that active photosynthesis promoted N and carbon assimilation and accumulation in rice plants. There was also a high positive correlation between chlorophyll fluorescence and transpiration. Higher F_v/F_m, qP and NPQ would increase dry-matter accumulation and grain yield at harvest. Furthermore, Φ_{PSII} showed significant positive correlations with dry matter, N uptake, yield and *WP*, with significant correlation coefficients of 0.38–0.46. It was essential for crop growth and yield to stimulate the potential of chlorophyll fluorescence of leaves [44]. Dry-matter accumulation and N uptake were negatively correlated with *HI*, *IE* and *PFP*, with significant correlation coefficients ranging from −0.40 to −0.89. In fact, dry-matter accumulation and N uptake increased with increasing N-fertilizer application rate, but N-use efficiency decreased with more N applied in both years. A similar negative correlation was found between *PFP* and *WP*.

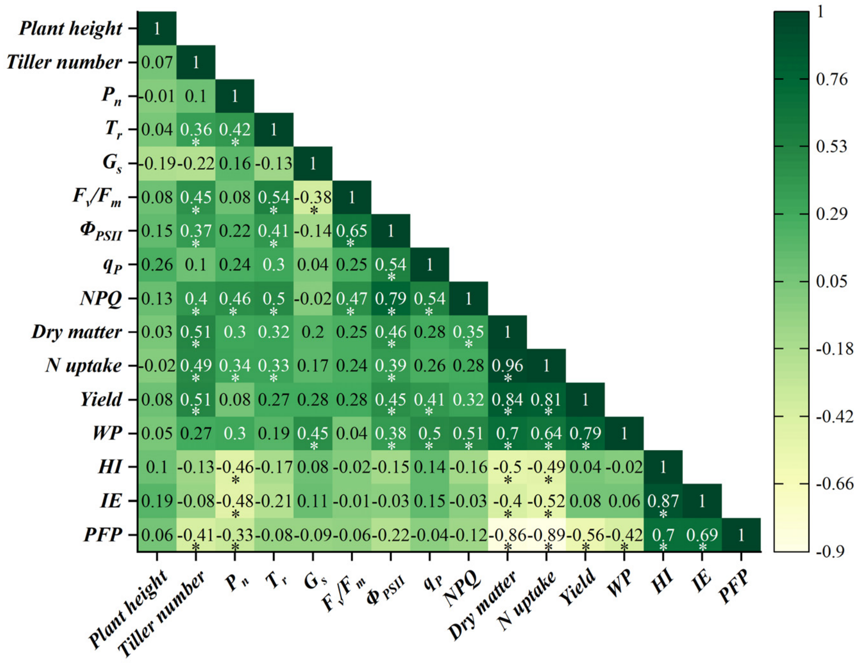

Figure 8. Correlation analysis between morphological and photosynthetic characteristics, biomass and N accumulation, yield and efficiency indices based on two years of rice experiments. Numbers and * in the boxes indicate the Pearson correlation coefficients and statistical significance ($p < 0.05$).

4. Discussion

Understanding the growth processes and physiological mechanisms of the rice plant is essential for the integrated response of water-saving irrigation and N-fertilizer reduction on paddy fields, which is a fundamental component of crop stress tolerance [34]. At the tillering stage, fluorescence parameters and photosynthetic indicators of CID were lower than those of CF, while this pattern reversed at the heading stage (Table 2 and Figure 5). Initially, the straw decomposition in topsoil may lead to a temporary reduction of the effective N of the root zone due to microbial N immobilization [13]. Previous studies have shown that when rice was exposed to water or N stress, physiological traits were significantly decreased and malondialdehyde contents enhanced [31,45], resulting in reduced photosynthetic components and yield attributes [46,47]. Moreover, CID produced a higher yield than CF in both two seasons (Table 3), which was at least partly attributable to a greater proportion of filled spikelets per panicle. Liang et al. [48] indicated that filled grains of rice increased under mild water stress. N application significantly increased water productivity (Figure 7) which is consistent with previous studies [29,49]. Higher N-use efficiency was observed in the CID or low N treatment. This may be attributed to the fact that N uptake and root elongation in rice plants can be promoted under low nutrient availability and WSI conditions [50].

The photochemistry and photochemical extinction coefficient of PSII decreased with the reduction of N-fertilizer input under continuously flooded irrigation conditions, (Table 2), which may be associated with the declined activity of the photochemical system due to a lack of N nutrients [44]. Fluorescence under CF was greater than CID at the late tillering stage and vice versa at the heading stage. CID may be more conducive to straw decomposition, and high soil N availability after vegetative growth could mitigate the adverse impacts of water stress by increasing F_v/F_m and qP, thus improving the photosynthetic efficiency of rice plants [51,52]. There was the compensation effect of straw-returning on the photosynthetic physiology of SN225 under water-saving irrigation (Figure 5). Straw return combined with N reduction reduces the thermal dissipation of light energy by increasing the photochemical efficiency and potential quantum yield of PSII. This helps to slow premature leaf decay, prolong the functional period of leaves, and increase photosynthetic productivity and biomass [53,54].

Compared to the CF regime, we also observed an increase in F_v/F_m, Φ_{PSII}, and qP of CID at the heading stage (Table 2), and a positive correlation with biomass and yield (Figure 8), in agreement with previous studies [55]. The CID regime created alternating wet and dry conditions in rice fields, where the soil transformed between aerobic and anaerobic environments, stimulating the microbial decomposition of straw. The addition of straw promoted the conversion of soil N into a slow-release source of N to enhance the nutrient supply for reproductive growth, thereby reducing reliance on mineral fertilizer [56]. Moreover, AWD was reported to increase the root biomass of rice and its oxidative activity, which may mitigate the adverse impacts of straw return [57]. Maneepitak et al. [58] suggested that adaptive physiological responses to water deficit and straw decomposition alleviated either stress on rice growth. This may be one of the mechanisms for optimizing straw management and water–nitrogen resource input in intensive agricultural areas such as the rice irrigation areas in southern China.

Our two-year field experiment showed that, compared with N300, SN225 and SN150 saved the application of nitrogen fertilizer by 25% and 50%, respectively, and that the yields decreased by 6.6–7.1% and 23.1–27.8%, respectively (Table 3), *HI*s increased by 2.7–8.3% and 9.2–10.1%, respectively; *IE*s increased by 3.8–9.0% and 10.2–10.5%, respectively; and *PFP*s increased by 23.4–23.9% and 49.1–53.7%, respectively (Figure 7). Generally, rice plant growth exhibits stress after the wheat–straw return. Microbial-derived straw decomposition consumes additional N and increases phytotoxic substances, such as organic acids and toxic reductants, thus constraining the root growth of rice seedlings [59], especially under anaerobic paddy soil with continuous flooded irrigation [60]. It is further reflected in the negative impact on the morphological growth and biomass and N accumulation of the above-ground parts (Figure 6). Straw decomposition with high N fixation and mineralization results in N deficiency in rice seedlings, especially during the early growth stages [61,62]. Consequently, a sufficient N supply is favorable for straw decomposition and alleviates the competition pressure.

In our study, it was necessary to ensure that the 225 kg N ha^{-1} application rate mitigated the late stress under straw return and improved the agronomic benefits. Decomposed straw not only improved soil structure and organic matter content but also released slowly as a nitrogen source, which is of positive significance for morphological physiology and yield formation after heading and flowering [63,64]. A study on farmland soil microbial communities indicated that straw return with chemical fertilizer reduction altered the soil microbial community structure, which was beneficial to improve soil fertility [65]. Although further field experiments are needed to characterize processes involved in the release, migration, transformation and uptake of exogenous nitrogen from straw in paddy soil, this study suggested that the CID regime may allow farmers to apply straw return with

N reduction and save irrigation without diminishing rice morpho-physiological growth and yield production.

5. Conclusions

Straw return under CF negatively affected rice tillering capacity, leaf photosynthesis, and chlorophyll fluorescence. Although the adverse effects were also manifested during the vegetative growth for SN225 under CID, it showed compensatory effects on photosynthetic physiology, fluorescence traits and N uptake at the reproductive growth stage. Compared with CF, CID tended to increase rice yield and *WP*; however, there was no significant difference in the yield between the CF and CID regime. The interaction between water regime and fertilizer management on morphological, physiological and yield indicators of rice did not show statistical significance, except for panicles. Compared with N300, SN225 had a 6.6–7.1% yield reduction but saved 25% on N-fertilizer inputs, with a corresponding 3.8–9.0% increase in *IE* and a 23.4–23.9% increase in *PFP*. Taken together, our results suggest that the CID regime offsets the negative effects of straw decomposition in early growth, and that straw return with appropriate N reduction under CID could maintain grain yield while improving agronomic performance and water–N utilization.

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