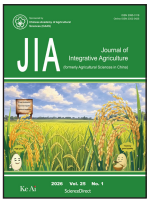
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RESEARCH ARTICLE

Optimizing nitrogen application and planting density improves yield and resource use efficiency *via* regulating canopy light and nitrogen distribution in rice

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Highlights

- Nitrogen extinction coefficient (K_N), light extinction coefficient (K_L) and the ratio of K_N to K_L (K_N/K_L) values were significantly influenced by N rate, planting density, and their interaction.
- K_L negatively correlated with radiation use efficiency (RUE), while K_N and K_N/K_L positively correlated with N use efficiency for grain production (NUEg).
- Optimizing the distribution of light and N within the canopy can jointly enhance yield and resource use efficiency under N2D2.

Abstract

Coordinating light and nitrogen (N) distribution within a canopy is essential for improving rice yield and resource use efficiency. However, limited research has examined light and N distribution in response to planting density and N rate, and their relationships with grain yield, radiation use efficiency (RUE), and N use efficiency for grain production (NUEg) in rice. A two-year field experiment was conducted with two hybrid varieties under three N levels, 0 kg ha^{-1} (N1), 90 kg ha^{-1} (N2) and 180 kg ha^{-1} (N3), and two planting densities, 22.2 hills m^{-2} (D1) and 33.3 hills m^{-2} (D2). Results showed 3.4% higher yield and 4.4% higher NUEg under N2D2 compared with N3D1. The extinction coefficient for N (K_N) and light (K_L) and their ratio (K_N/K_L) at heading stage were significantly influenced by N rate, planting density, and their interaction. K_N decreased with the increase of N input or planting density. Compared to N1, K_N decreased by 43.5 and 58.8% under N2 and N3, respectively, while K_N under D2 decreased by 16.0% compared to D1. Higher K_L and K_N/K_L values occurred under low N rates, with opposite trends under high N rates. Increased planting density led to decreased K_L and K_N/K_L values. N2D2 demonstrated higher K_L and K_N, and thus comparable K_N/K_L, compared to N3D1. Correlation analysis revealed K_L negatively correlated with RUE, while K_N and K_N/K_L positively correlated with NUEg. These findings indicate that increasing planting density under reduced N input could maintain rice yield while enhancing resource use efficiency through regulation of canopy light and N distribution.

Keywords: canopy light and N distribution, nitrogen input, planting density, high yield and high efficiency, hybrid rice

1. Introduction

The global population is projected to reach approximately 9.3 billion by 2050, necessitating a 70–100% increase in crop production (Tian *et al.* 2021). Rice (*Oryza sativa* L.), a globally distributed crop, serves as the primary food source for over 65% of China's population (Peng *et al.* 2009). Rice yield has significantly improved following the two green revolutions (Lou *et al.* 2023). The extensive application

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of chemical fertilizers, particularly nitrogen (N) fertilizer, has been instrumental in increasing rice yield. However, farmers frequently apply excess N fertilizer beyond rice requirements to achieve higher yields (Wang and Peng 2017). Furthermore, the adoption of modern rice cultivars with semi-dwarf traits has increased N input due to enhanced lodging resistance (Yang 2015; Huang *et al.* 2018). The current average N input rate in Chinese rice production has reached 209 kg N ha^{-1}, approximately 90% higher than the global average (Chen *et al.* 2014). In certain rice production regions, such as Jiangsu Province, N fertilizer application rates up to 300 kg ha^{-1} result in low N use efficiency (NUE), substantial N loss, and significant environmental issues including water eutrophication and soil acidification (Wang and Peng 2017). Therefore, enhancing rice's high-yield and high-efficiency potential is crucial for achieving sustainable agricultural development through green rice production.

Rice yields are determined by biomass accumulation and harvest index (HI). Enhancing biomass accumulation remains crucial for improving rice yield, as the potential for HI improvement is currently limited (Huang *et al.* 2013). Photosynthesis serves as the foundation for biomass formation in crops. While single leaf photosynthesis is important, increasing canopy photosynthesis represents the most fundamental approach to enhance dry matter accumulation and assimilate supply in rice (Long *et al.* 2006; Gu *et al.* 2014). Light functions as the energy source for crop photosynthesis, while nitrogen acts as the primary driver of light energy absorption. The crop canopy serves as the main site for light energy interception. An optimal canopy structure facilitates light distribution, while the vertical distribution of N within the canopy significantly affects material synthesis, efficient light energy utilization, and NUE for photosynthesis (Hikosaka 2005). Thus, optimizing light and N distribution in the canopy remains critical for achieving high yield and efficiency in rice production.

Research has demonstrated that to maximize canopy photosynthesis, plants should distribute more N to upper leaves and less N to shaded lower leaves. This gradient distribution of N should align with the light distribution in the canopy (Hirose and Werger 1987; Gastal and Lemaire 2002). The gradient distribution of N represents an adaptation to the light gradient in the canopy, promoting maximum canopy photosynthesis and enhanced NUE (Kull 2002). This gradient N distribution can increase canopy photosynthesis by 20% compared to uniform distribution (Hirose and Werger 1987). The light extinction coefficient (K_L) and N extinction coefficient (K_N) values indicate the gradients of light and N in the canopy. A lower K_L and higher K_N indicate more uniform light distribution and steeper N distribution, respectively (Anten *et al.* 1995; Gu *et al.* 2017; Zhu *et al.* 2022).

In practical conditions, the N gradient exhibits less steepness than the light gradient in the canopy (Moreau *et al.* 2012). The ratio of K_N to K_L (K_N/K_L) characterizes the match between light and N distribution in the canopy. Significant correlations between K_N/K_L and grain yield and NUE have been observed in rice (Ouyang *et al.* 2021; Zhu *et al.* 2022), maize (Wang *et al.* 2022), and rape (Liu T *et al.* 2020). K_L, K_N, and K_N/K_L values are affected significantly by rice varieties (Huang *et al.* 2019; Zhu *et al.* 2022). Previous research demonstrated that the *japonica/indica* hybrid rice Yongyou 4949, characterized by high yield and high NUE, exhibited lower K_L, higher K_N and K_N/K_L values compared to Yangliangyou 6 and Huanghuazhan (Huang *et al.* 2019). Zhu *et al.* (2022) further confirmed that N-efficient varieties with high yield potential demonstrated superior canopy structure (higher K_N/K_L), resulting in enhanced canopy photosynthesis and dry matter accumulation.

Nitrogen fertilizer and planting density are two critical cultivation management practices that influence grain yield and resource use efficiency (Guan *et al.* 2022; Chong *et al.* 2023; Wei *et al.* 2024). Research on rape demonstrated that N fertilizer significantly affects the distribution of light and N in the canopy (Liu T *et al.* 2020). The application of controlled-release urea (Li *et al.* 2024) and high-density tolerance varieties (Wang *et al.* 2022) has been shown to enhance maize yield and NUE by optimizing the canopy distribution of light and N. In rice studies, Zhu *et al.* (2022) examined the effects of N fertilizer on K_L, K_N, and K_N/K_L values of N-efficient varieties under 0 and 180 kg N ha^{-1} treatments. However, the influence of planting density and its interaction with N rate on light and N distribution in the canopy remains unclear for *indica* hybrid rice. This study utilized two hybrid rice varieties as test materials with various N rates and planting density treatments in field conditions. The research objectives were to (1) assess the effects of N rate, planting density, and their interaction on K_L, K_N, and K_N/K_L values and (2) investigate the relationships between K_L, K_N, and K_N/K_L values and grain yield, NUE and radiation use efficiency (RUE).

2. Materials and methods

2.1. Experimental sites

Field experiments were conducted for two years (2021 and 2022) at the experimental farm of Yangtze University in Jingzhou, Hubei Province, China. The experimental field contained calcareous alluvial soil with the following characteristics: pH 6.5, organic matter 20.7 g kg^{-1}, total N 1.8 g kg^{-1}, available phosphorus 29.7 mg kg^{-1}, and available potassium 128.9 mg kg^{-1}. A weather station near the experimental field measured daily minimum and maximum temperatures and solar radiation during the rice growing season in 2021 and 2022. From transplanting (TP) to heading (HD), the average daily minimum and maximum temperatures and solar radiation were 25.3°C and 26.2°C, 32.1°C and 34.1°C, and 16.5 and 21.2 MJ m^{-2} d^{-1} in 2021 and 2022, respectively. From heading to physiological maturity (PM), these values were 23.3°C and 23.4°C, 32.2°C and 32.3°C, and 16.2 and 16.9 MJ m^{-2} d^{-1}, respectively (Fig. 1). Additionally, from 7 days before the panicle initiation stage (PI) to PI, the average daily minimum and maximum temperatures and solar radiation were 26.9°C and 28.5°C, 33.1°C and 35.7°C, and 19.2 and 25.5 MJ m^{-2} d^{-1} in 2021 and 2022, respectively.

2.2. Experimental design

The experiment employed a split-split plot design with three replications, where N levels, planting densities, and

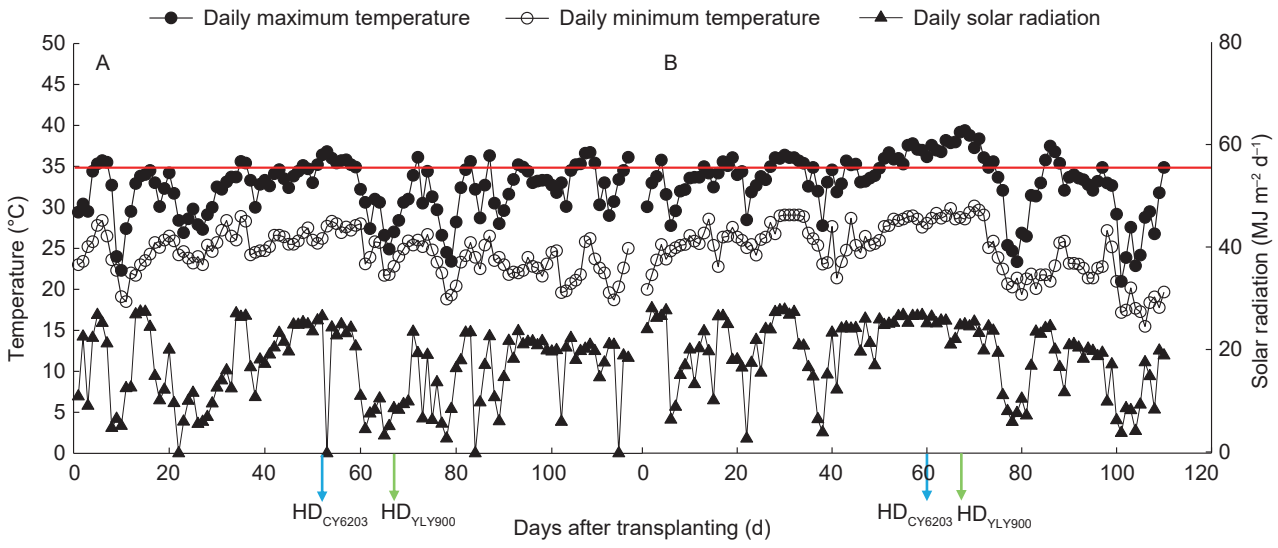


Fig. 1 Daily maximum and minimum temperatures and solar radiation during the rice growing season from transplanting to maturity at the experimental farm of Yangtze University in Jingzhou, Hubei Province, China in 2021 (A) and 2022 (B). The blue and green lines on the horizontal axis indicate the dates when Chuanyou 6203 (CY6203) and Yliangyou 900 (YLY900) first reached heading stage (HD) under varying nitrogen and planting density treatments, respectively.

rice cultivars were allocated to main plots, subplots, and sub-sub plots, respectively. Each sub-sub plot measured 25 m^2 (5.0 m×5.0 m) in both planting years. The three N levels consisted of 0 (N1), 90 (N2), and 180 kg N ha^{-1} (N3). Two planting densities were established: D1 (22.2 hills m^{-2} with 15 cm×30 cm spacing) and D2 (33.3 hills m^{-2} with 15 cm×20 cm spacing). The study utilized two high-yielding *indica* hybrid rice cultivars, Yliangyou900 (YLY900) and Chuanyou 6203 (CY6203). For N2 and N3 treatments, nitrogen was applied as urea in three distributions: 40% as basal fertilizer, 30% at mid-tillering (MT), and 30% at PI. Each plot received 40 kg P ha^{-1} calcium superphosphate and 50 kg K ha^{-1} potassium chloride as basal fertilizer. An additional 50 kg K ha^{-1} was applied as top dressing at the panicle initiation stage. Pre-germinated seeds were sown in a seedbed, and seedlings aged 32 and 34 days were transplanted on 9 June, 2021 and 13 June, 2022, respectively. Two seedlings per hill were transplanted following standard cultural practices.

2.3. Sampling and measurements

Dry matter accumulation At MT, PI, and HD, six hill plants were sampled from each plot. After recording tiller numbers, the plant samples were divided into straw and panicles (when present). The dry weight of each organ was determined after oven-drying at 80°C until reaching constant weight.

Grain yield and yield components At PM, grain yield was measured from a 5 m^2 sampling area in each plot's center and adjusted to a standard moisture content of 0.14 g H_2O g^{-1} fresh weight. Additionally, six hill plants were sampled per plot to determine total dry weight, HI, and yield components, including panicles m^{-2}, spikelets/panicle, grain-filling percentage, and grain weight, following the method of Huang *et al.* (2022).

Canopy light interception and RUE Canopy light interception measurements were conducted between 1,100 and 1,300 h on clear-sky days at MT, PI, HD, and PM using an AccuPAR LP-80 (Decagon Devices Inc., Pullman, WA, USA) in 2021 and 2022. Light intensity inside the canopy was measured by positioning the light bar between two rows slightly above the water surface. Subsequently, incoming light intensity was recorded above the canopy. Six readings were taken per plot, three in the horizontal direction and three in the vertical direction. Canopy light interception (IP), intercepted photosynthetically active radiation (IPAR), and RUE during each growth period were calculated according to Huang *et al.* (2019).

Vertical distribution of light and N in the canopy At HD, the canopy within two hills of representative plants was separated into 20 cm horizontal layers from the base to the top to analyze light and N vertical distribution. The leaf area of each layer was determined, and the leaf area index (LAI) was calculated based on leaf area and ground area. Each layer's leaf sample was dried, weighed, and ground to determine leaf N concentration using an elemental analyzer. The specific leaf N (SLN) of each layer was calculated based on leaf N content and leaf area. On the same day, canopy light distribution of each layer was measured with an AccuPAR LP-80 between 1,100 and 1,300 h. The following eq. describes the relationship between canopy light distribution and canopy structure: $I=I_o \cdot \exp(-K_L F)$ (Gallagher and Biscoe 1978), where F is the cumulative LAI from the canopy top, I and I_o are light intensity on a horizontal level at F and the canopy top, respectively, K_L is the light extinction coefficient. The N gradient within the canopy can be described by an exponential function as $SLNi=(N_o-N_b)\exp(-K_N F)+N_b$ (Anten *et al.* 1995), where SLN*i* is the SLN (g m^{-2}) of the *i*th layer of the canopy, N_o is SLN of the top leaves, N_b is the base value of SLN for photosynthesis, and its value was 0.3 g m^{-2} (Yin and Laar 2005), K_N is the extinction coefficient for effective leaf N.

Total N uptake and NUE Dry samples from PM (straw, filled grain, and half-filled grain+empty grain+panicle rachis) were ground to determine tissue N concentrations using micro-Kjeldahl digestion, distillation, and titration (Zhao *et al.* 2021). total N uptake (TN) (the product of N concentration and dry weight of each above-ground part) and NUE for grain production (NUEg) (grain yield/TN) were then calculated.

2.4. Statistical analysis

Analysis of variance was conducted using Statistix 9.0, and means were compared based on the least significant difference (LSD) test at the 0.05 probability level. All figures were generated using Origin 2023. Parameters K_L and K_N were estimated using iterative nonlinear least regression using the Gauss method in PROC NLIN of SAS.

3. Results

3.1. Grain yield and yield components

The grain yield of both YLY900 and CY6203 was significantly affected by N input, planting density, and their interaction (Fig. 2). Increasing N input under D1 significantly improved the grain yield of both varieties. Similarly, increasing the N rate from N1 to N2 under D2 significantly enhanced the yield. However, further increases in N input showed no significant effect on yield. Among the six combinations of N rate and planting density, YLY900 yields in 2021 and 2022 ranged from 6.51–8.95 and 4.70–8.50 t ha^{-1}, respectively. The yields of CY6203 ranged from 6.67–11.14 and 6.20–8.85 t ha^{-1}, respectively. The two-year average yields of YLY900 in N2D2, N3D1, and N3D2 were 8.54, 8.67, and 8.70 t ha^{-1}, respectively. The yields of CY6203 were 9.97, 9.23 and 9.97 t ha^{-1}, respectively.

The yield differences caused by N input were primarily due to the number of total spikelets and grain-filling percentage (Table 1). Compared with N1, total spikelet numbers increased by 19.3 and 29.1% in N2 and N3. The grain-filling percentage increased by 1.8 and 3.1%, averaged across varieties, planting densities, and years, respectively. Higher grain yields under D2 were also attributed to increased total spikelets m^{-2}, specifically, a 20.8% increase compared to D1. Additionally, panicles m^{-2}, grain-filling percentage, and grain weight of CY6203 were consistently and significantly higher than those of YLY900 in both years, explaining its higher yield. The yield difference between years was primarily attributed to grain filling percentage, with an 11.2% lower grain filling percentage observed in 2022 compared to that in 2021.

3.2. Dry weight and harvest index

Dry weights during the TP–MT, MT–PI, PI–HD, and HD–PM stages increased with higher N application or planting density (except for CY6203 in 2022) (Fig. 3). Total dry weight at PM reached 16.5 and 16.9 t ha^{-1} under N2 and N3, averaged across varieties, planting densities, and years, representing increases of 21.0 and 23.8% compared to N1, respectively. The total dry weight attained 16.8 t ha^{-1} under D2, showing a 15.2% increase compared to D1. While the average dry weight at HD was marginally lower, both post-flowering dry weight and total dry weight were significantly higher in 2022 than in 2021. Regarding varieties, CY6203 exhibited higher total dry weight than YLY900 in both years. HI showed no significant difference between N1 and N2, but increased by 7.4% in N3 compared to N2 (Fig. 4). Higher planting density enhanced HI, with D2 showing a 4.1% increase over D1. Additionally, HI values were lower in 2022 compared to 2021.

3.3. Canopy light interception and RUE

Both pre- and post-flowering IP and IPAR increased with higher N input, maintaining consistency across both years (Table 2). However, RUE demonstrated variations across periods and between years. Pre-flowering RUE increased significantly with higher N application in 2021, while in 2022, it initially decreased before increasing. Post-flowering RUE showed an initial increase followed by a reduction. Higher planting density enhanced pre-flowering IP by an average of 5.5% but had no significant impact on post-flowering IP. It also improved pre- and post-flowering RUE by averages of 7.5 and 13.5%, respectively. Among the six combinations of N rate and planting density, pre-flowering RUE was 4.0% lower under N2D2 than N3D1, while post-flowering RUE was 19.8% higher.

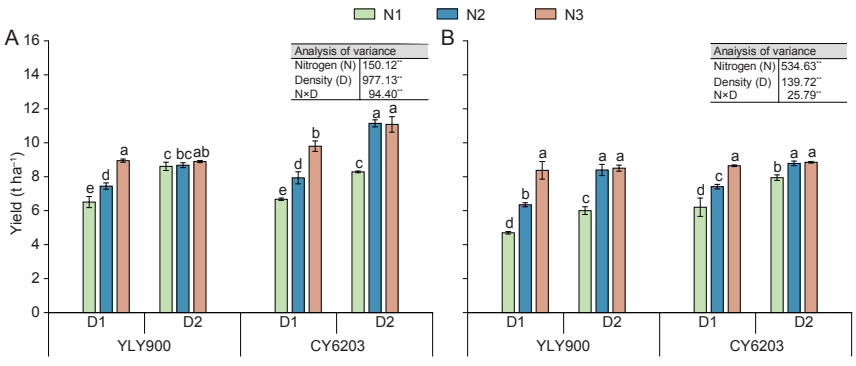


Fig. 2 Grain yield responses of Yliangyou 900 (YLY900) and Chuanyou 6203 (CY6203) cultivars under varying nitrogen application rates and planting densities in 2021 (A) and 2022 (B). Bars mean SE (n=3). N1–N3, nitrogen applications of 0, 90 and 180 kg N ha^{-1}, respectively. D1, 22.2 (30 cm×15 cm) hills m^{-2}; D2, 33.3 (20 cm×15 cm) hills m^{-2}. Different letters above columns denote statistical significance at the P<0.05 level among treatments within each variety.

Table 1 Yield components for Yliangyou 900 (YLY900) and Chuanyou 6203 (CY6203) under different N and planting density treatments in 2021 and 2022

Variety	Nitrogen[1)]	Density[2)]	2021				2022			
			Panicles m^{-2}	Spikelets/ panicle	Grain filling (%)	Grain weight (mg)	Panicles m^{-2}	Spikelets/ panicle	Grain filling (%)	Grain weight (mg)
YLY900	N1	D1	141.4 d	250.0 c	77.7 c	20.7 c	126.4 e	265.9 d	64.3 c	21.7 bc
		D2	169.7 c	267.2 ab	78.2 c	21.4 b	231.2 a	208.9 f	66.5 b	21.1 cd
	N2	D1	164.7 c	260.9 b	83.0 a	21.8 ab	186.3 c	246.3 e	69.9 a	21.0 d
		D2	198.8 b	272.0 a	71.2 d	22.2 a	192.9 c	291.4 c	59.3 e	22.7 a
	N3	D1	194.6 b	240.4 d	79.6 b	21.8 a	173.7 d	302.3 b	67.2 b	21.9 b
		D2	230.4 a	240.8 d	72.0 d	22.1 a	201.7 b	315.4 a	61.6 d	21.4 bcd
CY6203	N1	D1	159.7 f	191.4 bc	75.1 d	25.8 b	188.5 d	168.8 d	67.8 d	25.6 a
		D2	183.0 e	197.7 b	79.1 c	25.7 b	237.9 a	170.2 d	74.3 b	25.7 a
	N2	D1	195.2 d	188.6 c	74.5 d	26.0 ab	218.5 b	169.8 d	69.2 d	25.0 b
		D2	225.4 b	192.2 bc	84.9 a	26.3 a	217.9 b	199.0 c	81.9 a	24.4 c
	N3	D1	207.4 c	207.9 a	84.8 a	25.1 c	199.9 c	222.8 a	81.9 a	26.1 a
		D2	275.3 a	169.8 d	81.8 b	25.8 b	240.9 a	211.3 b	72.5 c	26.1 a
Analysis of variance										
Nitrogen (N)			162.8**	3.9 ns	12.3**	3.4 ns	4.6*	41.1**	7.2*	2.7 ns
Density (D)			250.8**	0.1 ns	13.9**	4.7 ns	123.8**	0.6 ns	0.9 ns	0.1 ns
Variety (V)			127.5**	394.7**	39.7*	611.6**	466.4**	774.3**	125.5**	1,653.1**
N×D			11.5**	13.4**	42.4**	0.1 ns	39.0**	20.1**	25.1**	2.7 ns
V×N			2.2**	2.6 ns	53.1**	2.9 ns	0.5 ns	2.3 ns	14.6**	5.6*
V×D			2.8**	13.1**	221.6**	0.2 ns	5.8*	0.6 ns	32.1**	1.2 ns
V×N×D			7.0**	3.5 ns	80.0**	0.8 ns	8.8**	9.6**	32.6**	8.1**

[1)] N1–N3, nitrogen applications of 0, 90 and 180 kg N ha^{-1}, respectively.
[2)] D1, 22.2 (30 cm×15 cm) hills m^{-2}; D2, 33.3 (20 cm×15 cm) hills m^{-2}.
Values followed by different lowercase letters within a column denote significant differences among treatments for the same cultivar (P<0.05). In the ANOVA results, * and ** indicate statistical significances at 0.05 and 0.01 probability levels, respectively; ns, no significant difference.

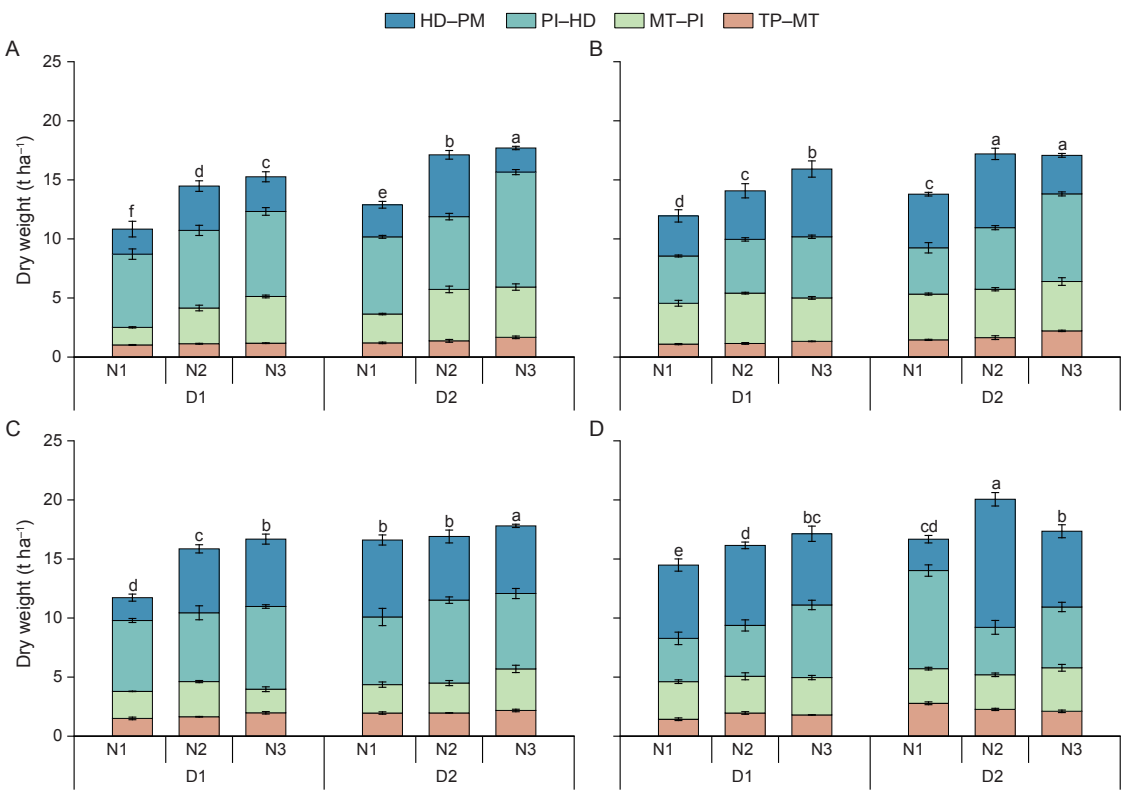


Fig. 3 Dry weight measurements for Yliangyou 900 (YLY900) (A and C) and Chuanyou 6203 (CY6203) (B and D) under varying nitrogen and planting density treatments in 2021 (A and B) and 2022 (C and D). N1–N3, 0, 90 and 180 kg N ha^{-1}. D1, 22.2 (30 cm×15 cm) hills m^{-2}; D2, 33.3 (20 cm×15 cm) hills m^{-2}. Bars mean SE (n=3). Different letters above columns denote statistical significance at the P<0.05 level among treatments within the same variety. MT, mid-tillering stage; PI, panicle initiation stage; HD, heading stage; PM, physiological maturity stage.

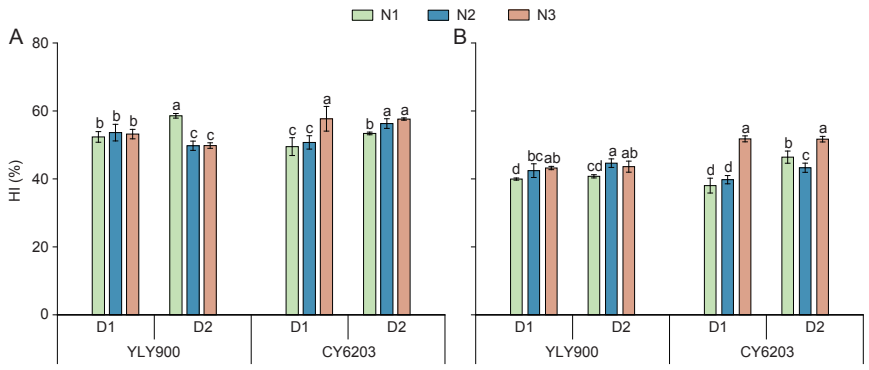


Fig. 4 Harvest index values for Yliangyou 900 (YLY900) and Chuanyou 6203 (CY6203) under varying nitrogen application rates and planting density treatments in 2021 (A) and 2022 (B). Bars mean SE (*n*=3). Different letters above columns denote statistical significance at the *P*<0.05 level among treatments within the same variety. HI, harvest index. N1–N3, 0, 90 and 180 kg N ha^{-1}. D1, 22.2 (30 cm×15 cm) hills m^{-2}; D2, 33.3 (20 cm×15 cm) hills m^{-2}.

Table 2 Intercepted percentage (IP), intercepted photosynthetically active radiation (IPAR) and radiation use efficiency (RUE) at major growth periods for Yliangyou 900 (YLY900) and Chuanyou 6203 (CY6203) under different N and planting density treatments in 2021 and 2022

Variety	Nitrogen[1)]	Density[2)]	2021[3)]						2022[3)]					
			TP–HD			HD–PM			TP–HD			HD–PM		
			IP (%)	IPAR (MJ m^{-2})	RUE (g MJ^{-1})	IP (%)	IPAR (MJ m^{-2})	RUE (g MJ^{-1})	IP (%)	IPAR (MJ m^{-2})	RUE (g MJ^{-1})	IP (%)	IPAR (MJ m^{-2})	RUE (g MJ^{-1})
YLY900	N1	D1	52.2 c	580.6 d	1.50 e	81.3 f	524.9 f	0.43 c	46.2 e	580.7 d	1.69 bc	87.9 c	668.5 e	0.37 e
		D2	52.6 c	655.8 c	1.75 c	84.4 e	547.7 e	0.54 b	51.1 c	642.3 c	1.57 d	88.2 c	670.9 e	0.97 a
	N2	D1	58.6 b	669.8 ab	1.64 d	91.4 c	622.0 c	0.55 b	51.5 c	646.5 c	1.62 cd	94.4 a	726.4 c	0.68 d
		D2	59.3 b	583.3 d	1.80 bc	89.2 d	612.1 d	0.86 a	54.4 b	683.1 b	1.69 bc	92.5 b	711.7 d	0.76 c
	N3	D1	59.4 b	660.1 bc	1.84 b	93.4 b	666.1 b	0.42 c	48.0 d	590.8 d	1.86 a	91.9 b	741.5 b	0.80 b
		D2	60.7 a	679.3 a	2.30 a	95.3 a	687.9 a	0.38 d	56.6 a	696.4 a	1.73 b	94.1 a	759.0 a	0.72 cd
CY6203	N1	D1	52.6 d	512.0 d	1.67 c	86.7 c	495.9 e	0.63 e	49.8 d	687.7 c	1.20 d	91.6 bc	496.9 e	1.25 c
		D2	53.5 d	591.6 c	1.82 b	87.2 c	518.8 d	0.96 c	54.1 b	746.3 a	1.88 a	93.0 a	504.9 d	0.56 e
	N2	D1	59.3 c	614.4 b	1.68 c	92.1 b	543.7 c	0.77 d	48.0 e	662.0 d	1.42 c	90.1 d	549.6 c	1.30 b
		D2	61.0 b	507.9 d	1.85 b	93.7 a	576.4 a	1.17 a	51.6 c	712.2 b	1.29 d	90.8 cd	554.1 c	2.06 a
	N3	D1	60.1 bc	593.7 c	1.66 c	92.3 b	562.7 b	1.03 b	51.9 c	705.5 b	1.57 b	93.5 a	612.1 a	1.08 d
		D2	62.6 a	625.3 a	2.21 a	92.1 b	583.3 a	0.54 f	55.0 a	747.4 a	1.46 c	92.1 b	602.9 b	1.06 d
Analysis of variance														
Nitrogen (N)			576.7**	901.1**	193.47**	413.8**	1,708.5**	301.03**	49.7**	18.6**	15.42**	75.0**	1,946.4**	376.43**
Density (D)			16.2**	2.0 ns	279.95**	4.4 ns	67.3**	210.94**	418.9**	396.1**	3.64 ns	1.1 ns	0.9 ns	104.15**
Variety (V)			173.6**	9,175.2**	0.47 ns	358.5**	23,119.2**	2,135.88**	15.0 ns	2,990.3**	484.02**	9.9 ns	64,240.4**	1,035.18**
N×D			1.1 ns	1.1 ns	40.21**	2.6 ns	2.5 ns	711.07**	11.0**	8.8**	25.43**	3.9*	5.1*	213.37**
V×N			0.9 ns	6.1**	30.68**	56.7**	224.3**	16.27**	80.7**	79.4**	8.57*	129.9**	47.2**	337.97**
V×D			2.1 ns	0.2 ns	0.02 ns	0.2 ns	9.4**	10.01**	16.5**	8.9*	18.05**	0.1 ns	0.1 ns	76.47**
V×N×D			0.1 ns	0.2 ns	2.29 ns	7.2**	10.1**	207.68**	17.9**	15.6**	39.55**	18.2**	22.0**	757.09**

[1)] N1–N3, 0, 90 and 180 kg N ha^{-1}, respectively.
[2)] D1, 22.2 (30 cm×15 cm) hills m^{-2}; D2, 33.3 (20 cm×15 cm) hills m^{-2}.
[3)] TP, transplanting; HD, heading; PM, maturity.
Values followed by different lowercase letters within a column denote significant differences among treatments for the same cultivar (*P*<0.05). In ANOVA, * and ** indicate significance at 0.05 and 0.01 probability levels, respectively, while ns indicates no significant difference.

Between experimental years, pre-flowering RUE was 11.5% lower in 2022 than 2021, while post-flowering RUE was 39.4% higher. IPAR increased with planting density, though significant differences varied by growth period and planting years. CY6203 demonstrated significantly higher post-flowering IP and RUE but lower IPAR.

3.4. Total N uptake and NUE

Higher N input enhanced total N uptake but reduced NUEg, with N2 and N3 increasing total N uptake by 43.7 and 53.2% while decreasing NUEg by 12.3 and 16.3%, respectively, compared to N1 (Table 3). Increased planting density enhanced total N uptake, showing 18.5% higher values under D2 than D1. However, its effect on NUEg varied between years, with significant improvement in 2021 but no significant difference in 2022. N2D2 demonstrated 4.4% higher NUEg compared to N3D1. Both total N uptake and NUEg were significantly influenced by variety, variety-N fertilizer interaction,

Table 3 Nitrogen uptake and N use efficiency for Yliangyou 900 (YLY900) and Chuanyou 6203 (CY6203) under different N and planting density treatments in 2021 and 2022

Variety (V)	Nitrogen (N)[1]	Density (D)[2]	2021[3]		2022[3]	
			N uptake (kg ha^{-1})	NUEg (kg kg^{-1})	N uptake (kg ha^{-1})	NUEg (kg kg^{-1})
YLY900	N1	D1	107.5 f	60.5 b	123.4 f	38.1 a
		D2	123.4 e	69.8 a	172.2 e	34.9 b
	N2	D1	147.5 d	50.5 c	196.4 d	36.2 b
		D2	184.5 b	47.1 d	211.2 c	34.8 b
	N3	D1	179.3 c	49.9 c	231.5 b	32.3 c
		D2	214.5 a	41.5 e	267.2 a	39.8 a
CY6203	N1	D1	118.9 e	56.2 ab	130.6 e	47.5 a
		D2	143.2 d	57.9 a	164.7 d	48.3 a
	N2	D1	162.3 c	48.9 c	200.8 b	45.2 b
		D2	202.2 a	55.1 b	252.4 a	44.6 b
	N3	D1	178.8 b	54.8 b	191.2 c	36.9 c
		D2	199.0 a	55.7 b	198.5 b	34.8 d
Analysis of variance						
N			1,845.5**	94.7**	5,439.2**	155.1**
D			2,125.4**	11.3**	2,039.9**	0.1 ns
V			16.1 ns	2.4 ns	317.4**	119.8**
N×D			72.9**	76.8**	66.4**	4.2*
V×N			67.5**	50.1**	1,269.2**	146.1**
V×D			0.9 ns	38.4**	2.3 ns	1.7 ns
V×N×D			32.3**	85.6**	196.4**	11.3**

[1] N1–N3, nitrogen application rates of 0, 90 and 180 kg N ha^{-1}, respectively.
[2] D1, 22.2 (30 cm×15 cm) hills m^{-2}; D2 represents 33.3 (20 cm×15 cm) hills m^{-2}.
[3] NUEg, nitrogen use efficiency for grain production.
Values followed by different lowercase letters within a column indicate statistically significant differences among treatments for the same cultivar (P<0.05). In the ANOVA analysis, * and **, significant differences at 0.05 and 0.01 probability levels, respectively; ns, no significant difference.

and planting years. Total N uptake was 19.3% higher in 2022 than 2021, while NUEg was 26.9% lower. CY6203 exhibited 9.4% higher NUEg than YLY900, averaged across N levels, planting densities, and experimental years.

3.5. Vertical distribution of light and N in the canopy

K_L and K_N were determined by analyzing the relationship between cumulative LAI and relative photosynthetically active photon flux density (PPFD) (Fig. 5), and the relationship between cumulative LAI and SLN per layer (Fig. 6). Both K_L and K_N values exhibited a decrease with increasing LAI. K_N, K_L, and K_N/K_L were significantly influenced by N rate, planting density, and N rate×planting density interaction (except K_L in 2022) (Table 4). K_N showed consistent patterns across both years, decreasing with higher N rates or planting densities. Compared to N1, K_N decreased by 43.5 and 58.8% under N2 and N3, respectively. The K_N under D2 showed a 16.0% reduction compared to D1. K_L and K_N/K_L values were higher under low N input but showed an inverse trend under high N treatments. Higher planting density resulted in decreased K_L and K_N/K_L values compared to D1. Regarding varieties, CY6203 exhibited a 23.4% higher K_N/K_L value than YLY900, averaged across N rate, planting density, and experimental years. N2D2 demonstrated higher K_L but similar K_N and K_N/K_L compared to N3D1. The values of K_N, K_L, and K_N/K_L varied between years, with 2022 showing an 11.4% higher K_L, but 36.8% lower K_N and 41.5% lower K_N/K_L than 2021.

3.6. Correlation analysis

As shown in Fig. 7, grain yield demonstrated significant positive correlations with panicles m^{-2} and grain-filling percentage, with correlation coefficients of 0.63 and 0.52, respectively. The number of panicles m^{-2} exhibited a significant positive correlation with dry weight at HD. Significant positive correlations were also observed between dry weight at HD and pre-flowering IP, IPAR, and RUE. Analysis revealed that pre-flowering RUE had a significant negative correlation with K_L, indicating that more uniform light distribution with lower K_L in the canopy enhanced rice RUE. Grain-filling percentage showed a significant positive correlation with HI, which in turn demonstrated a significant positive correlation with NUEg. Further analysis indicated that NUEg exhibited significant positive correlations with K_N and K_N/K_L, with correlation coefficients of 0.59 and 0.64, respectively.

4. Discussion

4.1. Effects of N application and planting density on grain yield, RUE, and NUE in hybrid rice

The benefits of appropriate increases in N application and planting density for improving rice yield through enhanced

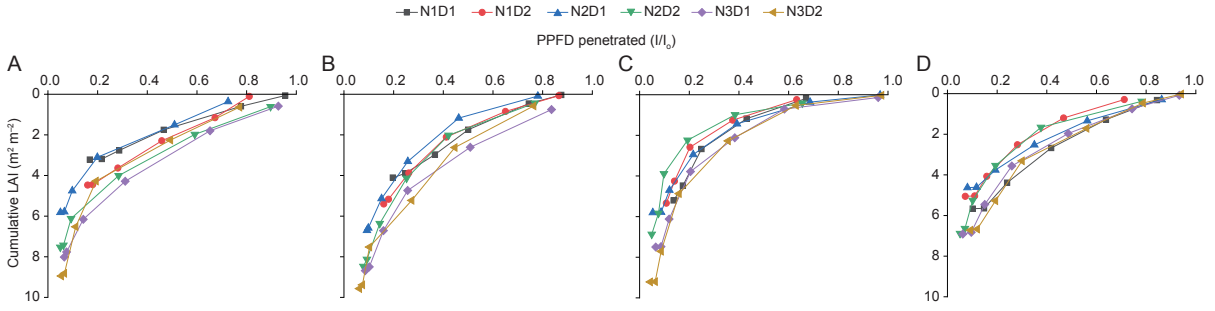


Fig. 5 Cumulative leaf area index (LAI) calculated from the canopy apex *vs.* relative photosynthetically active photon flux density (PPFD) penetration for Yliangyou 900 (YLY900) (A and C) and Chuanyou 6203 (CY6203) (B and D) under varying nitrogen application rates and planting density treatments in 2021 (A and B) and 2022 (C and D). N1–N3, 0, 90 and 180 kg N ha^{-1}, respectively. D1, 22.2 (30 cm×15 cm) hills m^{-2}; D2 indicates 33.3 (20 cm×15 cm) hills m^{-2}.

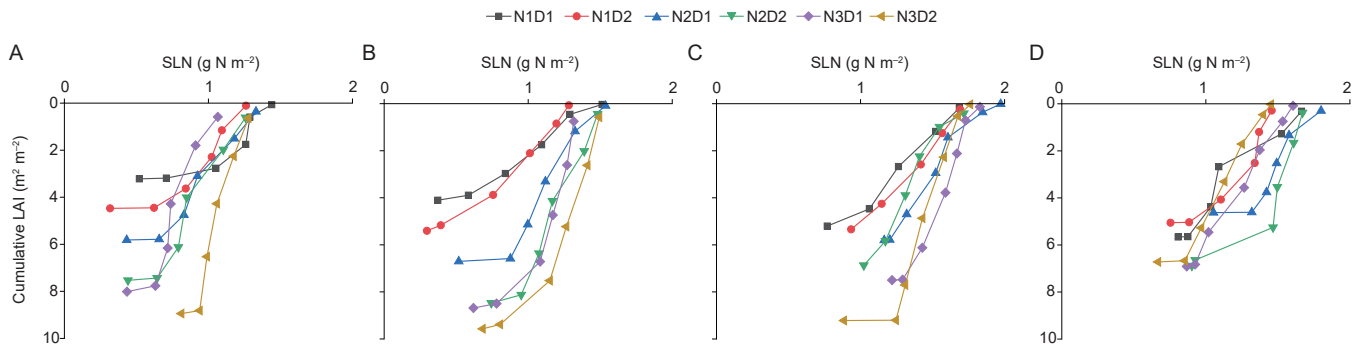


Fig. 6 Cumulative leaf area index (LAI) calculated from the canopy top *vs*. specific leaf nitrogen (SLN) for Yliangyou 900 (YLY900) (A and C) and Chuanyou 6203 (CY6203) (B and D) under varying nitrogen and planting density treatments in 2021 (A and B) and 2022 (C and D). N1–N3, 0, 90 and 180 kg N ha^{-1}, respectively. D1, 22.2 (30 cm×15 cm) hills m^{-2}; D2, 33.3 (20 cm×15 cm) hills m^{-2}.

Table 4 Nitrogen extinction coefficient (K_N), light extinction coefficient (K_L) and the ratio of K_N to K_L (K_N/K_L) values for Yliangyou 900 (YLY900) and Chuanyou 6203 (CY6203) under different N and planting density treatments in 2021 and 2022

Variety	Nitrogen[1)]	Density[2)]	2021			2022		
			K_N	K_L	K_N/K_L	K_N	K_L	K_N/K_L
YLY900	N1	D1	0.26 a	0.50 a	0.52 b	0.17 a	0.32 e	0.54 a
		D2	0.27 a	0.35 c	0.77 a	0.14 b	0.38 c	0.36 b
	N2	D1	0.22 b	0.47 a	0.46 c	0.10 c	0.46 b	0.23 c
		D2	0.17 c	0.40 b	0.43 c	0.10 c	0.49 a	0.20 cd
	N3	D1	0.14 d	0.34 c	0.43 c	0.06 d	0.35 d	0.19 d
		D2	0.06 e	0.33 c	0.18 d	0.07 d	0.33 de	0.21 cd
CY6203	N1	D1	0.36 a	0.33 a	1.10 a	0.19 a	0.35 c	0.55 a
		D2	0.31 b	0.31 ab	1.01 b	0.13 b	0.43 b	0.31 c
	N2	D1	0.15 c	0.32 a	0.48 c	0.10 c	0.49 a	0.21 d
		D2	0.09 d	0.28 bc	0.33 d	0.10 c	0.42 b	0.24 d
	N3	D1	0.10 d	0.28 bc	0.34 d	0.11 bc	0.36 c	0.31 c
		D2	0.09 d	0.27 c	0.32 d	0.12 b	0.32 d	0.39 b
Analysis of variance								
Nitrogen (N)			748.31**	21.93**	513.78**	451.92**	167.15**	262.57**
Density (D)			74.13**	44.01**	8.08*	17.75**	0.52 ns	26.32**
Variety (V)			0.24 ns	282.24**	31.37*	156.07**	0.71 ns	56.34*
N×D			5.62*	8.18**	14.76**	25.04**	19.42**	64.34**
N×V			90.40**	6.39*	95.33**	67.80**	9.09**	40.28**
D×V			0.05 ns	15.12**	5.36*	0.57 ns	6.17*	0.34 ns
N×D×V			19.71**	6.96**	24.99**	2.05 ns	5.28*	3.75 ns

[1)] N1–N3, 0, 90 and 180 kg N ha^{-1}.
[2)] D1, 22.2 (30 cm×15 cm) hills m^{-2}; D2, 33.3 (20 cm×15 cm) hills m^{-2}.
Values followed by different lowercase letters within a column denote significant differences among treatments for the same cultivar (P<0.05). In ANOVA, * and ** indicate statistical significance at 0.05 and 0.01 levels, respectively, while ns indicates no significant difference.

panicle numbers and total spikelets have been extensively documented (Hou *et al.* 2019; Fu *et al.* 2021; Chong *et al.* 2023). The present study supports these findings. Rice yield was significantly affected by the interaction between N fertilizer and planting density (Zhou *et al.* 2019). The effect of increased N input on grain yield was more substantial under D1 compared to D2 (Fig. 2). Additionally, elevated N input under D2, particularly at high N rates, resulted in excessive population density, reduced ventilation and light transmission, and increased disease and pest susceptibility, leading to yield reduction (Hou *et al.* 2019).

Both increasing N input and planting density enhanced dry weight and HI at PM, with a more pronounced effect on dry weight (Figs. 3 and 4; Huang *et al.* 2018; Chen *et al.* 2019). Contemporary high-yield theory indicates that dry matter accumulation correlates strongly with RUE (Liu K *et al.* 2020). This study revealed that pre-flowering RUE increased, while post-flowering RUE initially increased then decreased with higher N input (Table 2). Higher N application levels elevated leaf N concentration and population LAI, leading to enhanced photosynthetic rate and RUE (Lafarge *et al.* 2002; Li *et al.* 2009). However, certain studies indicate that N fertilizer application did not influence RUE (Liu K *et al.* 2020). Conversely, increased planting density enhanced RUE. This enhancement likely occurs because higher planting density reduces pre-canopy closure incident solar radiation waste by increasing tillering number and leaf area, thereby improving canopy light interception, RUE, and grain yield (Chen *et al.* 2019; Fu *et al.* 2021; Chong *et al.* 2023).

Regarding N absorption and utilization, current and

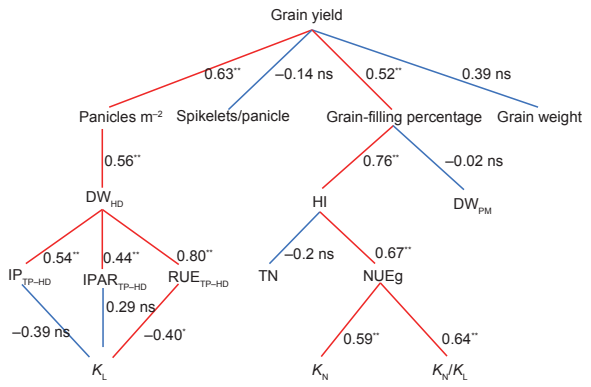


Fig. 7 A schematic diagram illustrating how management practices enhance yield, radiation use efficiency (RUE) and nitrogen use efficiency for grain production (NUEg) through their effects on N extinction coefficient (K_N), light extinction coefficient (K_L) and the ratio of K_N to K_L (K_N/K_L). DW, dry weight; TP, transplanting stage; HD, heading stage; PM, maturity stage; HI, harvest index; IP, Interception percentage; IPAR, intercepted photosynthetically active radiation; TN, total nitrogen uptake. ns, not significant at the 0.05 probability level. * and **, significant at the 0.05 and 0.01 probability levels, respectively.

previous studies demonstrate that increased N application enhanced total N absorption while reducing NUEg (Table 3; Huang *et al.* 2018; Zhou *et al.* 2023). Appropriate N input prevents excessive rice root growth and facilitates greater N transport to above-ground parts, enabling high yield and NUE (Xu *et al.* 2023). Higher planting density establishes optimal source–sink relationships by regulating dry matter distribution among organs, thereby enhancing plant N uptake and NUE (Zhu *et al.* 2023).

Furthermore, observations revealed that average yield, total RUE, and NUE under N2D2 exceeded those under N3D1. These findings suggest that dense planting with reduced N application maintains rice yield while improving resource use efficiency, thereby minimizing environmental impacts from N input (Fu *et al.* 2021; Chong *et al.* 2023). The aforementioned indicators varied between years, potentially due to climatic conditions. The pre-flower temperature in 2022 significantly exceeded that of 2021, particularly during panicle initiation. Sánchez *et al.* (2014) identified 33.1°C as the high-temperature threshold at PI, while this study recorded an average daily maximum temperature of 35.7°C during panicle initiation in 2022. Previous research demonstrated that grain filling percentage exhibited highest sensitivity to elevated temperatures at PI (Wu *et al.* 2016), with decreased grain filling percentage primarily resulting from reduced spikelet fertility rather than poor grain filling (Cheabu *et al.* 2019). Consequently, high temperature at PI led to reduced pre-flowering dry weight and grain-filling percentage, resulting in lower pre-flowering RUE, grain yield, and NUE.

4.2. Canopy light and N distribution under different N levels and planting densities

The method has undergone extensive testing across various crop types, with K_L typically ranging between 0.3 and 1.0 (Monsi and Saeki 2005). The K_L values observed in this study ranged from 0.30 to 0.50 (Table 4), aligning with previous research findings (Monsi and Saeki 2005). Cultivation practices demonstrated significant influence on K_L. The study revealed higher K_L values under low and medium N rates, with a decreasing trend as N input increased. Additionally, higher planting density corresponded to decreased K_L values. Various management practices, including N fertilizer application, increased planting density, water management, and organic fertilizer usage, contributed to K_L reduction (Gu *et al.* 2017). Research by Zhu *et al.* (2022) indicated that applying 180–200 kg N ha^{-1} resulted in lower K_L compared to no N treatment. Similarly, K_L decreased with increasing LAI. Enhanced N input and planting density expanded LAI through increased tiller numbers and promoted leaf growth, leading to reduced K_L (Fig. 5; Gu *et al.* 2017). However, research on oilseed rape reported increased K_L with higher N application (Liu T *et al.* 2020), contrasting with our findings. This difference likely stems from variations in canopy structures among crops and differential K_L responses to N fertilizer across crop types.

In this study, K_N was utilized to assess canopy N distribution: the highest K_N value was observed under zero N conditions, decreasing with increased N application (Table 4). Previous research confirmed that plants under low N conditions exhibited steeper leaf N distribution compared to those with adequate N supply (Gu *et al.* 2017; Liu T *et al.* 2020; Zhu *et al.* 2022). The K_N response to N fertilizer appears related to N availability. Increased N input enhanced soil N availability, subsequently reducing leaf N transport and decreasing K_N. Under low N conditions, restricted canopy expansion and accelerated senescence of older leaves, coupled with N redistribution to younger leaves, resulted in more pronounced vertical N gradient distribution and elevated K_N (Dreccer *et al.* 2000; Tian *et al.* 2022). Higher planting density reduced canopy light penetration through mutual shading, triggering N redistribution from older to younger leaves (Hirose and werger 1987) and creating steep SLN gradients (Hirose *et al.* 1988). However, our findings showed K_N decreased with increased planting density under medium and low N treatments, attributed to the negative correlation between K_N and LAI, as illustrated in Fig. 6 (Liu T *et al.* 2020). The high planting density treatment of 33.3 hills m^{-2} did not constitute excessive density, thus minimizing leaf shading under low N conditions and potentially explaining the absence of increased K_N. Under high N application, the difference in K_N between planting densities showed no statistical significance (except for YLY900 in 2021). This may be attributed to delayed leaf senescence due to increased N absorption under high N conditions (Table 3), resulting in reduced N transport from older to younger leaves. Additionally, lower K_N values in 2022 compared to 2021 likely resulted from higher N accumulation and lower pre-flowering dry weight caused by elevated temperatures at PI, leading to more uniform canopy N distribution in 2022.

Research suggests that N gradient distribution within a canopy serves to maximize carbon assimilation (HiRose and Werger 1987). However, the N distribution remains suboptimal. Anten *et al.* (1995) and Hikosaka (2014)

demonstrated that $K_N/K_L \geq 1$ when light and N distribution reached optimal levels. In this study, the average K_N/K_L for YLY900 and CY6203 under six combinations of N level and planting density was 0.38 and 0.47, ranging from 0.18–0.77 and 0.21–1.10, respectively (Table 4). K_N/K_L peaked under zero N rate and decreased with N application. Higher planting density typically led to decreased K_N/K_L, primarily due to reduced K_N. Compared to N3D1, N2D2 exhibited higher K_L and K_N but similar K_N/K_L. These findings indicate that dense planting with reduced N application decreased light transmittance while enhancing N gradient distribution, maintaining coordinated distribution of canopy light and N.

4.3. Optimizing canopy light and N distribution synergistically improves grain yield and radiation/N use efficiency

Extensive research demonstrates that aligning canopy N gradient distribution with light gradient distribution maximizes canopy photosynthesis, leading to enhanced yield and resource use efficiency in crops (Gu *et al.* 2017; Huang *et al.* 2019). This study revealed K_L had a significant negative correlation with pre-flowering RUE. Additionally, RUE strongly correlated with dry matter accumulation and grain yield (Fig. 7). Lower K_L values indicate more uniform light distribution in the canopy, reducing light saturation in upper leaves and light deficiency in lower leaves. This enhancement improves canopy photosynthetic capacity and RUE, ultimately increasing dry matter accumulation and grain yield (Long *et al.* 2006; Gu *et al.* 2014). Further analysis revealed that both K_N and K_N/K_L showed significant positive correlations with NUEg. NUEg correlated closely with HI, and increased HI improved yield through enhanced grain-filling percentage. These findings indicate that greater N gradient distribution within the canopy and higher consistency with light distribution lead to improved yield and NUE. Previous research confirms the relationship between K_N/K_L values and rice yield and NUE (Gu *et al.* 2017; Huang *et al.* 2019; Zhu *et al.* 2022). Consequently, comparable K_N/K_L values enabled N2D2 treatment to achieve similar yields and marginally higher NUE compared to N3D1. However, given the limited scope of three N fertilizer and two planting density treatments, and substantial N rate gradients, determining the optimal combination requires additional research.

Analysis of previous research, including our prior study (K_N/K_L value of 0.25 on average, Huang *et al.* 2019), the current study (K_N/K_L value of 0.25 on average, Table 4), and the work of Gu *et al.* (2017) (K_N/K_L value of 0.34 on average), reveals K_N/K_L values consistently below 1. These findings indicate that the matching degree of canopy light and N distribution in high-yield varieties used in large-scale production remains substantially below optimal levels (Hikosaka 2014). Importantly, K_N/K_L is influenced by both total N content and N partitioning within leaves (Dreccer *et al.* 2000). Research by Liu T *et al.* (2020) on rape demonstrated that K_N/K_L could be enhanced by reducing SDS-soluble proteins N or increasing the extinction coefficient of water-soluble proteins N. Additionally, Gu *et al.* (2017) proposed that K_N/K_L might correlate with cytokinin content in flag leaves. However, the matching mechanism of light and N distribution within rice canopy remains poorly understood. Therefore, future research will investigate the physiological mechanisms through which cultivation management practices can improve K_N/K_L.

5. Conclusion

The study demonstrates that elevated N input or planting density results in decreased K_N. Under low N conditions, K_L and K_N/K_L values were typically higher compared to high N conditions. Conversely, higher planting density generally led to reduced K_L and K_N/K_L values. Furthermore, K_N, K_L, and K_N/K_L values were influenced by the interaction between N rate and planting density. K_N, K_L, and K_N/K_L values were closely related to dry matter production, RUE and NUEg. The findings suggest that increasing planting density while reducing N input could synergistically enhance yield and NUE through optimized canopy light and N distribution. Further research is required to elucidate the physiological mechanisms through which cultivation management practices can optimize canopy light and N distribution.

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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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