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Agronomic and Physiological Performance of High-Quality *Indica* Rice under Moderate and High Nitrogen Conditions in Southern China

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Abstract: High-quality rice (*Oryza sativa L.)* is increasingly widely planted in China with the improvement of people's living standards and the achievement of rice breeding efforts in recent years. However, the agronomic and physiological performances of high-quality *indica* rice (HQIR) under different nitrogen(N) application conditions in southern China are little known. Two-year consecutive field experiments were conducted with two HQIR and two ordinary-quality *indica* rice (OQIR) varieties under moderate and high N application rates, with yield and yield components, biomass, N uptake, and their related traits investigated. We found that grain yields of HQIR were slightly decreased, but grain yields of OQIR were significantly increased by 6.60%–8.88% under high N rate compared with moderate N rate in both years. Thereby, OQIR produced 8.34%–11.87% and 22.00%–22.50% higher grain yield than HQIR under moderate and high N rates, respectively. The different responses of grain yield to N application rates were mainly due to decreased grain setting rate in HQIR and increased spikelets m^{-2} in OQIR under high N rate. Furthermore, high N rate significantly reduced pre-anthesis AE and improved grain-leaf area ratio, while did not increase post-anthesis DM compared with moderate N rate in HQIR, which might result in carbon metabolic deterioration and imbalance of source-sink relationship and subsequently lower supply of carbohydrate to panicle. Our results suggest that a moderate N rate (165 kg N ha^{-1}) is beneficial for HQIR varieties to balance the maximum grain yield and high quality in southern China.

Keywords: grain yield; biomass; N application rate; high-quality rice

1. Introduction

Rice (*Oryza sativa L.*) is a vital important staple food for more than 60% of the population and contributes nearly 40% of the people's total calorie intake in China [1]. Over the past several decades, the high-yielding traits were always regarded as the principal targets for rice breeding and selecting to meet the population growth of China [2]. For instance, with the development of hybrid rice in 1976 and "super" rice in 1996 in China, the newly released rice varieties which have higher canopy photosynthesis and larger sink size showed about 10% higher yield potential than their check varieties [1–3]. Correspondingly, the national total rice yield and average rice yield have increased 3.09 Mt $year^{-1}$ and 0.127 t ha^{-1} $year^{-1}$ from 1976–1995, and 1.26 Mt $year^{-1}$ and 0.039 t ha^{-1} $year^{-1}$ from 1996–2020, respectively, in despite of the national total rice production area showing a decreasing trend (FAOSTAT, 2020) [4]. These achievements have contributed much to national food self-sufficiency and food security.

Presently, with the development of social economy and the continuous improvement of living standards, the consumer demand for rice food has shifted from quantity to high-quality in China

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[5,6]. However, there has long been a contradiction in achieving high yield and superior quality simultaneously for rice breeders [7,8]. Most high-yielding hybrid *indica* rice varieties generally show poor rice quality, like higher chalkiness degree, lower cooking and eating quality [9,10]. The reasons for this outcome are that most rice yield- or quality-related traits are quantitative, and yield and quality are generally negatively correlated with each other [11–13]. Hence, it is difficult to develop new elite rice varieties with both high yield and superior quality using traditional breeding approaches [13,14]. Fortunately, based on technological innovation of rice breeding (i.e., molecular marker-assisted breeding, molecular design breeding), the improvement of quality of high-yielding rice varieties has been increasingly highlighted in breeding efforts and more and more attentions have been paid on high-quality rice breeding [9,13,14]. So far, over 50% varieties released by province and state have reached the national and ministerial standards of high-quality rice since 2017, which greatly accelerates the popularizing rate of high-quality varieties in rice production in China [15]. Particularly in late-season rice (grown from July to November) of double-rice cropping system of southern China, more than 80% of the late rice varieties planted by farmers have high quality as the optimal temperature in the late-season is conducive to the formation of rice quality.

In comparison with the ordinary-quality rice, the high-quality rice varieties usually have lower yield potential but higher price per unit yield and overall benefits [6,8]. As we all known, nitrogen (N) input plays a vital role in rice production and has significant effects on rice yield and quality. To get more returns, however, rice farmer unrealistically applied a large amount of nitrogen (N) fertilizer to realize higher yield of high-quality rice varieties [16]. Many studies indicated that the overuse of N fertilizer was prevalent in rice production of China, subsequently leading to rice lodging, increased pests and diseases, low N use efficiency, and higher environmental costs [17,18]. In fact, potential yields of most high-yielding rice varieties do not depend on greater N fertilizer input under moderate and high soil fertility conditions [19,20]. On the other hand, excessive N fertilizer input may increase grain protein content and alter starch properties, resulting in remarkable decline in cooking and eating quality for high-quality rice [21–23]. Previous studies showed that optimizing N management, such as reducing total N and/or late-stage N application rate, is beneficial to balance rice yield and quality [16,22]. Most results indicated that the rational N application rate of simultaneously obtaining high yield and superior quality varied with varieties and was 180–270 kg N ha^{-1} for high-quality *japonica* rice (HQJR) [21–23], but such rational N application rate was 135–165 kg N ha^{-1} for high-quality *indica* rice (HQIR) [24–26], which is close to the N application rate of producing maximum yield in ordinary-quality *indica* rice (OQIR) [20,27].

However, the abovementioned studies focused more on the effect of N management on balancing rice yield and quality. The agronomic and physiological responses of yield formation to N application rates are not detailed in HQIR varieties. In this study, we hypothesized that HQIR and OQIR had similar responses in terms of yield formation under different N application rates. Therefore, to verify the hypothesis, two-year field experiments were carried out with two HQIR and two OQIR varieties under moderate and high N rates. The objectives of this study were to explore yield performance of two types of rice varieties with contrasting quality under moderate and high N conditions, and to further reveal the relevant physiological mechanism related to yield formation. The results may provide an insight into the fundamental of balancing high yield and superior quality of HQIR by adopting a reasonable N management.

2. Materials and Methods

2.1. Plant materials

The tested rice varieties included Yexiangyoulisi (YXY), Wanxiangyou-982 (WXY), Jiyou T025 (**JY**) and Keyou-5 (KY), which are all hybrid late *indica* rice. The YXY and WXY are high-quality *indica* rice (HQIR) varieties, while JY and KY are ordinary-quality *indica* rice (OQIR) varieties, the related key quality properties were showed in Table 1. In addition, the YXY and JY were first released in 2017, and WXY and KY were first released in 2019.

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Table 1. The related key quality properties of tested varieties.

Type	Variety	Length-width ratio	Percentage of chalky grains (%)	Chalkiness degree (%)	Gel consistency (mm)	Amylose content (%)
HQIR	YXY	4.0	5.0	0.9	69	13.9
	WXY	3.9	9.0	1.8	73	15.0
OQIR	JY	3.3	23.0	4.8	30	25.9
	KY	2.9	33.0	8.2	36	18.5

Note: Data obtained from China rice data center, https://www.ricedata.cn/variety/index.htm.

2.2. Experimental design

Field experiments were conducted in Jiangxi Shanggao Rice Science and Technology Backyard in 2020 and 2021, which located in Sixi Township, Shanggao County, Jiangxi Province, China (115° 06′ E, 28° 20′ N, 38 m altitude). The soil during the two experimental years were clay loam. The upper 20 cm of soil properties in 2020 were: pH 5.49, 29.51 g kg^{-1} organic C, 18.73 mg kg^{-1} available P, 65.13 mg kg^{-1} available K, and total 1.98 g kg^{-1} N content. In 2021, the soil properties were pH 5.62, 34.95 g kg^{-1} organic C, 19.29 mg kg^{-1} available P, 76.31 mg kg–1 available K, and 2.09 g kg^{-1} total N content. Climate parameters including daily average temperature and solar radiation were collected during the growth period from sowing to maturity from an automatic weather station (Vantage Pro 2, Davis instruments Corp., Hayward, CA, USA) located near the experimental site (Figure 1).

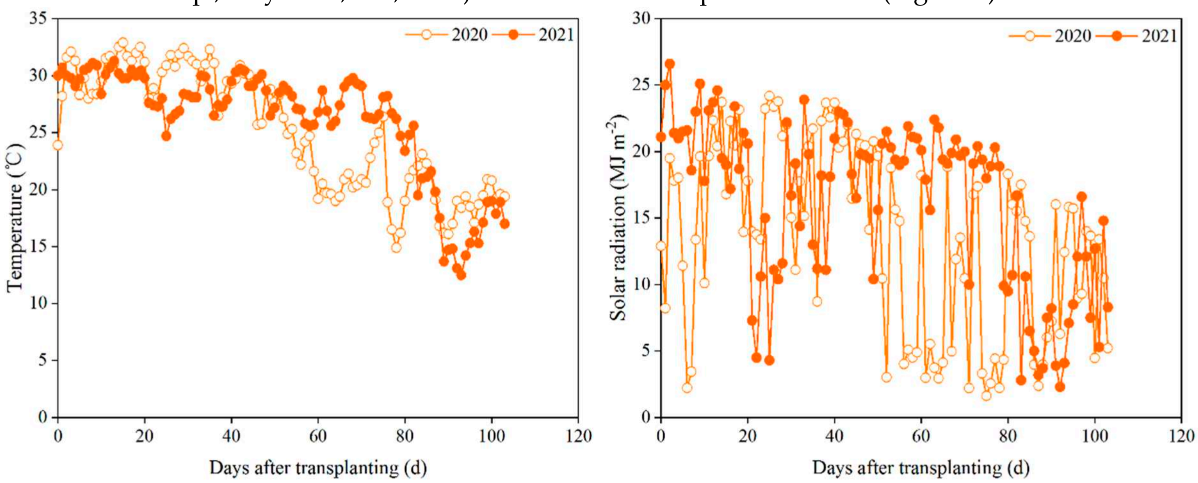

Figure 1. Daily average temperature and solar radiation during the late rice growing seasons in Shanggao County, Jiangxi Province, China in 2020 and 2021.

The experiments were all arranged in a split-plot design with N application rates as main plots and rice varieties as subplots. The experiments were replicated three times with a main plot size of 120 m^2 and subplot size of 30 m^2. Each main plot separated by a ridge with plastic film inserted into the soil to a depth of 0.3 m to minimize leakage and nutrient loss. N application rates were 165 kg N ha^{-1} (moderate N rate) and 225 kg N ha^{-1} (high N rate). For both moderate and high N rates, urea was used as the N fertilizer and was split-applied with 50% as basal (1 day before transplanting), 30% at early-tillering (7 days after transplanting), and 20% at panicle initiation.

Pre-germinated seeds were sown on June 27th in 2020 and June 24th in 2021. The 25-day-old seedlings were transplanted at a hill spacing of 25 cm × 14 cm with two seedlings per hill. The heading date of four rice varieties was on September 8th to 11th in both years, and physiological maturity date was October 26th in 2020 and October 16th in 2021. The amount and method of P and K fertilizer were consistent during the two years; rice plants received 105 kg ha^{-1} P_2O_5 and 180 kg ha^{-1} K_2O. The P was applied as basal, while the K was split equally at basal and panicle initiation. The regime for water management was in the sequence of flooding, midseason drainage, reflooding, and moist intermittent irrigation. Weeds, pests, and diseases were intensively controlled using chemical treatments.

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2.3. Sampling and measurements

2.3.1. Yield and yield components

At maturity, ten hills on a diagonal from the centre of each subplot were sampled to determine the aboveground total biomass and yield components. The sampled plants were separated into straw, filled grains, unfilled grains, and rachis. Panicle number was recorded from the 10 hills and the panicles were hand threshed. The filled grains were separated from unfilled grains using a seed winnowing machine (SXJ-80A, Hangzhou, China) and then were oven-dried at 70 °C to a constant weight. The number of filled and unfilled grains were calculated using an automatic seed counter (DC-3, Zhengzhou, China). Grain yield was determined from 5 m^2 in each plot, and yields were then adjusted to the standard moisture content of 0.135 g H_2O g^{-1} fresh weight.

2.3.2. Biomass and related properties

At heading stage, ten hills, excluding two borders, were sampled from each subplot. The rice plants were separated to leaves, stems and panicles, and then were oven-dried at 70 °C to a constant weight to determine aboveground total dry weight. At maturity, the total biomass including straw, filled grains, unfilled grains, and rachis were determined from abovementioned 2.3.1. Apparent exportation of pre-anthesis stem and leave dry matter (pre-anthesis AE), contribution of pre-anthesis AE, post-anthesis dry matter (pre-anthesis DM), contribution of post-anthesis DM, and harvest index were calculated by the following formulas.

$$\text{Pre-anthesis AE} = \text{stem and leaf dry weight at heading} - \text{stem and leaf dry weight at maturity.} \quad (1)$$

$$\text{Contribution of pre-anthesis AE} = (\text{pre-anthesis AE/grain yield}) \times 100 \quad (2)$$

$$\text{Pre-anthesis DM} = \text{biomass at maturity} - \text{biomass at heading} \quad (3)$$

$$\text{contribution of post-anthesis DM} = (\text{Pre-anthesis DM/grain yield}) \times 100 \quad (4)$$

$$\text{Harvest index} = \text{filled spikelet weight/aboveground total biomass)} \times 100 \quad (5)$$

2.3.3. Leaf area index (LAI) and grain-leaf ratio

Green leaves from six hills at heading stages was measured with a leaf area meter (LI-3000C, LI-COR, Lincoln, NE, USA). LAI was calculated as leaf area/the specific land area. Grain-leaf ratio was calculated as spikelets m^{-2} (filled grains m^{-2} or grain weight m^{-2})/leaf area m^{-2}.

2.3.4. Radiation use efficiency (RUE) and net photosynthetic rate (Pn)

Canopy light interception was measured between 11:00 h and 13:00 h at middle-tillering, panicle initiation, booting, heading, 15 days after heading (HD15), and maturity using the SunScan Canopy Analysis System (Delta-T Devices Ltd., Burwell, Cambridge, UK). The measuring methods and computing methods referenced to Zhang et al. [28]. Briefly intercepted radiation during the whole growing season was the summation of intercepted radiation during each growth period. RUE (aboveground total biomass/intercepted radiation during the whole growing season) was calculated.

The *Pn* was measured on five flag leaves for each subplot at heading, 15 days after heading (HD15) and 30 days after heading (HD30) using a portable photosynthesis system (LI-6400, Li-Cor, Lincoln, NE, USA). The measurements were collected between 9:00 and 11:00 when photosynthetic active radiation above the canopy was 1000–1200 μmol m^{-2} s^{-1}. Meanwhile, a light intensity of 1200 μmol m^{-2} s^{-1}, a leaf temperature of 30 °C, a constant CO_2 concentration of 380 μmol mol^{-1} and a relative humidity of 70% were set up in the sample chamber. Moreover, a chlorophyll meter (SPAD-502, Minolta Camera Co. Ltd., Japan) was used to measure the SPAD value for the corresponding leaves.

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2.3.5. Plant N uptake and N use efficiency

The aboveground plants from heading and maturity stages were ground to a fine powder to determine plant N concentration using a fully automatic Kjeldahl apparatus (Kjeltec 8400, FOSS Analytical A/S, Hilleroed, Denmark). N uptake, post-anthesis N uptake, pre-anthesis N exportation and N use efficiency for grain production (NUE_g) were calculated by the following formulas.

$$\text{N uptake} = \text{N concentration} \times \text{dry matter weight.} \quad (6)$$

$$\text{Post-anthesis N uptake} = \text{N uptake at maturity} - \text{N uptake at heading} \quad (7)$$

$$\text{Pre-anthesis N exportation} = \text{N uptake of stem and leaf at heading} - \text{N uptake of stem and leaf at maturity.} \quad (8)$$

$$NUE_g = \text{grain yield/N uptake at maturity.} \quad (9)$$

2.4. Statistical Analysis

Crop data were analysed using analysis of variance (ANOVA) in Statistix 8.0 (Analytical software, Tallahassee, FL, USA), and the means of the treatments were examined with the least significant (LSD) test at the 5% probability level. Graphs were drawn using Origin 2018 (OriginLab Corp, Northampton, MA, USA).

3. Results

3.1. Grain yield and its components

N application rate and variety had significant effects on grain yield and its components, except for the effect of N application rate on grain weight in 2020 and 2021; Interaction effects between N application rate and variety were observed on spikelets m^{-2}, grain setting rate, grain yield in both years and grain weight in 2021(Table 2). Compared to moderate N rate, grain yields of HQIR were slightly decreased, while grain yields of OQIR were significantly increased by 6.60%–8.88% under high N rate in both years. High N rate significantly increased panicles m^{-2} of HQIR and OQIR, but decreased spikelets per panicle of HQIR, which resulted in significantly increased in spikelets m^{-2} of OQIR. In addition, high N rate also led to a marked decline in grain setting rate of HQIR, while had no effect for OQIR.

OQIR produced higher grain yield of 8.34%–11.87% under moderate N rate and 22.00%–22.50% under high N rate than HQIR in both years. Although panicles m^{-2} of OQIR were significantly lower than HQIR, OQIR had significantly higher spikelets per panicle and spikelets m^{-2} than HQIR under two N rates. However, significant higher grain setting rate was only observed in OQIR than that in HQIR under high N rate. Moreover, OQIR had higher grain weight than YXY (one of the varieties of HQIR) but lower grain weight than WXY.

Table 2. Grain yield and its components of HQR and OQR varieties under moderate and high N rates.

Year	N rate	Variety	Panicles (m^{-2})	Spikelets (panicle^{-1})	Spikelets ($\times 10^3$ m^{-2})	Grain setting rate (%)	Grain weight (mg)	Grain yield (t hm^{-2})
2020	Moderate N	YXY	311.19 a	146.71 b	45.64 c	73.89 a	19.81 d	7.51 c
		WXY	298.76 b	144.99 b	43.31 d	72.74 a	23.38 a	7.64 c
		$Mean_{HQR}$	*304.97 B*	*145.85 B*	*44.48 C*	*73.32 A*	*21.60 B*	*7.58 C*
		KY	283.00 c	172.82 a	48.90 a	74.43 a	21.54 c	8.63 a
		JY	279.62 c	170.19 a	47.58 b	70.16 b	22.53 b	8.33 b
		$Mean_{OQR}$	*281.31 D*	*171.51 A*	*48.24 B*	*72.29 AB*	*22.03 A*	*8.48 B*
	High N	YXY	327.69 a	140.33 b	45.97 c	69.95 b	19.72 d	7.35 c

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		WXY	315.90 b	137.70 b	43.50 d	67.63 c	23.13 a	7.46 c
		Mean$_{HQR}$	*321.80 A*	*139.02 C*	*44.74 C*	*68.79 C*	*21.42 B*	*7.41 C*
		KY	300.14 c	170.09 a	51.04 a	73.67 a	21.73 c	9.19 a
		JY	293.48 c	169.24 a	49.66 b	69.67 b	22.62 b	8.90 b
		Mean$_{OQR}$	*296.81 C*	*169.66 A*	*50.35 A*	*71.67 B*	*22.17 A*	*9.04 A*
2021	Moderate N	YXY	301.02 a	146.17 b	43.00 b	81.95 a	20.71 c	8.47 b
		WXY	286.38 b	142.67 b	40.85 c	81.58 a	23.68 a	8.79 b
		Mean$_{HQR}$	*293.70 B*	*144.42 B*	*42.42 C*	*81.76 A*	*22.19 B*	*8.63 C*
		KY	281.67 b	164.66 a	46.37 a	82.15 a	23.24 b	9.37 a
		JY	280.29 b	163.18 a	45.73 a	82.61 a	23.51 a	9.34 a
		Mean$_{OQR}$	*280.98 C*	*163.92 A*	*46.05 B*	*82.35 A*	*23.38 A*	*9.35 B*
	High N	YXY	325.49 a	136.08 b	44.27 c	77.39 b	20.57 c	8.18 b
		WXY	305.99 b	133.88 b	40.96 d	76.99 b	23.43 b	8.44 b
		Mean$_{HQR}$	*315.74 A*	*134.98 C*	*42.62 C*	*77.19 B*	*21.00 B*	*8.31 C*
		KY	300.95 bc	163.12 a	49.09 a	82.09 a	23.39 b	10.29 a
		JY	293.61 c	160.18 a	47.02 b	81.31 a	23.74 a	10.08 a
		Mean$_{OQR}$	*297.28 B*	*161.65 A*	*48.06 A*	*81.73 A*	*23.56 A*	*10.18 A*
Analysis of variance								
2020	N rate		**	*	**	**	ns	*
	Variety		***	***	***	***	***	***
	N rate ×Variety		ns	ns	***	**	ns	**
2021	N rate		*	*	*	*	ns	*
	Variety		***	***	***	**	***	***
	N rate ×Variety		ns	ns	***	*	**	***

Note: Within a column, different lowercase letters between varieties in the same N rate indicate significant differences at the $p < 0.05$ level; different uppercase letters between varietal types across two N rates indicate significant differences at the $p < 0.05$ level. * , ** and *** represent significant differences at the $p < 0.05$, $p < 0.01$ and $p < 0.001$ probability levels, respectively; ns means no significance.

3.2. Biomass production

Significant effects on biomass at heading and maturity stages, pre-anthesis AE and post-anthesis DM and its contribution to grain yield, as well as harvest index were observed among N application rate, variety, and their interaction in two years, except for interaction effect on the contribution of post-anthesis DM to grain yield (Table 3 and Figure 2). Compared to moderate N rate, high N rate significantly increased biomass of HQIR and OQIR at heading and maturity stages, post-anthesis DM of OQIR, and contribution of post-anthesis DM to grain yield of HQIR and OQIR (excluding 2020). On the other hand, high N rate markedly reduced pre-anthesis AE and harvest index of HQIR, and the contribution of pre-anthesis AE to grain of HQIR and OQIR.

At heading stage, HQIR produced more biomass than OQIR under moderate and high N rates. On the contrary, OQIR had more biomass at maturity stage and subsequently showed significantly higher post-anthesis DM and its contribution to grain yield than OQIR. However, in comparison with OQIR, higher pre-anthesis AE (excluding high N rate in 2020) and its contribution to grain yield were observed in HQIR under two N rates. Moreover, OQIR showed higher harvest index than HQIR under two N application rates in both years.

Table 3. Biomass production and its contribution to grain yield of HQR and OQR varieties under moderate and high N rates.

Year	N rate	Variety	Biomass ($g\ m^{-2}$)		Pre-anthesis AE ($g\ m^{-2}$)	Contribution of pre-anthesis AE (%)	Post-anthesis DM ($g\ m^{-2}$)	Contribution of post-anthesis DM (%)
			Heading	Maturity				
2020	Moderate N	YXY	1020.44 a	1401.26 c	261.17 a	34.75 a	380.82 d	50.70 c
		WXY	1017.14 a	1423.75 b	248.60 b	32.55 b	406.61 c	53.22 c
		Mean$_{HQR}$	*1018.79 B*	*1412.50 D*	*254.89 A*	*33.65 A*	*393.72 C*	*51.96 C*
		KY	926.18 c	1449.41 b	216.34 d	25.07 d	523.23 a	60.61 a

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		JY	943.90 b	1424.06 a	234.17 c	28.10 c	480.16 b	57.62 b
		Mean$_{OQR}$	*935.04 D*	*1436.73 C*	*225.26 B*	*26.58 C*	*501.70 B*	*59.12 A*
	High N	YXY	1097.13 a	1488.93 c	223.21 ab	30.37 a	391.80 d	53.28 d
		WXY	1090.88 a	1504.64 b	208.60 c	27.96 b	413.76 c	55.48 c
		Mean$_{HQR}$	*1094.00 A*	*1496.78 B*	*215.91 B*	*29.17 B*	*402.78 C*	*54.38 B*
		KY	980.86 c	1553.18 a	215.52 bc	23.45 d	572.32 a	62.29 a
		JY	1018.90 b	1547.35 a	229.42 a	25.79 c	528.45 b	59.39 b
		Mean$_{OQR}$	*999.88 C*	*1550.26 A*	*222.47 B*	*24.62 D*	*550.39 A*	*60.84 A*
2021	Moderate N	YXY	1019.01 a	1424.81 d	309.24 a	36.52 a	405.80 d	47.93 d
		WXY	1012.80 a	1452.75 c	277.29 b	31.56 b	439.95 c	50.05 c
		Mean$_{HQR}$	*1015.90 B*	*1438.78 D*	*293.27 A*	*34.04 A*	*422.88 C*	*48.99 D*
		KY	903.15 c	1473.05 b	230.22 d	24.57 c	569.90 a	60.81 a
		JY	949.54 b	1501.22 a	243.39 c	26.07 c	551.68 b	59.10 b
		Mean$_{OQR}$	*926.35 D*	*1487.13 C*	*236.81 C*	*25.32 C*	*560.79 B*	*59.95 B*
	High N	YXY	1089.88 a	1501.06 c	272.30 a	33.28 a	411.18 d	50.27 b
		WXY	1072.48 b	1520.58 b	253.93 b	30.07 b	448.10 c	53.08 b
		Mean$_{HQR}$	*1081.18 A*	*1510.82 B*	*263.12 B*	*31.68 B*	*429.64 C*	*51.67 C*
		KY	929.89 d	1575.81 a	222.42 d	21.62 d	645.92 a	62.80 a
		JY	961.56 c	1583.48 a	235.86 c	23.39 c	621.92 b	61.70 a
		Mean$_{OQR}$	*945.73 C*	*1579.64 A*	*229.14 C*	*22.51 D*	*633.92 A*	*62.25 A*
Analysis of variance								
2020	N rate		***	***	**	**	**	*
	Variety		***	***	**	***	***	***
	N rate ×Variety		***	***	***	*	***	ns
2021	N rate		***	***	**		**	*
	Variety		***	***	***	**	***	***
	N rate ×Variety		***	***	***	***	***	ns

Note: Within a column, different lowercase letters between varieties in the same N rate indicate significant differences at the $p < 0.05$ level; different uppercase letters between varietal types across two N rates indicate significant differences at the $p < 0.05$ level. * , ** and *** represent significant differences at the $p < 0.05$, $p < 0.01$ and $p < 0.001$ probability levels, respectively; ns means no significance.

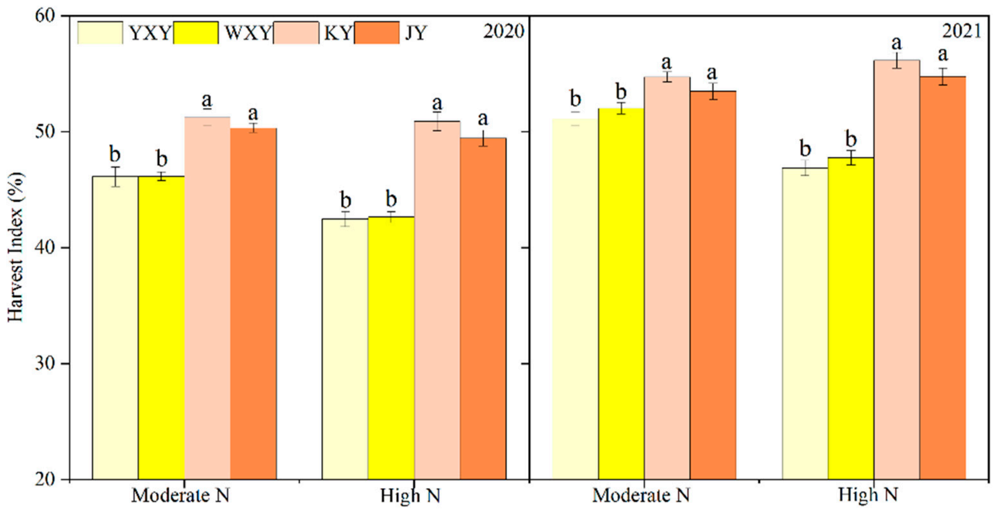

Figure 2. Harvest index of HQR and OQR varieties under moderate and high N rates. Note: Different lowercase letters between varieties in the same N rate indicate significant differences at the $p < 0.05$ level.

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3.3. Net photosynthetic rate (Pn), RUE, and sink-source relationship

Compared to moderate N rate, high N rate improved SPAD values of HQIR and OQIR at HD, HD15d and HD30d, excluding SPAD values of HQIR at HD and of OQIR at HD15d in 2020 (Table 4). Meanwhile, high N rate significantly enhanced *Pn* of HQIR and OQIR at HD15d in 2020 and HD30d in 2021, and of OQIR at HD30d in 2020 and HD in 2021. At HD and HD15d, significant higher SPAD values and *Pn* of OQIR were found than those of HQIR, while OQIR showed lower SPAD values and *Pn* than HQIR at HD30d in both years.

High N rate significantly increased intercepted radiation and RUE of HQIR and OQIR, compared to moderate N rate in 2020 and 2021. OQIR showed markedly higher intercepted radiation but lower RUE than HQIR under two N rates (Figure 3).

In comparison with moderate N rate, high N rate significantly increased LAI of HQIR and OQIR at heading, but significantly decreased spikelets-leaf ratio, filled grains-leaf ratio and grain weight-leaf ratio of HQIR in 2020 and 2021(Table 5). Furthermore, HQIR had higher LAI and lower spikelets-leaf ratio, filled grains-leaf ratio and grain weight-leaf ratio than OQIR under two N rates.

Table 4. SPAD value and net photosynthetic rate (*Pn*) of HQR and OQR varieties under moderate and high N rates.

Year	N rate	Variety	SPAD value			*Pn* (μmol CO_2 m^{-2} s^{-1})		
			HD	HD15d	HD30d	HD	HD15d	HD30d
2020	Moderate N	YXY	34.89 d	30.89 d	21.01 b	17.96 c	15.43 b	12.21 a
		WXY	35.99 c	32.10 c	21.89 a	18.10 c	16.02 b	11.46 b
		Mean$_{HQR}$	*35.44 C*	*31.50 C*	*21.45 B*	*18.03 B*	*15.73 C*	*11.84 A*
		KY	39.06 a	33.00 b	16.55 d	23.25 a	16.84 a	10.34 c
		JY	37.98 b	34.21 a	18.77 c	22.68 b	16.99 a	10.59 c
		Mean$_{OQR}$	*38.52 B*	*33.61A*	*17.66 D*	*22.96 A*	*16.92 B*	*10.47 C*
	High N	YXY	35.62 d	31.89 c	23.41 b	18.39 c	17.56 b	12.37 a
		WXY	37.89 c	33.78 b	26.99 a	18.84 c	18.00 b	12.00 b
		Mean$_{HQR}$	*36.76 C*	*32.84 B*	*25.20 A*	*18.62 B*	*17.78 B*	*12.19 A*
		KY	42.00 a	34.88 a	17.56 d	25.51 a	20.45 a	11.00 d
		JY	39.44 b	33.83 b	19.83 c	21.78 b	18.00 b	11.34 c
		Mean$_{OQR}$	*40.72 A*	*34.36 A*	*18.69 C*	*23.65 A*	*19.23 A*	*11.17 B*
2021	Moderate N	YXY	33.84 c	29.50 c	21.37 b	17.80 b	15.12 c	11.99 a
		WXY	36.41 b	33.57 a	24.46 a	18.26 b	15.93 b	11.54 b
		Mean$_{HQR}$	*35.13 D*	*31.54 C*	*22.92 B*	*18.03 C*	*15.53 C*	*11.77 B*
		KY	39.32 a	32.19 b	15.96 d	23.02 a	16.03 b	10.01 c
		JY	38.57 a	34.29 a	16.65 c	22.88 a	16.94 a	9.99 c
		Mean$_{OQR}$	*38.95 B*	*33.24 B*	*16.30 D*	*22.95 B*	*16.49 AB*	*10.00 D*
	High N	YXY	35.90 c	32.78 c	22.63 b	18.19 d	16.31 c	12.32 a
		WXY	38.33 b	34.23 b	27.36 a	18.73 c	16.00 c	11.94 b
		Mean$_{HQR}$	*37.11 C*	*33.50 B*	*25.00 A*	*18.46 C*	*16.16 BC*	*12.13 A*
		KY	41.78 a	33.84 b	16.96 d	25.28 a	17.34 a	10.62 d
		JY	42.24 a	36.55 a	18.93 c	24.41 b	16.98 b	11.05 c
		Mean$_{OQR}$	*42.01 A*	*35.20 A*	*17.94 C*	*24.85 A*	*17.16 A*	*10.84 C*

Note: Within a column, different lowercase letters between varieties in the same N rate indicate significant differences at the $p < 0.05$ level; different uppercase letters between varietal types across two N rates indicate significant differences at the $p < 0.05$ level.

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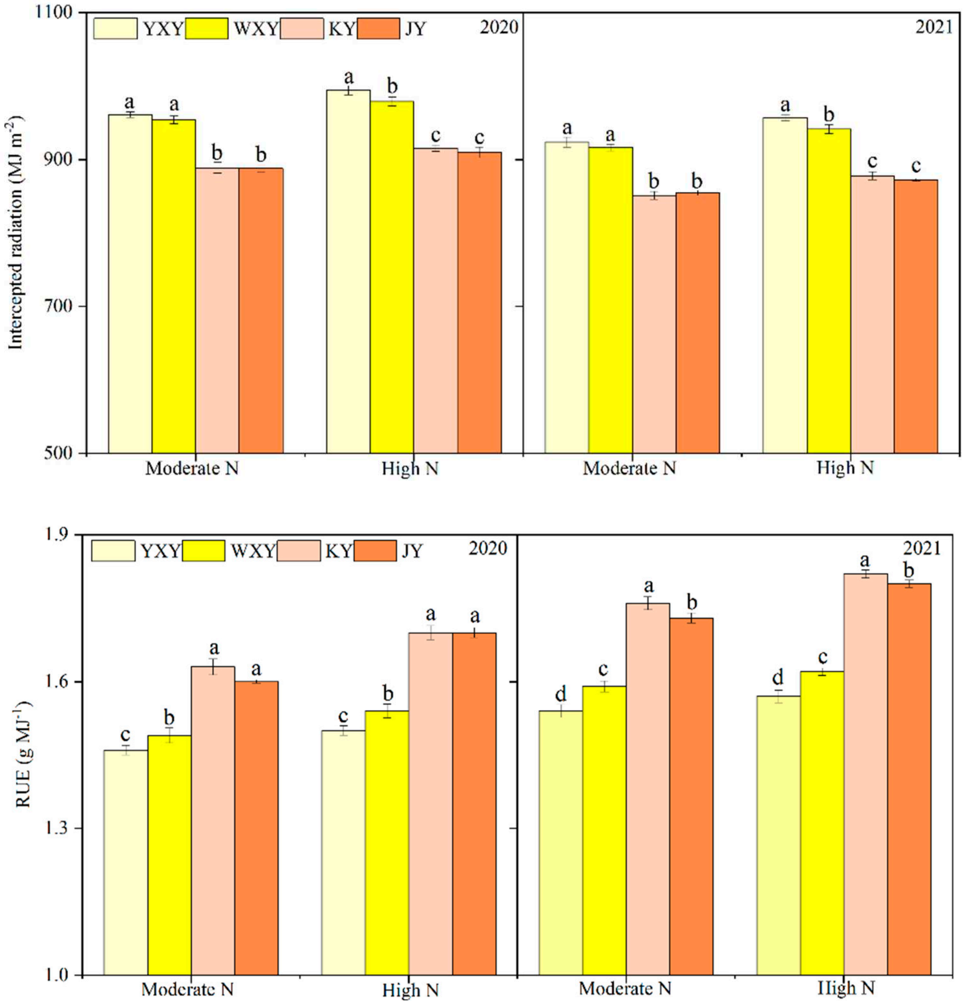

Figure 3. Intercepted radiation and RUE of HQR and OQR varieties under moderate and high N rates. Note: Different lowercase letters between varieties in the same N rate indicate significant differences at the *p <0.05* level.

Table 5. LAI and grain-leaf area ratio of HQR and CMR varieties under moderate and high N rates.

N rate	Variety	2020				2021			
		LAI	Spikelets-leaf area ratio (cm⁻²)	Filled grains-leaf area ratio (cm⁻²)	Grain weight-leaf area ratio (mg cm⁻²)	LAI	Spikelets-leaf area ratio (cm⁻²)	Filled grains-leaf area ratio (cm⁻²)	Grain weight-leaf area ratio (mg cm⁻²)
Moderate N	YXY	7.08 a	0.64b	0.48c	9.44c	7.13 a	0.62b	0.51b	10.48c
	WXY	6.99 a	0.62c	0.45d	10.54b	6.94 a	0.59b	0.48c	11.26b
	Mean*HQR*	7.04 B	0.63B	0.46B	9.99B	7.03 B	0.60B	0.49B	10.87B
	KY	6.51 b	0.75a	0.56a	12.05a	6.51 b	0.73a	0.60a	14.07a
	JY	6.36 b	0.75a	0.52b	11.82a	6.39 b	0.72a	0.59a	13.90a
	Mean*OQR*	6.43 D	0.75A	0.54A	11.94A	6.45 D	0.72A	0.60A	13.98A
High N	YXY	7.68 a	0.60b	0.42c	8.24c	7.60 a	0.58b	0.45c	9.27c
	WXY	7.36 b	0.59b	0.40d	9.25b	7.44 b	0.55b	0.42d	10.03b
	Mean*HQR*	7.52 A	0.59C	0.41C	8.74C	7.52 A	0.57C	0.44C	9.65C
	KY	6.76 c	0.76a	0.56a	12.09a	6.72 c	0.73a	0.61a	14.19a
	JY	6.57 d	0.76a	0.53b	11.91a	6.52 d	0.72a	0.59b	14.04a
	Mean*OQR*	6.66 C	0.76A	0.54A	12.00A	6.62 C	0.73A	0.60A	14.11A

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Note: Within a column, different lowercase letters between varieties in the same N rate indicate significant differences at the $p < 0.05$ level; different uppercase letters between varietal types across two N rates indicate significant differences at the $p < 0.05$ level.

3.4. Plant N uptake and N use efficiency

Compared with moderate N rate, high N rate significantly increased N uptake of HQIR by 25.38%–25.39% at heading and 14.50%–17.40% at maturity, and of OQIR by12.96%–17.90% at heading and 2.75%–18.81% at maturity (Table 6). In contrast, high N rate significantly decreased the post-anthesis N uptake of HQIR by 28.72%–33.06% in two years and of OQIR by 8.98% in 2020 (but increased by 55.73% in 2021). However, high N rate significantly increased pre-anthesis N exportation of HQIR and OQIR by 26.84%–37.23% and 17.06%–22.51%, respectively. Finally, the significant declines in NUE_g of HQIR by 14.72%–17.90% and of OQIR by 5.42%–8.40% were found under high N rate compared to moderate N rate.

Compared with HQIR, OQIR showed significantly higher N uptake at heading under moderate N rate and N uptake at maturity under two N rates. Similarly, significant higher post-anthesis N uptake under high N rate and pre-anthesis N expropriation under two N rates were observed in OQIR than in HQIR. Accordingly, OQIR also had higher NUE_g under two N rates than HQIR.

Table 6. Aboveground plant N uptake and NUEg of HQR and OQR varieties under moderate and high N rates.

Year	N rate	Variety	N uptake at heading (kg ha^{-2})	N uptake at maturity (kg ha^{-2})	Post-anthesis N uptake (kg ha^{-2})	Pre-anthesis N exportation (kg ha^{-2})	NUE_g (kg kg^{-1})
2020	Moderate N	YXY	123.47 c	149.87c	26.40b	44.55b	50.22bc
		WXY	122.38 c	157.87b	35.49a	41.78b	48.41c
		Mean$_{HQR}$	122.92 C	153.87D	30.95AB	43.16C	49.31B
		KY	129.81 b	164.59a	34.78a	55.29a	52.45a
		JY	134.72 a	162.73a	28.01b	59.37a	51.22ab
		Mean$_{OQR}$	132.26 B	163.66C	31.40A	57.33B	51.84A
	High N	YXY	156.24 ab	177.80b	21.56b	62.18b	41.37b
		WXY	152.01 bc	174.57b	22.56b	56.29c	42.76b
		Mean$_{HQR}$	154.13 A	176.18B	22.06C	59.23B	42.06C
		KY	151.50 c	184.54a	33.04a	68.41a	49.83a
		JY	160.38 a	184.49a	24.11b	69.89a	48.23a
		Mean$_{OQR}$	155.94 A	184.52A	28.58B	69.15A	49.03B
2021	Moderate N	YXY	125.62 bc	142.64d	17.02c	50.92c	59.36b
		WXY	124.42 c	146.90c	22.49ab	47.23d	59.85ab
		Mean$_{HQR}$	125.02 D	144.77D	19.75B	49.07C	59.60A
		KY	128.88 ab	152.56b	23.68a	56.89b	61.45a
		JY	136.72 a	155.11a	18.38bc	61.22a	60.24ab
		Mean$_{OQR}$	132.80 C	153.84C	21.03B	59.05B	60.84A
	High N	YXY	159.63 a	172.13b	12.50c	64.66bc	47.54c
		WXY	153.87 b	167.80c	13.94c	59.81c	50.32b
		Mean$_{HQR}$	156.75 A	169.97B	13.22C	62.24B	48.93C
		KY	145.35 c	181.80a	36.45a	68.64b	56.59a
		JY	154.68 b	183.73a	29.05b	76.04a	54.87a
		Mean$_{OQR}$	150.01 B	182.77A	32.75A	72.34A	55.73B

Note: Within a column, different lowercase letters between varieties in the same N rate indicate significant differences at the $p < 0.05$ level; different uppercase letters between varietal types across two N rates indicate significant differences at the $p < 0.05$ level.

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4. Discussion

4.1. Yield responses of HQIR to N application rates

N is an essential nutrient for rice growth, development, and yield formation in almost all environments. Over the past several decades, most previous studies have demonstrated that the continuously increase of rice yield in China and the world is mainly attributed to genetic improvement and N fertilizer input [17,19,29,30]. On further improving rice yield potential, China had made two breakthroughs in breeding for hybrid and "super" rice varieties since the semidwarf rice varieties were successfully bred in 1956 [1,2]. In addition, many modern high-yielding rice varieties usually have great N responsiveness and higher lodging resistance [19]. On this account, rice farmers often apply a large amount of N fertilizers to obtain the highest grain yield of high-yielding rice varieties [16,17,20]. Ultimately, a synchronous increased tendency is observed between total rice grain yields and total N fertilizers consumption in China during the past several decades [4]. In fact, numerous studies have shown that there is a quadratic function relationship between grain yield (per unit area yield) and N application rates in most high-yielding rice varieties [20,27,30,31]. These results suggest that higher yields of high-yielding rice varieties do not depend on much more N fertilizer inputs.

In this study, we find that different yield responses of HQIR and OQIR to moderate and high N application rates were mainly explained by the difference in spikelets m^{-2} and/or grain setting rate. High N rate significantly increased OQIR's yield by 6.60%–8.88% but had no or slightly adverse effect on HQIR's yield in comparison with moderate N rate (Table 2). The results indicate that HQIR can obtain the highest grain yield under the moderate N rate (165 kg N ha^{-1}), which is in accord with the recommended optimum N application rates (135–165 kg N ha^{-1}) from previous reports for HQIR grown in late-season of double-rice cropping system [24–26]. Meanwhile, our results also suggest that further increase in N fertilizer input is beneficial to gain the maximum grain yield for OQIR compared with the moderate N rate. However, previous studies revealed that OQIR could produce the maximum grain yield under moderate N rates (120–190 kg N ha^{-1}) in the single- and double-rice cropping systems in southern China [27,32]. The difference in OQIR maybe because the site-specific N management technology was adopted in previous studies, which would significantly improve rice grain yield and N use efficiency as well as reduce N loss [17,27]. To the end, OQIR produced 8.34%–11.87% and 22.00%–22.50% higher grain yield than did HQIR under moderate and high N rates, respectively.

4.2. Agronomical and physiological responses of HQIR to N application rates

In the present study and previous studies, the high N rate did not increase spikelets m^{-2} but led to a significant decline in grain setting rate of HQIR [24–26]. On the contrary, significant increases in spikelets m^{-2} and no effect on grain setting rate of OQIR were observed under high N rate (Table 2). Fu et al. [31] have found that high N rate could reduce the grain setting rate of spikelets at the panicle base of "super" rice without the increased spikelets per panicle. In general, "super" rice varieties have numerous spikelets per panicle, but they often fail to achieve their high yield potential because of poor grain-filling of inferior spikelets, particularly under high N rates [33]. The main reason may be due to lower partitioning of assimilates in developing inferior spikelets resulted from low activity of enzymes involved in carbohydrate metabolism [33,34]. On the other hand, high N rate could significantly increase plant (panicles, stems, and leaves) N concentration, which might result in enhancement of plant N metabolism and overconsumption of carbohydrate, thus decreasing carbohydrate supply to panicles [35]. However, the spikelets per panicle of HQIR (140–150 spikelets $panicle^{-1}$) and OQIR (160–170 spikelets $panicle^{-1}$) in our study are less than that of "super" rice (more than 180 spikelets $panicle^{-1}$). The decreased grain setting rate of HQIR under high N rate are probably related to the above-mentioned interpretations.

In addition, HQIR had 8.99%–13.59% higher LAI than OQIR, and the LAI of HQIR and OQIR were increased by 6.82%–6.97% and 2.64%–3.58%, respectively, under high N rate compared with moderate N rate (Table 5). Meanwhile, we also found that high N rate significantly decreased pre-anthesis AE in HQIR but increased post-anthesis DM in OQIR compared with moderate N rate (Table 3); HQIR had obviously higher canopy intercepted radiation but lower RUE than OQIR under moderate and high N application rates. These results confirm that higher LAI of HQIR might lead to canopy closure and result in further aggravated carbohydrate metabolism under high N rate [23,31]. Generally, grain-leaf area ratio, including spikelets-leaf area ratio, filled grains-leaf area ratio, and grain weight-leaf area ratio, is an important parameter to evaluate the relationship between source and sink, and is taken as a comprehensive index to breed and select high-yielding rice varieties [36]. Thereby, it is an efficient approach to improving rice grain yield by increasing the grain-leaf area ratio [37]. In our study, grain-leaf ratios were significantly decreased in HQIR, but there was no effect in OQIR under high N rate compared with moderate N rate (Table 4). The results indicate that high N rate may result in an imbalance of source and sink relationship in HQIR. On the other hand, HQIR had higher or close N uptake at heading but lower pre-anthesis N exportation, as well as higher *Pn* at the late grain filling stage than OQIR under high N rate (Tables 4 and 6). The results suggest that the carbon and nitrogen metabolisms of HQIR could be disturbed by excessive N fertilizer input, resulting in lower supply of carbohydrate for panicle [38]. In comparision with 2021, grain setting rate and grain yield of HQIR and OQIR were significantly decreased in 2020, which resulted from lower daily average temperature (4.17 °C) and daily average solar radiation (3.81 MJ m^{-2}) in 2020. Nevertheless, the agronomical and physiological mechanism underlying lower grain setting rate of HQIR under high N rate need to be further studied in future.

5. Conclusions

The present study showed that the yield responses of HQIR and OQIR to moderate and high N application rates were different, which mainly explained by the difference in spikelets m^{-2} and/or grain setting rate. Compared with moderate N rate, slightly decreased grain yield of HQIR was due to decreased grain setting rate, whereas significant increased grain yield of OQIR was attributed to increased spikelets m^{-2} under high N rate. High N rate reduced pre-anthesis AE and its contribution, as well as grain-leaf area ratio of HQIR, but did not increase its post-anthesis DM compared with moderate N rate. Therefore, the mechanism underlying lower grain setting rate of HQIR under high N rate might be aggravated carbohydrate metabolism and imbalance source-sink relathionship. These results suggest that mederate N rate is beneficial for HQIR to balance the maximum grain yield and higher quality.

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