



# Coordination of high grain yield and high nitrogen use efficiency through large sink size and high post-heading source capacity in rice



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## ABSTRACT

Breeding green varieties that have high yield potential and require less resource input is the ideal way to cope with the challenges that human is facing with respect to food security and environmental pollution. However, few studies have focused on how high yield and high resource use efficiency is coordinated in rice (*Oryza sativa* L.). Here three varieties with different sink size, namely Yongyou4949 (YY4949) with large sink size, Yangliangyou6 (YLY6) with medium sink size, and Huanghuazhan (HHZ) with small sink size, were used in field and pot experiments in 2015–2017. The objective was to examine how enlarged sink size coordinate high yield and high nitrogen (N) use efficiency (NUE). It was found that YY4949 produced a grain yield of 9.60–11.79 t ha<sup>-1</sup> in 2015–2017, which was higher than that of YLY6 by 0.3–1.75 t ha<sup>-1</sup>, and that of HHZ by 1.3–2.18 t ha<sup>-1</sup>. N use efficiency for grain production (NUEg) of YY4949 reached 47.7–58.3 kg kg<sup>-1</sup> depending on the weather condition, which was 5.3–12.8% higher than that of YLY6 and 15.8–20.7% higher than that of HHZ. The concomitantly higher grain yield and NUEg of YY4949 were due to: (1) higher efficiency of spikelet production in respect of dry matter, N, accumulated temperature and radiation; (2) higher biomass production and N accumulation after flowering; (3) higher RUE after flowering due to the better canopy structure. In conclusion, rice breeding in the future should continue to enlarge the sink size especially through the improvement in production efficiency of sink size, while simultaneously increase the post-heading biomass production capacity.

## 1. Introduction

At its current rate of growth, the global population is set to reach ~10 billion people by 2050 (UN, 2017). Increasing crop production to maintain food security while reducing agriculture's environmental impacts is the dual challenges that human is facing in the future (Cassman, 2003; Cui et al., 2018). Moreover, this objective has to be realized under the condition of changing climate (Peng et al., 2004). Hence the traditional goal of pursuing super-high yield has been replaced by achieving high yield, high quality, high efficiency, environment-friendly, and food safety simultaneously at the beginning of 21st century (Cassman, 2003; Zhang, 2007).

Rice is one of the staple food crops in the world, providing the diets and livelihoods of over 3.5 billion people (Godfray et al., 2010). Until recently, increasing yield potential has been the major goal in China's rice breeding programs due to the huge population pressure (Ling, 2008). In the last half of century, rice yield potential has been improved

substantially in China due to the introduction of semi-dwarfism and the utilization of heterosis (Yuan, 1994; Khush, 2001). Together with the application of improved agronomic practices, the average rice grain yield in China increased from 2.08 t ha<sup>-1</sup> in 1961 to 6.75 t ha<sup>-1</sup> in 2013 (Wang and Peng, 2017). Nevertheless, this led to severe environmental problems, such as widespread soil acidification (Guo et al., 2010), devastating water pollution (Diaz and Rosenberg, 2008), and excessive greenhouse gas emissions (Zhang et al., 2016). Since 2013, China government started to transform the way of agriculture production through a series of policies, for example in 2017, the Ministry of Agriculture in China implemented Green Varieties, a new varietal evaluation and certification system for the release of major crop varieties that require less fertilizer, pesticide or water (Wang et al., 2018). This will definitely promote the transformation of China's rice breeding from super-high yield potential to coordination of high yield potential and high resource use efficiency.

Agronomic traits that facilitate the simultaneous increase of grain

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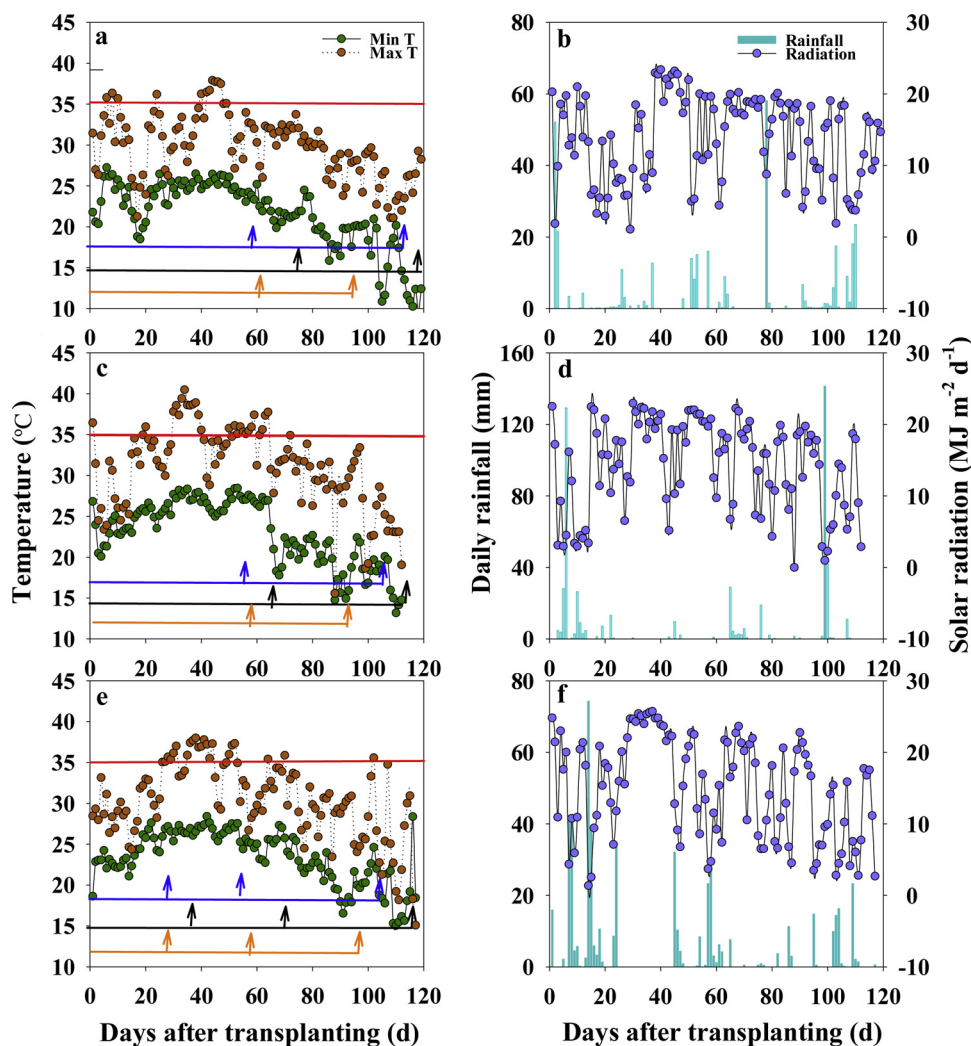


Fig. 1. Daily minimum temperature and maximum temperature (a, c and e), solar radiation and rainfall (b, d and f) during rice growing season from transplanting to maturity at Wuxue County, Hubei Province, China in 2015 (a and b), 2016 (c and d) and 2017 (e and f). Horizontal lines in Fig. 1a, c, and e denote growth duration (from transplanting to maturity) of three rice varieties, and arrows in Fig. 1a, c represent heading and maturity, and arrows in Fig. 1e represent panicle initiation, heading and maturity, respectively. The blue, black and yellow color represent YY4949, YLY6 and HHZ, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

yield and resource use efficiency could be used as selection criterion, and will greatly enhance the efficiency of rice breeding. The agronomic and physiological mechanisms underlying genetic improvement in rice yield potential have been extensively investigated (Peng et al., 2000; Tabien et al., 2008; Breseghello et al., 2011; Zhu et al., 2016). With the progress of genetic improvement, one notable alteration in plant type of the high-yielding rice varieties is the enlarged panicles (Yamamoto et al., 2001). Breeding large-panicle varieties by increasing the number of spikelets per panicle and grain size has been an effective approach to improve grain yield (Zhang et al., 2013). Sink size is the product of number of spikelets per panicle and grain weight. Significantly higher yield potential was also observed in the varieties with large sink size in comparison to conventional varieties (Laza et al., 2004; Jiang et al., 2014). Over-application of nitrogen (N) fertilizer and low N use efficiency (NUE) in China's rice production has been widely reported (Peng et al., 2002, 2006). This is partly due to that modern high-yielding rice varieties have larger response of grain yield to N input (Zhang and Kokubun, 2004; Tabien et al., 2008), and therefore led to a misunderstanding that super hybrid rice *per se* is responsible for the low NUE in rice production in China (Wang and Peng, 2017). Recent studies have demonstrated that genetic improvement in rice also significantly increased NUE (Zhu et al., 2016; Huang et al., 2018). Wada and Wada (1991) studied the relationship between leaf senescence and sink size using rice varieties with different sink size, and found that sink size affected the amount of N remobilized from leaves to panicles. Shan et al. (2004) investigate N uptake and utilization characteristics of rice varieties with different sink size under hydroponic condition, and the

result showed that sink size had significant influence on N uptake and utilization efficiency of rice. Therefore, it is reasonable to hypothesis that large sink size could simultaneously increase grain yield and NUE. However, how breeding for large sink size coordinates high yield potential and high NUE especially under low N input condition is still obscure.

The *japonica/indica* hybrid rice with strong heterosis had significantly higher yield potential over hybrid *indica* rice (Yuan, 1994; Peng et al., 1999), but often failed to achieve the expected yield in production because of the poor grain filling (Yang et al., 2002). However, a series of *japonica/indica* hybrid varieties designated as “Yongyou” produced 8–10% higher grain yield than the high-yielding inbred *japonica* and hybrid *indica* varieties (Jiang et al., 2015b; Wei et al., 2016a). High yield of Yongyou varieties was mainly attributed to larger sink size resulted from more spikelets per panicle (Wei et al., 2016a) and high grain filling percentage of more than 80% (Meng et al., 2015). For example, Yongyou1540 and Yongyou4540 had approximately 350 spikelets per panicle and a grain filling percentage of nearly 90% at an N rate of 270 kg ha<sup>-1</sup> (Meng et al., 2016).

In the present study, comparison in grain yield and NUE among three varieties (Yongyou4949, Yangliangyou6, and Huanghuazhan) with different sink size was performed under reduced N fertilizer input condition in the Middle Reaches of the Yangtze River of China in 2015–2017. The objectives were to: 1) determine the advantage in grain yield and NUE of large sink size variety under reduced N fertilizer input condition, and 2) explore the mechanisms underlying the co-ordination of high grain yield and high NUE by large sink size.

## 2. Materials and methods

### 2.1. Plant materials

Three rice varieties, namely Yongyou4949 (YY4949), Yangliangyou6 (YLY6) and Huanghuazhan (HHZ) were used in present study. YY4949 is an *indica-japonica* hybrid variety developed by the Ningbo seed company with Yonggeng49 A as the female parent and F9249 as the male parent using the three-line method. YY4949 exhibited high yield potential due to its large sink size in the Middle Reaches of Yangtze River (Tang et al., 2016). YLY6 and HHZ are the representative varieties of super hybrid and inbred *indica* rice, respectively, and they are widely grown by farmers in the Lower and Middle Reaches of Yangtze River. YLY6 and HHZ produced around 160 and 120 spikelets per panicle, and the sink size were 1137 and 1056 g m<sup>-2</sup> in regional rice trials in Hubei Province, and were released in Hubei Province in 2005 and 2007, respectively. In this study, YY4949 was used as a large sink size variety, and YLY6 and HHZ were medium and small sink size varieties, respectively.

#### 2.1.1. Experiment site and design

Field experiments were conducted at Zhangbang Village (29°51' N 115°33' E), Wuxue County, Hubei Province, China, from 2015 to 2017. Wuxue County is located in the Middle Reaches of the Yangtze River. The soil in the experimental field was clay loam with the following properties: pH of 5.20, soil organic matter of 26.69 g kg<sup>-1</sup>, total N of 1.19 g kg<sup>-1</sup>, available P of 22.56 mg kg<sup>-1</sup>, and available K of 159.2 mg kg<sup>-1</sup>. Meteorological data, including daily minimum temperature, daily maximum temperature, daily solar radiation, and daily rain precipitation during the rice growing seasons were collected from the weather station located within 2 km of the experimental site in 2015–2017. Detailed information about climate data are shown in Fig. 1.

Three rice varieties were arranged in a complete randomized block design with three replications. Each plot covered 30 m<sup>2</sup> (5 m × 6 m), and plots were separated by a ridge 0.3 m wide with plastic film inserted into the soil to ensure the non-exchanging irrigation. Pre-germinated seeds were sown in seedbeds, after which 30 days old seedlings were transplanted on 19 June 2015, 22 June 2016 and 17 June 2017. Transplanting was performed at a hill spacing of 16.7 cm × 26.7 cm with two seedlings per hill in three experiment years. The rate of N application was 100 kg N ha<sup>-1</sup> in this study. The N fertilizer rate for single season rice in local farmers' practice is 180–200 kg N ha<sup>-1</sup>, which was similar to the national average value (Peng et al., 2002; Huang et al., 2018). In our previous study, reducing N input by 50% (90 kg N ha<sup>-1</sup>) compared with the farmers' practice resulted in maximum yield reduction of 12.8% in local area (Yuan et al., 2017). Thus, 100 kg N ha<sup>-1</sup> was used as low N input condition in the study. For N fertilizer, urea was split-applied with 40% as basal (1 day before transplanting), 30% at early tillering (7 days after transplanting) and 30% at panicle initiation. Phosphorus at a rate of 40 kg P ha<sup>-1</sup> as monocalcium phosphate was applied as a basal fertilizer, and K as potassium oxide at 100 kg K ha<sup>-1</sup> was split equally between the basal and panicle initiation. Fertilizer management practices remained consistent from 2015 to 2017. The experiment fields were kept flooded from transplanting until 10 days before maturity. Insects, weeds and diseases were intensively controlled by chemicals to avoid biomass and yield loss.

#### 2.2. Sampling and measurements

At heading stage (HD) in 2015 and 2016, and at the panicle initiation (PI), 14 days after PI (PI<sub>14</sub>), HD, 14 days after HD (HD<sub>14</sub>) in 2017, 12 hills of plants from each plot were sampled. After recording tiller number and plant height, plants were separated into leaves, stems, and panicles (when present). The area of green leaf was measured using

a leaf area meter (LI-3100, LI-COR, Lincoln, NE, USA), and expressed as leaf area index (LAI, surface area of leaves per unit ground). Leaf area duration (LAD) [ $1/2 \times (\text{leaf area at the first measurement} + \text{leaf area at the second measurement}) \times (\text{the second time (d) of the measurement} - \text{the first time (d) of the measurement})$ ] was calculated based on LAI and growth stages in 2017. Spikelets to leaf-area ratio at HD from 2015 to 2017 was calculated using the formula (Spikelets to leaf-area ratio = spikelets m<sup>-2</sup> at PM / LAI at HD). After then, the dry weights of leaves, stems and panicles were measured after being oven-dried to a constant weight at 70 °C. The aboveground dry weight was the summation of dry weights from different plant parts.

In 2017, the main stem was marked in early tillering stage. At HD, additional six panicles from main stems were sampled when exertion of 1/2–3/4 portion of the panicles from the leaf sheath in each plot. All panicles were used to count the number of primary branches, secondary branches, differentiated and degenerated spikelets per panicle. Spikelets per unit of dry matter (SD) and N accumulation (SN) were calculated based on spikelets m<sup>-2</sup> at PM and dry weight, N accumulation at PI<sub>14</sub>. Spikelets per unit of accumulation temperature (ST) and solar radiation (SR) were calculated based spikelets m<sup>-2</sup> at PM and accumulation temperature, accumulation solar radiation from PI to HD.

Canopy light interception was measured between 1100 and 1300 h on clear-sky days at mid-tillering, PI, PI<sub>14</sub>, HD, HD<sub>14</sub> and maturity (PM) using a line ceptometer (AccuPAR LP-80, Decagon Devices Inc., Pullman, WA, USA) in 2017. In each plot, light intensity inside the canopy was measured by placing the light bar in the middle of two rows and slightly above the water surface. And then light intensity was measured above the canopy. Three readings were taken in the vertical direction and another three in the horizontal direction, and in total, six measurements were performed in each plot. Canopy light interception (LI%) was calculated as the percentage of light intercepted by the canopy [ $100 \times (\text{light intensity above canopy} - \text{light intensity below canopy}) / \text{light intensity above canopy}$ ]. Intercepted radiation during each growth period was calculated using the average LI% and cumulative incident solar radiation during this growth period [ $1/2 \times (\text{LI\% at the beginning of the growth period} + \text{LI\% at the end of the growth period}) \times \text{cumulative incident radiation during the growth period}$ ]. Intercepted radiation from transplanting to HD and from HD to PM were the summation of intercepted radiation during each growth period. Radiation use efficiency (RUE) from transplanting to HD, HD to HD<sub>14</sub>, HD<sub>14</sub> to PM and HD to PM were calculated as the ratio of biomass to intercepted radiation during their corresponding periods. Solar radiation was from meteorological data.

In addition, the canopy was separated into horizontal layers to analyze light and N vertical distribution at HD in 2017. The canopy within 2 hills adjacent plants was cut from the base of the plants to the top at 20 cm layer thickness. The leaf area of each layer was determined and LAI was calculated. The leaf sample of each layer was dried and weighed. After then, dry leaf sample of each layer was ground to determine the 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 in each layer. At the same day, the canopy light distribution of each layer was measured, and measurements were taken diagonally across the rows and above the canopy. The relationship between canopy light distribution and canopy structure could be described by the formula  $I = I_0 \exp(-K_L F)$  (Gallagher and Biscoe, 1978), where F is the cumulative LAI from the canopy top, I and I<sub>0</sub> are light intensity on a horizontal level at F and the canopy top, respectively, K<sub>L</sub> is the light extinction coefficient. The gradient of N within the canopy could be described by an exponential function as  $SLN_i = (N_o - N_b) \exp(-K_N F) + N_b$  (Anten et al., 1995), where SLN<sub>i</sub> is the SLN (g m<sup>-2</sup>) of the i-th layer of the canopy, N<sub>o</sub> is SLN of the top leaves, N<sub>b</sub> is the base value of SLN for photosynthesis and its value was 0.3 g m<sup>-2</sup> (Yin and van Laar, 2005), K<sub>N</sub> is the extinction coefficient for effective leaf N. A smaller K<sub>L</sub> and higher K<sub>N</sub> indicates light and N distribution within the canopy is more appropriate.

**Table 1**  
Grain yield, yield components and harvest index (HI) for YY4949, YLY6 and HHZ at Wuxue County, Hubei Province, China in 2015, 2016 and 2017.

Variety	Yield (t ha <sup>-1</sup> )	Panicles m <sup>-2</sup>	Spikelets panicle <sup>-1</sup>	Spikelets m <sup>-2</sup> (×10 <sup>3</sup> )	Grain filling percentage (%)		Grain weight (mg)	Sink size (g m <sup>-2</sup> )	HI (%)
2015									
YY4949	11.79 a	206 b	279 a	57.3 a	94.0 a	21.5 b	1231 a		61.5 a
YLY6	10.04 b	208 b	170 b	35.3 c	90.4 b	28.5 a	1006 b		49.4 b
HHZ	9.61 b	276 a	159 b	43.7 b	93.3 ab	21.3 b	931 b		51.5 b
2016									
YY4949	9.69 a	191 b	278 a	53.1 a	87.9 a	20.0 b	1062 a		55.7 a
YLY6	8.72 b	211 b	181 b	38.0 b	84.2 ab	28.0 a	1064 a		49.5 b
HHZ	8.07 c	272 a	184 b	49.9 a	77.5 b	17.8 c	888 b		46.4 c
2017									
YY4949	9.60 a	188 b	309 a	57.7 a	79.5 b	19.4 b	1120 a		51.1 a
YLY6	9.30 a	218 b	179 b	39.0 b	89.3 a	26.3 a	1026 ab		49.6 ab
HHZ	8.30 b	284 a	198 b	56.1 a	78.2 b	17.4 c	976 b		46.0 b
ANOVA									
Year (Y)	***	ns	*	**	***	***	*		***
Variety (V)	***	***	***	***	ns	***	***		***
Y*V	ns	ns	ns	*	**	***	*		***

Within a column in each year, different letters indicate significant differences among different rice varieties by LSD ( $p < 0.05$ ). ns represent no significance at the  $P < 0.05$  level. \*, \*\*, \*\*\* indicate significance at the  $P < 0.05, 0.01, 0.001$  levels, respectively. ANOVA-analysis of variance.

The grain yield was determined from a 5 m<sup>2</sup> sampling area in the center of each plot and adjusted to 14% moisture content at PM in 2015, 2016 and 2017. In addition, plants of 12 hills from each plot were sampled to determine the aboveground dry weight, harvest index (HI) and yield components. After the panicle number was counted, plants were separated into leaves, stems, and panicles. The area of green leaf blade was determined at PM to calculate LAI and rate of LAI decrease [(LAI at HD-LAI at PM)/growth duration from HD to PM] in 2017. Panicles were hand-threshed and the filled spikelets were separated from unfilled spikelets by submerging them in tap water. Then empty spikelets were separated from half-filled spikelets by seed wind machine (FJ-1, China). Three 30 g subsamples of filled spikelets, total half-filled spikelets and three 2.0 g subsamples of empty spikelets were taken to quantify the number of spikelets per m<sup>2</sup>. The dry weights of leaves, stems, rachis, filled and unfilled spikelets were determined after oven-drying to a constant weight. The aboveground total dry weight was calculated as the summation of dry weight of leaves, stems, rachis, filled, half-filled and empty spikelets. Panicles m<sup>-2</sup>, spikelets per panicle, total spikelets m<sup>-2</sup>, 1000-grain weight, grain-filling percentage [ $100 \times$  filled spikelet number/total spikelet number], and HI [ $100 \times$  filled spikelet weight/aboveground total dry weight] were also calculated.

Dry samples from HD (leaf, stem, and panicle) and PM (leaf, stem, filled grains, and half-filled grains + empty grains + panicle rachis) in 2015–2017, and from PI<sub>14</sub> (leaf, stem) and HD<sub>14</sub> (leaf, stem, and panicle) in 2017 were ground to determine the plant tissue N concentration using an Elemental Analyzer (Elementar vario MAX CNS/CN, Elementar Trading Co., Ltd, Germany). The plant N contents at HD (TN<sub>HD</sub>) and PM (TN<sub>PM</sub>) were calculated as the product of N concentration and dry weight of each aboveground part. The specific leaf N (SLN) at PI<sub>14</sub>, HD, HD<sub>14</sub> and PM were calculated in 2017 as leaf N content per unit leaf area. The NUE-related parameters were calculated as follows:

N utilization efficiency for grain production (NUE<sub>g</sub>, kg kg<sup>-1</sup>) = GY/TN<sub>PM</sub>  
 N utilization efficiency for biomass production (NUE<sub>b</sub>, kg kg<sup>-1</sup>) = TDW/TN<sub>PM</sub>  
 N harvest index (HI) = GN/TN<sub>PM</sub>

Partial factor productivity of fertilizer N (FPF<sub>N</sub>, kg kg<sup>-1</sup>) = GY/N  
 Where GY is the grain yield, GN is the grain N content, TDW is the aboveground biomass at maturity, TN<sub>PM</sub> is the total N uptake in the plant at maturity, N is the rate of N fertilizer applied.

### 2.2.1. Statistical analysis

Analysis of variance was performed with Statistix 9.0 using the least significant difference (LSD) test at 0.05 probability level. All figures were constructed using SigmaPlot 12.5.

## 3. Results

### 3.1. Whether condition

The average daily maximum temperature and minimum temperature from transplanting to mature were 29.8 and 21.4 °C (Fig. 1a) in 2015, 31.0 and 22.9 °C (Fig. 1c) in 2016, and 30.3 and 23.3 °C (Fig. 1e) in 2017. The average daily solar radiation and total rainfall during the rice growing season were 13.7, 14.2 and 14.9 MJ m<sup>-2</sup> d<sup>-1</sup>, and 337.6, 520.9 and 526.0 mm (Fig. 1b, d, f) in 2015, 2016 and 2017, respectively. In general, 2016 and 2017 had higher temperature, solar radiation, and total rainfall than 2015 during the growing season. The average daily maximum temperature and minimum temperature in 2016 was 0.7 °C higher and 0.4 °C lower than that in 2017. YY4949, YLY6 and HHZ didn't encounter high temperature stress at HD in 2015 and 2017, but in 2016, YY4949 and HHZ suffered several hot days with the maximum temperature above 35 °C.

### 3.2. Grain yield, yield components and harvest index (HI)

There were significant differences in grain yield, yield components and HI among varieties in each year (Table 1). The grain yield of YY4949 was 11.79, 9.69, and 9.60 t ha<sup>-1</sup> in 2015–2017, which was higher than that of YLY6 by 0.3–1.75 t ha<sup>-1</sup>, and that of HHZ by 1.3–2.18 t ha<sup>-1</sup>. In terms of yield components, HHZ produced significantly higher panicles m<sup>-2</sup> than the other two varieties, but YY4949 had higher number of spikelets panicle<sup>-1</sup> than YLY6 and HHZ by 64.7% and 60.1% respectively averaged across 2015–2017. The product of panicles m<sup>-2</sup> and spikelets panicle<sup>-1</sup> was that YY4949 had higher spikelets m<sup>-2</sup> than YLY6 and HHZ in all three years. YY4949 had relative high grain filling percentage in 2015 and 2016, whereas differences among the three varieties were not consistent between the two years. The grain weight of YY4949 was consistently higher than HHZ, and significantly lower than YLY6 in 2015–2017. Sink size is the product of spikelets m<sup>-2</sup> and grain weight, which was 10.4% and 22.2% higher in YY4949 compared with YLY6 and HHZ respectively averaged across 2015–2017. The HI of YY4949 was 61.5%, 55.7%, and 51.1% in 2015–2017, which was averagely 13.3% and 16.9% higher than that of YLY6 and HHZ

**Table 2**

Nitrogen uptake and N use efficiency for YY4949, YLY6 and HHZ at Wuxue County, Hubei Province, China in 2015, 2016 and 2017.

Variety	TN <sub>HD</sub> (kg ha <sup>-1</sup> )	TN <sub>HD-PM</sub> (kg ha <sup>-1</sup> )	TN <sub>PM</sub> (kg ha <sup>-1</sup> )	NUE <sub>g</sub> (kg kg <sup>-1</sup> )	NHI (%)	NUE <sub>b</sub> (kg kg <sup>-1</sup> )	PPF <sub>N</sub> (kg kg <sup>-1</sup> )
2015							
YY4949	165 a	33.3 a	198 a	58.3 a	71.2 a	96.4 a	117.9 a
YLY6	171 a	9.6 b	180 a	51.7 b	63.3 a	102.1 a	100.4 b
HHZ	173 a	4.9 b	178 a	48.3 b	63.0 a	95.3 a	96.1 b
2016							
YY4949	144 a	33.0 a	177 a	54.9 a	70.0 a	95.0 b	96.9 a
YLY6	151 a	18.2 a	170 a	51.5 ab	67.4 a	110.5 a	87.2 b
HHZ	162 a	12.3 a	174 a	46.3 b	57.8 b	87.3 b	80.7 c
2017							
YY4949	150 b	52.2 a	202 a	47.7 a	63.1 a	86.4 a	96.0 a
YLY6	179 a	26.8 b	206 a	45.3 ab	61.7 ab	89.9 a	93.0 a
HHZ	154 b	48.8 ab	202 a	41.2 b	53.1 b	82.8 a	83.0 b
ANOVA							
Year (Y)	ns	***	**	**	**	**	***
Variety (V)	ns	**	ns	***	*	**	***
Y*V	ns	ns	ns	ns	ns	ns	ns

Within a column in each year, different letters indicate significant differences among Different rice varieties by LSD ( $p < 0.05$ ). ns represents no significance at the  $P < 0.05$  level. \*, \*\*, \*\*\* indicate significance at the  $P < 0.05, 0.01, 0.001$  levels, respectively. ANOVA-analysis of variance.

TN<sub>HD</sub>, TN<sub>HD-PM</sub>, TP<sub>PM</sub>, NUE<sub>g</sub>, NUE<sub>b</sub>, NHI and PPF<sub>N</sub> are plant nitrogen accumulation at heading stage, plant nitrogen accumulation from heading to maturity, plant nitrogen accumulation at maturity, nitrogen use efficiency for grain production, nitrogen use efficiency for biomass production, nitrogen harvest index, and partial factor productivity of fertilize N, respectively.

respectively in the three years (Table 1).

### 3.3. Plant N uptake and utilization

YY4949 had consistently low plant N accumulation before heading, and relative high plant N uptake at the grain filling period in 2015–2017 (Table 2). There was no significant difference in total N uptake at PM among the three varieties across the three years. NUE<sub>g</sub> was 5.3–12.8% higher in YY4949 than that of YLY6, but the difference was statistically significant only in 2015. Compared to HHZ, YY4949 had 15.8–20.7% higher NUE<sub>g</sub> across the three years. NHI and PPF<sub>N</sub> were highest in YY4949, followed by YLY6, while HHZ had the lowest across the three years. NUE<sub>b</sub> of YLY6 was the highest, followed by YY4949, and HHZ was the lowest in each year (Table 2).

### 3.4. Spikelet differentiation and degeneration

YY4949 had substantially higher primary and secondary branch number than YLY6 and HHZ in 2017. The number of differentiated spikelets and surviving spikelets per panicle were also significantly higher in YY4949 than in YLY6 and HHZ (Table 3). Despite the lower total dry weight of YY4949 relative to YLY6 at late spikelet differentiation stage (PI<sub>14</sub>) (Table 4), the increased dry weight per stem during the period from PI to PI<sub>14</sub> was 18.7% and 45.9% higher in YY4949 than that in YLY6 and HHZ (Fig. 2a), and the increased amount of N per stem at the same period was 40.4% and 59.8% higher in

**Table 3**

Spikelet differentiation and degeneration for YY4949, YLY6 and HHZ at Wuxue County, Hubei Province, China in 2017.

Variety	Primary branch no.	Secondary branch no.	No. of surviving spikelets panicle <sup>-1</sup>	No. of degenerated spikelets panicle <sup>-1</sup>	No. of differentiated spikelets panicle <sup>-1</sup>
YY4949	18.3 a	95.5 a	456 a	25.6 a	482 a
YLY6	13.7 b	56.9 b	278 b	10.6 b	288 b
HHZ	12.9 b	51.5 c	236 c	7.4 b	243 c

Within a column, different letters indicate significant differences among different rice varieties by LSD ( $p < 0.05$ ).

YY4949 than that in YLY6 and HHZ (Fig. 2b). The SD and SN were highest in YY4949, followed by HHZ, and YLY6 had the lowest one. YY4949 had lower accumulated temperature and radiation than YLY6 and HHZ during the period from PI to HD, but significantly higher ST and SR (Table 4).

### 3.5. Dry matter accumulation and the related parameters

#### 3.5.1. Growth duration and dry matter accumulation

Averaged across 2015–2017, the pre-flowering growth duration (TP-HD) of YY4949 was 14 and 3 d shorter than YLY6 and HHZ respectively, however, the post-flowering growth period (HD-PM) of YY4949 was 4 and 15 d longer than YLY6 and HHZ respectively (Table 5). The pre-flowering dry matter accumulation of YY4949 was the lowest among the three varieties, but its post-flowering dry matter accumulation was higher than YLY6 and HHZ by 0.4–4.7 t ha<sup>-1</sup> and 1.0–4.0 t ha<sup>-1</sup>, respectively in 2015–2017. The total dry weight at maturity of HHZ was the lowest among the three varieties, and the difference in total dry weight between YY4949 and HHZ was not consistent in the three years (Table 5).

#### 3.5.2. Canopy intercepted radiation and RUE

There was no difference in canopy intercepted percentage (LI%) among the three varieties during the period from HD to HD<sub>14</sub>, from HD<sub>14</sub> to PM and from HD to PM in 2017 (Table 6). Canopy intercepted radiation was significantly lower in YY4949 than that in YLY6 and HHZ during the period from TP to HD, but 20.7% and 18.5% higher than YLY6 and HHZ, respectively from HD to PM. There was similar RUE for YY4949 and YLY6 from TP to HD, which was significantly higher than that of HHZ. During the grain filling period, RUE of YY4949 was higher than that of YLY6, especially during the period from HD to HD<sub>14</sub> (Table 6).

#### 3.5.3. Light and N distributions with the canopy

The canopy ecophysiological characteristics including LAI, light and N distribution were determined at HD (Fig. 3 and Table 7). From top to bottom of the canopy, light transmission ( $I/I_0$ ) and SLN were decreasing with the increase of accumulative LAI. At the same level of canopy, YY4949 had higher light transmission and SLN than YLY6 and HHZ (Fig. 6). LAI at HD was 29.8% and 23.1% lower in YY4949 than that in

**Table 4**  
Spikelet production efficiency for YY4949, YLY6 and HHZ at Wuxue County, Hubei Province, China in 2017.

Variety	Spikelets $m^{-2}$ ( $\times 10^3$ )	Dry weight at $PI_{14}$ ( $g\ m^{-2}$ )	N content at $PI_{14}$ ( $g\ m^{-2}$ )	Accumulated temperature from PI to HD ( $^{\circ}C\ d$ )	Accumulated radiation from PI to HD ( $MJ\ m^{-2}\ d$ )	SD ( $no\ g^{-1}$ dry weight)	SN ( $no\ mg^{-1}$ N)	ST ( $no\ m^{-2}\ ^{\circ}C$ $d^{-1}$ )	SR ( $no\ MJ^{-1}$ $d^{-1}$ )
YY4949	57.7 a	653 b	14.1 a	809	567	90.3 a	4.2 a	72.9 a	104.0 a
YLY6	39.0 b	829 a	14.5 a	1014	612	45.9 b	2.6 b	37.5 c	62.2 b
HHZ	56.1 a	661 b	13.6 a	951	614	85.1 a	4.1 a	59.1 b	91.5 a

Within a column in each year, different letters indicate significant differences among different rice varieties by LSD ( $p < 0.05$ ). SD: spikelets per unit of dry matter, SN: spikelets per unit of N accumulation, ST: spikelets per unit of accumulated temperature, SR: spikelets per unit of accumulated radiation.

YLY6 and HHZ, respectively (Table 7). Canopy extinction coefficients for light ( $K_L$ ) of YY4949 was  $0.35\ m^2$  ground  $m^{-2}$  leaf, which was 29.3% lower than YLY6 and 14.8% lower than HHZ. Canopy extinction coefficients for N ( $K_N$ ) of YY4949, YLY6 and HHZ were 0.15, 0.11 and  $0.05\ m^2$  ground  $m^{-2}$  leaf, respectively, and the difference between YY4949 and HHZ was significant. Moreover,  $K_N/K_L$  was higher in YY4949 than that in YLY6 and HHZ (Table 7).

### 3.5.4. Specific leaf nitrogen (SLN)

Significant difference was observed in SLN among the three varieties at  $PI_{14}$ ,  $HD_{14}$ , and PM, but the difference was not significant at HD (Fig. 4). YY4949 had the highest SLN among the three varieties at  $PI_{14}$ , HD and  $HD_{14}$ , while at PM, SLN of YY4949 was lower than YLY6, but higher than HHZ (Fig. 4).

### 3.5.5. Rate of LAI decrease and leaf area duration (LAD)

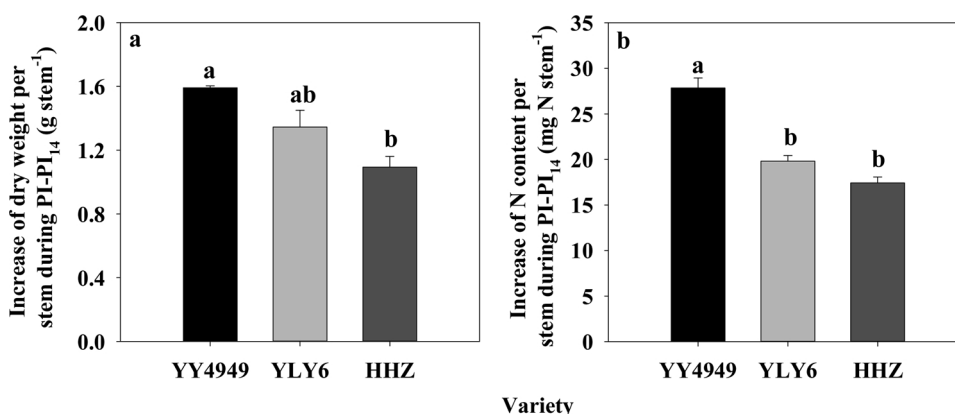
The rate of LAI decrease in YY4949 from HD to PM was significantly lower than that in YLY6 and HHZ (Fig. 5a). LAD at grain filling stage was significantly higher in YY4949 than that in HHZ, but significantly lower than in YLY6 (Fig. 5b).

### 3.6. Spikelets to leaf-area ratio in the heading stage

Spikelets to leaf-area ratio in YY4949 was the highest among the three varieties across the three years, and the difference was significant except for that between YY4949 and HHZ in 2017 (Fig. 6).

### 3.7. Correlations of grain yield and $NUE_g$ with grain N accumulation ( $TN_{grain}$ ), grain N concentration ( $N_{grain}$ ) and leaf N concentration ( $N_{leaf}$ ) at PM

The Grain yield positively correlated with the  $TN_{grain}$  significantly ( $P < 0.01$ ), but negatively correlated with the  $N_{grain}$  and  $N_{leaf}$  ( $P > 0.05$ ) at PM (Fig. 7). Similarly,  $NUE_g$  positively correlated with the  $TN_{grain}$  ( $P > 0.05$ ), but significantly negatively correlated with the  $N_{grain}$  ( $P < 0.01$ ) and  $N_{leaf}$  ( $P < 0.05$ ) at PM (Fig. 7).



**Fig. 2.** The increase of dry weight per stem (a) and N content per stem (b) for YY4949, YLY6 and HHZ during PI and  $PI_{14}$  at Wuxue County, Hubei Province, China in 2017. Data are means of replicates, and the vertical bars represent the standard error. Different letters above the columns indicated statistical significance at the  $p < 0.05$  level among different rice varieties.

**Table 5**  
Growth duration, biomass accumulation for YY4949, YLY6 and HHZ at Wuxue County, Hubei Province, China in 2015, 2016 and 2017.

Variety	Growth duration (d)		Biomass ( $t\ ha^{-1}$ )			
	TP-HD	HD-PM	TP-HD	HD-PM	DMT	TDW
2015						
YY4949	59	53	9.4 c	9.7 a	2.0 b	19.1 a
YLY6	73	46	13.4 a	5.0 b	4.1 a	18.4 ab
HHZ	61	33	11.1 b	5.7 b	3.0 ab	16.8 b
2016						
YY4949	55	48	8.6 b	8.1 a	1.2 a	16.7 b
YLY6	65	47	10.8 a	7.7 a	1.5 a	18.5 a
HHZ	57	34	9.6 b	5.6 b	1.5 a	15.2 c
2017						
YY4949	53	50	9.4 b	8.0 a	0.9 b	17.4 ab
YLY6	70	47	12.7 a	5.8 b	3.4 a	18.5 a
HHZ	58	40	9.7 b	7.0 ab	0.7 b	16.7 b

Within a column in each year, different letters indicate significant differences among different rice varieties by LSD ( $p < 0.05$ ).

DMT is the translocation of dry matter accumulated prior to flowering in the vegetative organs to grains during grain filling period.

## 4. Discussion

Due to the measurement of NUE parameters is complex and time-consuming, scientists are always trying to identify the readily measured agronomic or physiological traits that can be used as a proxy of NUE (Broadbent et al., 1987; de Datta and Broadbent, 1993; Singh et al., 1998; Koutroubas and Ntanos, 2003; Wu et al., 2016). Unfortunately, until now no such parameters could satisfy breeders' requirement. Based on our previous finding that grain yield, NUE, and sink size were concomitantly increased along with the rice genetic improvement in China (Zhu et al., 2016) and the genetic linking between panicle size and NUE (Huang et al., 2009; Hu et al., 2014), the present study examined the physiological mechanisms underlying the coordination of high grain yield and high NUE by large sink size especially at reduced N

**Table 6**

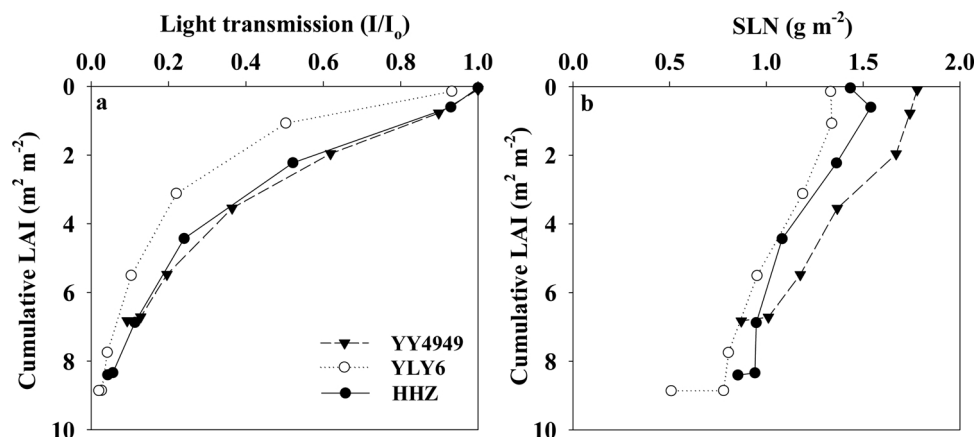
Incident radiation, intercepted percentage, intercepted radiation and radiation use efficiency (RUE) at major growth periods for YY4949, YLY6 and HHZ at Wuxue County, Hubei Province, China in 2017.

Growth stage	Variety	Incident radiation (MJ m <sup>-2</sup> )	Intercepted percentage (%)	Intercepted radiation (MJ m <sup>-2</sup> )	RUE (g MJ <sup>-1</sup> )
TP-HD	YY4949	958	67.6 b	648 c	1.45 a
	YLY6	1215	73.0 a	886 a	1.43 a
	HHZ	1005	69.9 ab	702 b	1.38 b
HD-HD <sub>14</sub>	YY4949	215	96.2 a	218 b	1.56 a
	YLY6	195	97.4 a	209 c	1.02 b
	HHZ	263	96.8 a	259 a	1.32 ab
HD <sub>14</sub> -PM	YY4949	406	96.8 a	466 a	0.99 a
	YLY6	352	96.2 a	320 c	1.22 a
	HHZ	363	96.4 a	352 b	1.00 a
HD-PM	YY4949	685	96.6 a	661 a	1.21 a
	YLY6	567	96.6 a	548 c	1.06 a
	HHZ	578	96.6 a	558 b	1.25 a

Within a column for each growth duration, different letters indicate significant differences among different rice varieties by LSD (P < 0.05).

input condition. Difference in sink size among the three varieties varied depending on the weather condition in each year, which was consistent with difference in NUEg among the three varieties. In general, the large sink size variety YY4949 had significantly higher grain yield and N utilization efficiency (namely NUEg) especially when no high temperature occurred at heading stage. There were three physiological causes for the higher grain yield and higher NUEg of YY4949: (1) higher efficiency of spikelet production in respect of dry matter, N, accumulated temperature and radiation; (2) higher biomass production and N accumulation after flowering; (3) higher RUE after flowering due to the better canopy structure.

In present study, the number of surviving spikelets per panicle was 64.1% and 93.2% higher in YY4949 than that in YLY6 and HHZ respectively, which contributed the larger sink size of YY4949. With the increasing of sink size, NUEg and NHI increased in rice (Shan et al., 2004). Under hydroponic condition, Dong et al. (2009) reported NUEg and NHI of large panicle varieties were higher than the other varieties. Enhancing the dry matter accumulation and N uptake at the late spikelet differentiation stage could promote large panicle formation (Kamiji et al., 2011). Despite YY4949 had lower dry weight and N accumulation than YLY6 at PI<sub>14</sub>, the increased dry weight and N content per stem during the period from PI to PI<sub>14</sub> were higher for YY4949, which lay the foundation for the formation of large panicle. Ansari et al. (2003) also found that the differentiated spikelet number per panicle



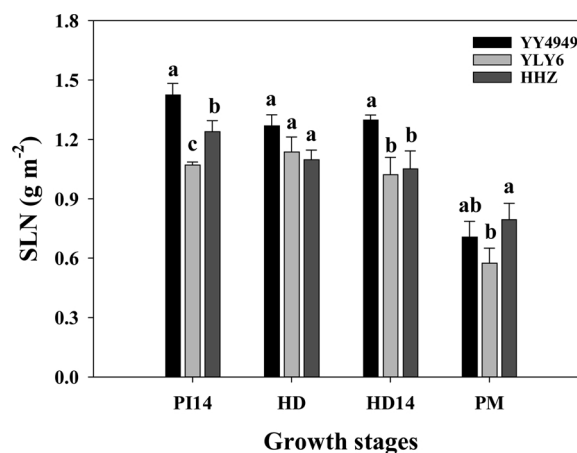
**Fig. 3.** Cumulative LAI calculated from the top of the canopy vs light transmission (I/I<sub>0</sub>) (a) and specific leaf nitrogen (SLN) (b) for YY4949, YLY6 and HHZ at heading in 2017 at Wuxue County, Hubei Province, China.

**Table 7**

Canopy light coefficient (K<sub>L</sub>, m<sup>2</sup> ground m<sup>-2</sup> leaf) and canopy nitrogen extinction coefficient (K<sub>N</sub>, m<sup>2</sup> ground m<sup>-2</sup> leaf) and their ratio (K<sub>N</sub>/K<sub>L</sub>) in YY4949, YLY6 and HHZ in 2017.

Variety	LAI (m <sup>2</sup> m <sup>-2</sup> )	K <sub>L</sub> (m <sup>2</sup> m <sup>-2</sup> )	N <sub>0</sub> (g m <sup>-2</sup> )	K <sub>N</sub> (m <sup>2</sup> m <sup>-2</sup> )	K <sub>N</sub> /K <sub>L</sub>
YY4949	6.83 b	0.35 b	1.78 a	0.15 a	0.41 a
YLY6	8.86 a	0.46 a	1.33 b	0.11 ab	0.24 ab
HHZ	8.41 a	0.40 ab	1.43 ab	0.05 b	0.12 b

Within a column, different letters indicate significant differences among different rice varieties by LSD (P < 0.05).



**Fig. 4.** Specific leaf N (SLN) for YY4949, YLY6 and HHZ at 14 d after panicle initiation (PI<sub>14</sub>), heading stage (HD), 14 d after heading (HD<sub>14</sub>), and mature (PM) at Wuxue County, Hubei Province, China in 2017. Data are means of replicates, and the vertical bars represent the standard error. Different letters above the columns indicated statistical significance at the p < 0.05 level among different rice varieties.

was mainly determined by dry matter accumulation and N uptake per productive stem during the panicle formation stage. In addition, the ability to form spikelets based on per unit dry weight and N uptake, namely, SD and SN was important for the formation of large panicle (Yao et al., 1995; Yoshida et al., 2006). Yoshinaga et al. (2013) reported the high SN was the main factor for the formation of large sink capacity. The increase of the effective accumulation temperature and total light radiation was conducive to increase the number of differentiated spikelet per panicle during the panicle formation stage (Wang et al., 2017). Here YY4949 had lower accumulation temperature and solar radiation during the period from PI to HD due to the shorter growth

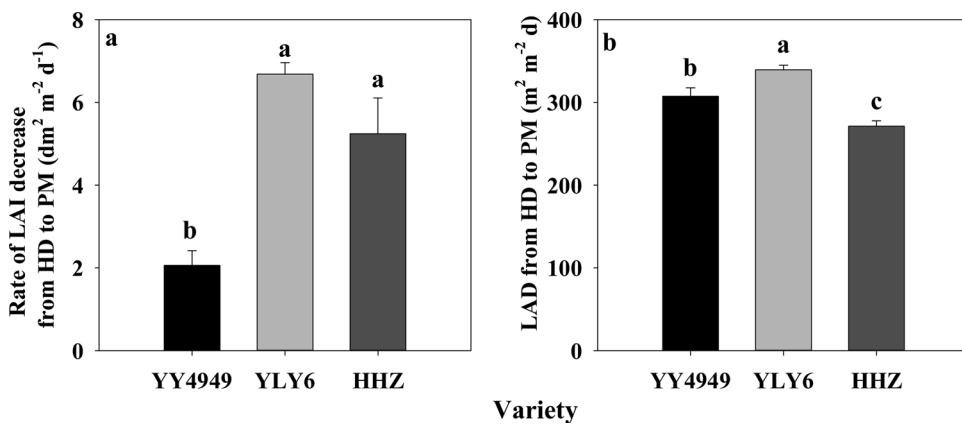


Fig. 5. Rate of LAI decrease from heading to maturity (a) and leaf area duration (LAD) at grain filling stage (b) for YY4949, YLY6 and HHZ in 2017 at Wuxue County, Hubei Province, China. Data are means of replicates, and the vertical bars represent the standard error. Different letters above the columns indicated statistical significance at the  $p < 0.05$  level among different rice varieties.

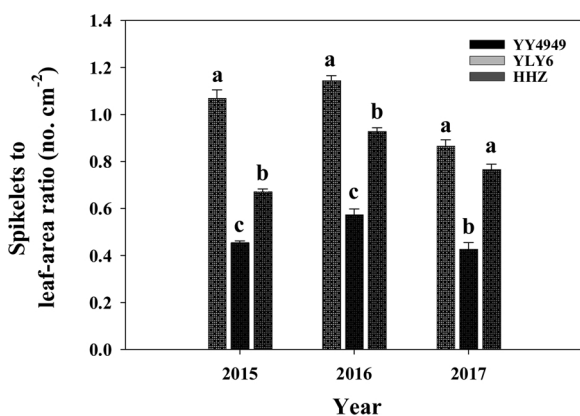


Fig. 6. Spikelets to leaf-area ratio at heading for YY4949, YLY6 and HHZ at Wuxue County, Hubei Province, China in 2015, 2016 and 2017. Data are means of replicates, and the vertical bars represent the standard error. Different letters above the columns indicated statistical significance at the  $p < 0.05$  level among different rice varieties.

duration, but significantly higher ST. More attention is deserved to focus on the genotypic variation in ST and the possible mechanisms.

Recently, several studies reported the importance of biomass accumulation after heading to the formation of high grain yield (Murchie et al., 2002; Deng et al., 2015). YY4949 had significantly higher biomass accumulation after heading than YLY6 and HHZ, which was consistent with the study of Yan et al. (2014) on the biomass accumulation of large panicle varieties. Compared with hybrid *indica* and conventional *japonica* rice, *japonica/indica* hybrids of Yongyou series had higher biomass production after heading (Meng et al., 2015; Wei et al., 2016b). The photosynthetic capacity of leaves and the speed of leaf senescence during the grain filling period directly affected dry matter accumulation, and then affected grain yield and NUE (Murchie et al., 1999). Compared with *japonica* super rice, *indica* super rice had significantly lower dry matter accumulation, crop growth rate, net assimilation rate and LAD after heading (Gong et al., 2014). Yongyou *indica/japonica* hybrid varieties had significantly higher LAI at HD and PM, LAD and Pn after heading than conventional *japonica* and hybrid *indica* rice (Jiang et al., 2015b). In present study, relatively higher LAD and slower leaf senescence contributed to significantly higher dry

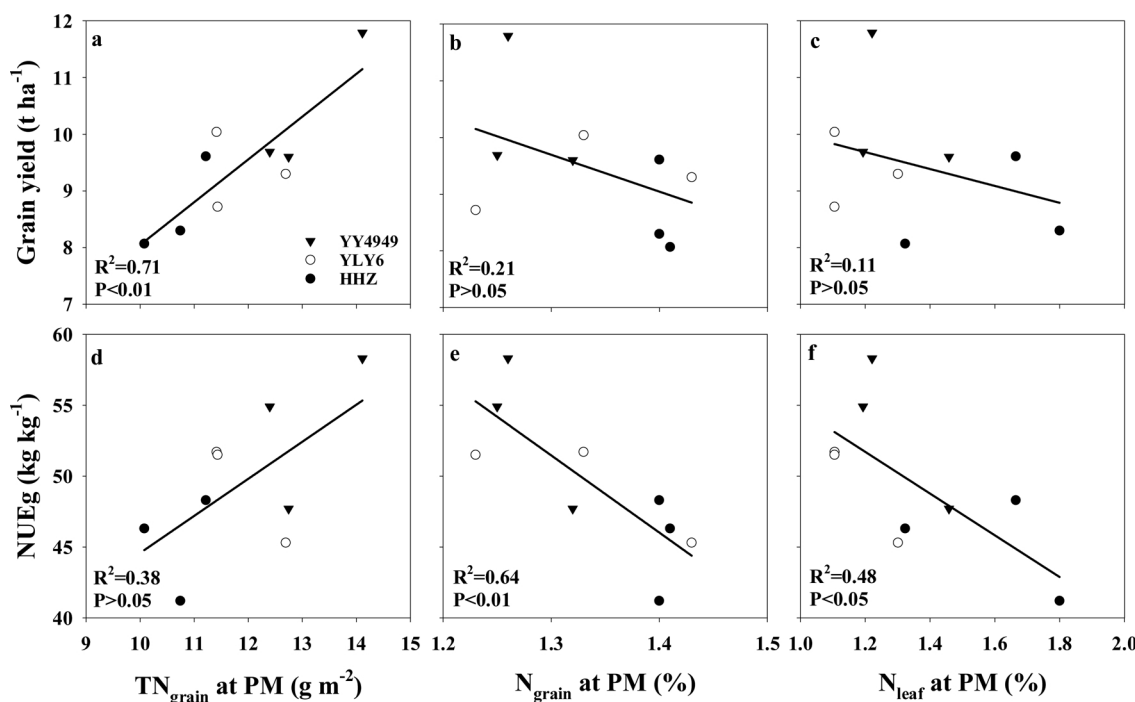


Fig. 7. Correlations of grain N accumulation (TN<sub>grain</sub>), grain N concentration (N<sub>grain</sub>) and leaf N concentration (N<sub>leaf</sub>) at mature (PM) with grain yield (a, b and c), and NUE for grain production (NUEg) (d, e and f) (n = 9) for YY4949, YLY6 and HHZ in 2015–2017.



matter accumulation after heading in YY4949. In terms of N uptake, YY4949 had significantly higher post-flowering N uptake than YLY6 and HHZ, despite no significant difference was observed in total N uptake at PM among the three varieties. Significantly higher N accumulation after heading of YY4949 may be attributed to longer grain filling period. In previous studies, better root structure and higher biological activity in the late growth stage was observed in Yongyou varieties compared to hybrid *indica* or conventional *japonica* varieties (Jiang et al., 2015a; Wei et al., 2018a).

Canopy photosynthesis was the essential determinant for biomass production (Gu et al., 2014). By improving the canopy architecture of rice, canopy photosynthesis and NUE can be significantly improved (Gu et al., 2017). In our study, compared with YLY6 and HHZ, YY4949 had significantly lower  $K_L$  and relative high light transmittance, which is consistent with the findings of Ma et al. (2007) and Jiang et al. (2015). Aside from the light, N also plays an important role in canopy photosynthesis. Numerous studies had summarized leaf photosynthesis was closely related to leaf N content (Lawlor, 2002; Gu et al., 2012). To maximize canopy photosynthesis, more N should be partitioned to the top leaves of the canopy to accommodate the high light intensities, less N should be portioned to shaded lower leaves, and a steeper N gradient is preferred (Field, 1983). The improved N distribution within the canopy can be reflected by the extinction coefficient for effective leaf N ( $K_N$ ) (Gu et al., 2017). In present study, YY4949 had relatively higher  $K_N$  compared with YLY6 and HHZ. The higher RUE during the grain filling stage was resulted from significantly lower  $K_L$  and higher  $K_N$  in YY4949. In addition, rice RUE was related to leaf photosynthesis, and higher RUE can be achieved by improving leaf photosynthetic traits (Huang et al., 2016). In this study, higher SLN was observed in YY4949 than that in YLY6 and HHZ at HD and HD<sub>14</sub>, which might be another reason why YY4949 had high RUE after flowering, especially in the stage from HD to HD<sub>14</sub>.  $K_N/K_L$  ratio was higher in YY4949 than in YLY6 and HHZ in our study.  $K_N/K_L$  is the parameter that reflects N partitioning efficiency at the whole canopy level and closely correlated with rice yield and NUEg (Gu et al., 2017). Therefore, optimized canopy structure is conducive to the coordination of high yield and high NUE in YY4949.

The spikelets to leaf-area ratio is an important index to assess sink-source relationship. Increasing spikelets to leaf-area ratio was beneficial to promote the accumulation of dry matter after heading and the translocation of photosynthate from vegetative organs to grains during the grain filling stage (Ling and Yang, 1986). Significantly higher spikelets to leaf-area ratio was observed in YY4949 than that in YLY6 and HHZ, which suggested YY4949 had better sink-source relationship, and therefore achieved high grain yield and NUE. In addition, increasing  $TN_{grain}$  and decreasing  $N_{grain}$  and  $N_{leaf}$  is beneficial to improve grain yield and NUE under reduced N input condition. It was worth noting grain yield negatively correlated with  $N_{grain}$  at PM only marginally ( $P > 0.05$ ) in the study, while Wei et al. (2018b) showed significantly negative correlation ( $P < 0.01$ ). The difference might be resulted from different N levels. increasing  $TN_{grain}$  at PM could improve grain yield at low N input (100 kg ha<sup>-1</sup> in our study), while under high N input condition, higher grain yield diluted N concentration in grain, and caused significantly negative correlation between grain yield and  $N_{grain}$  (Wei et al., 2018b).

In conclusion, YY4949 with shorter pre-flowering growth duration but larger sink size produced higher yield and NUE simultaneously compared with YLY6 and HHZ under reduced N input condition. The higher SD, SN and ST enabled YY4949 distribute longer growth duration after heading, which led to higher dry matter and N accumulation after heading for YY4949. Moreover, the optimized canopy structure of YY4949 resulted in more synergetic distribution of light and N within the canopy, and partly contributed to the higher RUE after heading. Overall, enlarged sink size and improved post-heading source capacity can facilitate the achievement of high yield and high resource use efficiency simultaneous under low N input condition. More endeavors

ought to focus on the physiological and genetic mechanisms and the interaction effect between genotype and environment.

## Acknowledgements

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