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Influence of tiller heterogeneity on yield components of rice grown under different nitrogen regimes

Y. Wang[a], J.W. Lu[a], T. Ren[a], S. Hussain[a,b], Q. Jia[a], J.L. Zhang[a], M. Yousaf[a], X.K. Li[a,*]

[a]*Key Laboratory of Arable Land Conservation (Middle and Lower Reaches of Yangtze River), Ministry of Agriculture; Microelement Research Center, College of Resources and Environment, Huazhong Agricultural University, Wuhan 430070, China.*
[b]*Department of Agronomy, University of Agriculture, Faisalabad 38040, Pakistan.*
*Corresponding author. E-mail: lixiaokun@mail.hzau.edu.cn

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Abstract

Increase in rice yield under excessive nitrogen (N) supply is negligible, hence it is necessary to analyze the limiting factors via yield components. The present study was carried out during 2014 and 2015 growing seasons in order to quantify the yield componenents of different types of tiller at various N levels. Tillers were divided into three different types (superior, medium and inferior) based on their productivity. The results indicated that the quantitative proportions and yield contributions were decreased in superior tillers, increased in the inferior tillers, while remained stable in the medium tillers with increasing supply of N fertilizer. The increased rate of spikelets per panicle in the superior tillers was higher under all N application levels; however, a high quantitative proportion and the lower number of spikelets per panicle of the inferior tillers might have resulted in the reduced population of spikelets per panicle. The rates of grain filling percentage and grain weight in medium and inferior tillers were decreased with increasing N applications, which led to a decrease in population grain filling and grain weight. The present study suggested that the enhancement of grain filling and weight of the inferior tillers would be an effective approach to further improve the per acre yields of rice. The acquisition of more accurate yield component data, in the perspective of tiller, might be helpful for researches regarding the development of augmented rice breeding architectures.

Keywords: Rice; Nitrogen; Yield components; Heterogeneity; Tiller.

Introduction

Rice (*Oryza sativa* L.) is a major food crop for more than 50% of the world's population. Rice yield components including panicle numbers, spikelets per panicle, grain filling percentage and grain weights, are the key parameters for rice yield estimation. These attributes collectively not only affect the final yields, but also alter plant architectures (Yoshida, 1981). Moreover, yield components are significantly related to organ formation, as well as nutrient transportation and accumulation in the plants (Li et al., 2014). Typically, individual components have a significant positive correlation to the grain yields; however, increasing any one of them might not lead to high yield production, due to strong restriction and compensation mechanisms among the four factors through path analysis (Tong et al., 2011). Hence, coordinated development among the different yield components might possibly leads to higher yields (Liu et al., 2013).

Every yield component is largely established at a particular growth stage of the crop. For instance, the number of panicles (m^{-2}) is mainly dependent on the tiller performance during the vegetative growth stage, whereas, the spikelets per panicle, grain filling and grain weights are determined during the reproductive growth stage (Tadahiko, 1997). In essence, formation of component is a process of continuous increase and accumulation of dry matter.

Nitrogen (N), a key macro-element in many organic compounds of rice plants (Sandhu et al., 2012), is closely related with the leaf photosynthesis and dry matter production (Azizian and Sepaskhah, 2014). At early tillering stage, panicle numbers can be increased with the application of N, which not only fulfills the nutrient's demand for tiller growth, but also regulates the endogenous auxin and cytokinin levels to promote tiller bud germination (Liu et al., 2011). During early reproductive growth stage, the maximum number of spikelets was determined through the differentiation of branches and spikelets. While at the panicle initiation stage, the increase in plant N concentrations significantly regulated the number of differentiated spikelets via the promotion of secondary rachis-branch differentiation (Kobayashi et al., 1994). In addition, the N concentrations at this stage affected the grain plumpness and hull size, thus further altered the grain weight (Yang et al., 2002).

A striking increase in rice population yields has been observed following the application of N fertilizer, where the increased number of productive tillers was generally considered as the key factor for N-induced high yields (Jian et al., 2014). Nevertheless, not every tiller possesses high productivity; typically, the panicles of late-emerging tillers did not significantly contribute to the grain yields of rice (Wang et al., 2007). The application of N triggered the heterogeneity in rice tiller yields and the major sources of such variations were differences of various tillers on the growth stage, photosynthetically active radiation and straw C/N ratio (Wang et al., 2016). Individual tiller yields correspond to their own yield components. In previous studies, the yield components of rice populations were recorded under the conditions of contrasting N levels, which were the average value of all rice tillers (Qiao et al., 2013). Significant differences in panicle characteristics were observed among the different tillers at high N levels; hence, the mean value of yield components was not an effective representation of the tillers that exhibited different productivity rates.

In the present study, tillers were divided into different types (superior, medium and inferior) according to their productivity level under field conditions. The specific objectives were to (i) quantify the proportion of the three types of tillers under different N levels; and (ii) compare the yield components of the three types of tillers under different N levels. The findings of this study may elucidate the mechanisms that drive the changing tendencies in rice yield components following the application of N fertilizer.

Materials and Methods

Site description

The field experiments were conducted in the early and late rice-growing seasons of 2014 and 2015 in two adjacent fields in Wuxue County (30°11′ N 115°59′ E), Hubei

Province, in Central China. The soil type was hydromorphic paddy soil, which is a silty clay loam in texture and derived from quaternary yellow sediment. Prior to the early rice experimentation, soil samples from the upper 20-cm layer were extracted for chemical analyses (Table 1).

Table 1. Soil properties in plow layer (0-20 cm) of on-farm experimental site in 2014 and 2015.

Year	pH	Organic matter	Total N	Available P	Available K
		($g\ kg^{-1}$)		($mg\ kg^{-1}$)	
2014	5.51	29.0	1.42	10.9	90.6
2015	5.58	26.9	1.66	14.2	121.4

Crop management

Rice variety Liangyou 287 (LY287) was grown in the early season (ES), whereas Fengyuanyou 299 (FYY299) was grown in the late season (LS). These two *indica* cultivars have been widely cultivated by local farmers due to their high yield and extensive adaptability. In the ES experiment, pre-germinated seeds were sown in a seedbed on 27 March and the seedlings were transplanted on 1 May at a hill spacing of 0.167 m × 0.191 m, with a single seedling per hill. For the LS experiment, pre-germinated seeds were sown in a seedbed on 25 June and the seedlings were transplanted at the same density to ES following the early rice harvest. The plot size for each replicate was 5.0 × 10.0 m^2. In order to prevent seepage and nutrient flow, each plot was separated by 0.2-m-wide borders, which were covered with a double-layered plastic film (0.3 m deep in the soil). Flooding was maintained in the field during transplanting until 10 d prior to physiological maturity. Weeds, diseases, birds and insects were intensively controlled throughout the growing season to avoid yield losses during both years.

Experimental design and treatments

The proposed study was arranged in a randomized complete block design with three replications. There were four N fertilizer treatments: (i) N_0 (no N fertilizer application); (ii) $N_{82.5}$ (82.5 kg N ha^{-1}); (iii) N_{165} (165 kg N ha^{-1}, which is the recommended rate for rice in Hubei province; Wang et al., 2012); and (iv) $N_{247.5}$ (247.5 kg N ha^{-1}). The N fertilizer was applied as urea with 50% at basal, 25% at the tillering stage (15 days after transplanting; DAT) and 25% at the panicle initiation stage (40 DAT). All treatments received phosphorus (as calcium superphosphate; 33 kg P ha^{-1}) and zinc (as zinc sulfate heptahydrate; 5 kg Zn ha^{-1}) as a basal application. Potassium chloride was applied at 62 kg K ha^{-1} with 70% as a basal stage, while the remaining 30% was applied during the panicle initiation stage.

Measurements

At the physiological maturity stage, the crop was harvested from a 5-m^2 sampling area within each plot and the grain yield was determined and adjusted to a moisture content of 0.14 g H_2O g^{-1} fresh weight. Prior to the yield determination, four hills were sampled from the non-sampling area in order to determine the yield components. Individual rice plants were separated into different tillers and were subsequently dissected into straw and panicles. The number of panicles form each hill was quantified to determine the number of panicles per m^2. Panicles were threshed manually, while the filled spikelets, unfilled spikelets and grain weight were quantified by a seed analysis instrument (SC-G, Wanshen Detection Technology Co., Ltd., Hangzhou, China).

Tillers classification

To reduce the effects of tiller yield heterogeneity on yield components and to further analyze the causes of population yield component variability influenced by N applications, all tillers within the same N treatments were classified into different types (superior, medium and inferior) based on their production. A ratio was obtained by dividing the grain yields of individual tillers by the grain yields of the optimally producing tillers. Tillers were denoted as inferior tillers (when the ratio was < 50%), medium tillers (when the ratio was 50-75%) and superior tillers (when the ratio was > 75%).

Increase rate of yield components for different types of tillers

Population yield components are typically altered following the application of N fertilizer and this population increase rate may be divided into three parts according to different tiller types, which can be expressed as:

$$\text{Increase rate of spikelets per panicle}\left(\%\right)=\frac{NS_i-P_s}{P_s}\times\frac{N_i}{TN}\times 100 \qquad (1)$$

$$\text{Increase rate of grain filling}\left(\%\right)=\frac{N_i\times\left(NFG_i-NG_i\times P_f\right)}{TNG\times P_f}\times 100 \qquad (2)$$

$$\text{Increase rate of grain weight}\left(\%\right)=\frac{N_i\times\left(GY_i-NFG_i\times P_w\right)}{TNFG\times P_w}\times 100 \qquad (3)$$

where N_i is the number of different types of tillers, NS_i is the number of spikelets per panicle of different types of tillers, NG_i is the number of grains of different types of tillers, NFG_i is the number of filled grains of different types of tillers, GY_i is the grain yield of different types of tillers; TN is the total tiller number, TNG is the total number of grains of all tillers, TNFG is the total number of filled grains of all tillers; P_s is the population spikelets per panicle at N_0 treatment, P_f is the population grain filling at N_0 treatment and P_w is the population grain weight at N_0 treatment.

Data collection for yield components

An exhaustive literature survey of peer-reviewed articles published during 1995−2016 was undertaken using the China Knowledge Resource Integrated (CNKI) database (Beijing, China) and the ISI-Web of Science (Thomson Reuters, NY, USA). The keywords employed for searching the literature were rice, *oryza sativa*, nitrogen, yield, yield components. Studies had to meet specific criteria prior to being included in the data set. Initially, the references had at least two N fertilizer levels, where one was no-N treatment and the other was a recommended N fertilizer treatment. Secondly, the references possessed at least one of the yield components (panicles, spikelets per panicle, grain filling percentage or grain weight).

The final data set collected from the literature survey consisted of 53 published studies, covering 980 observations, including 206 measured observations of grain yields, 208 observations of panicles, 200 observations of spikelets per panicle, 170 observations of grain filling and 194 observations of grain weights.

Data analysis

The data were analyzed using SPSS 19.0 software (Chicago, IL, USA) and the mean of the treatments were compared on the basis of the least significant difference test (LSD) at 5% probability. The graphs were plotted using the Origin 8.0 software program (Microcal Software, Northhampton, MA).

Results

Heterogeneity in tillers yield

The application of N fertilizer increased the maximum grain yields of individual tillers, while it decreased the minimum grain yields of individual tillers (Figure 1). Hence, the increased range of grain yields per tiller was observed with increasing N rates for both cultivars (Table 2). In comparison with the N_0 treatment, the mean tiller yield of LY287 was increased following the addition of N during both years; however, the tiller yield of FYY299 was decreased under the $N_{247.5}$ treatment (Figure 1). These results indicated that a huge number of tillers with poor productivity were generated under high N conditions, which might have decreased the mean grain yields per tiller. The coefficient of variation (CV) of individual tiller yields for these two varieties was increased with enhanced N rates in 2014. However, a slight decrease regarding the CV of both varieties was observed when the N rate was increased from N_{165} to $N_{247.5}$ in 2015 (Table 2). The heterogeneity of rice tiller yields was increased with elevated N rates; however, this variation in tiller yields had its upper limit.

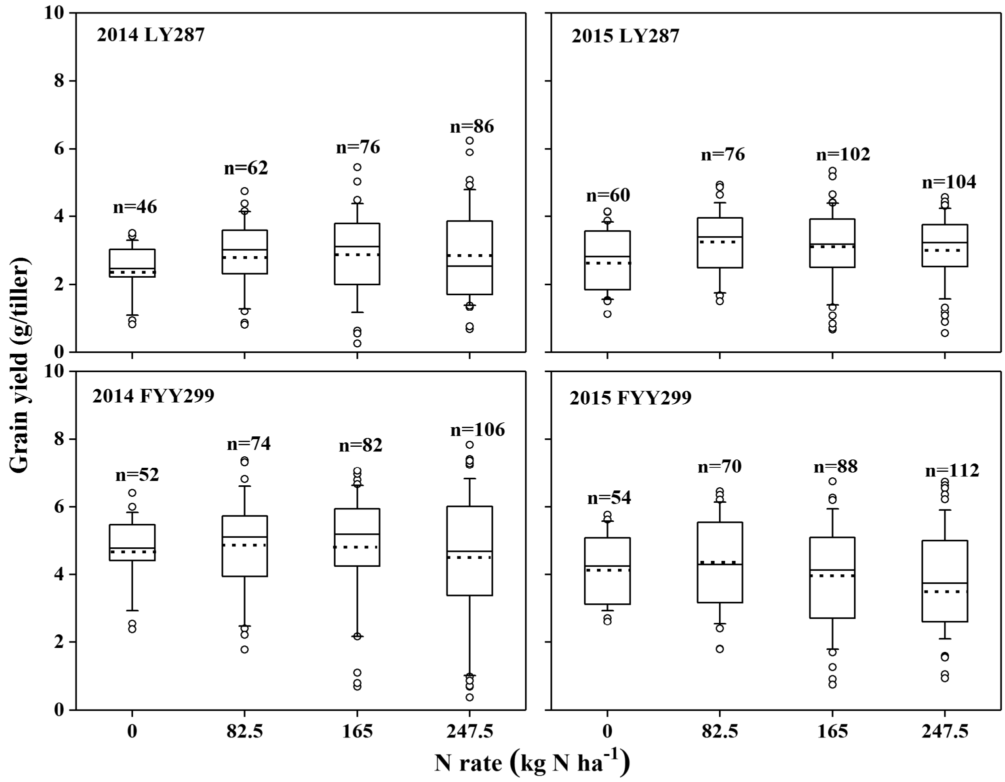

Figure 1. Distribution of different tillers in grain yield affected by N levels in 2014 and 2015. The upper and lower limits of each box represent 25th and 75th percentiles, the upper and lower whisker caps indicate 10th and 90th percentiles, the circles indicate the outliers and the horizontal solid and dashed lines within the box indicate the median and mean, respectively. "n" indicate tiller number of twelve rice plants. LY287, early rice variety Liangyou 287; FYY299, late rice variety Fengyuanyou 299.

Table 2. Heterogeneity in rice tiller yields under different N applications in 2014 and 2015.

Variety	N rate (kg N ha^{-1})	Range (g)	Coefficient of variation (%)
2014			
LY287	0	2.41 ^{c}	33.1 ^{b}
	82.5	2.98 ^{bc}	36.6 ^{ab}
	165	4.15 ^{ab}	42.5 ^{ab}
	247.5	4.68 ^{a}	49.4 ^{a}
FYY299	0	3.35 ^{b}	22.3 ^{b}
	82.5	4.34 ^{ab}	27.9 ^{b}
	165	4.62 ^{ab}	30.9 ^{b}
	247.5	5.98 ^{a}	43.3 ^{a}
2015			
LY287	0	2.43 ^{b}	26.4 ^{b}
	82.5	2.67 ^{ab}	27.9 ^{ab}
	165	3.43 ^{a}	33.8 ^{a}
	247.5	3.16 ^{ab}	30.4 ^{ab}
FYY299	0	3.15 ^{b}	24.2 ^{b}
	82.5	4.66 ^{ab}	31.4 ^{ab}
	165	5.99 ^{a}	39.7 ^{a}
	247.5	5.28 ^{ab}	38.6 ^{a}

Range is the difference value between the maximum and minimum tiller grain yield.
Coefficient of variation indicate the degree of dispersion for grain yield of all tillers.
LY287, early rice variety Liangyou 287; FYY299, late rice variety Fengyuanyou 299.
Means followed by different letters in a column represent significant difference ($P < 0.05$) for the different N levels.

Quantitative proportion and yield contributions of different types of tillers

To study the yield components of tillers with different productivity responses to N fertilizer, the tillers were divided into three types (superior, medium and inferior) based on tiller production (Table 3). Under N_0 treatment, the superior tiller had the highest quantitative proportion and yield contribution followed by medium tiller, whereas the poorest quantitative proportion and yield contribution was observed from inferior tiller. The quantitative proportion of the superior tiller was decreased with increasing N rates; however, the quantitative proportion of the inferior tiller was increased at higher N applications. In contrast to the superior and inferior tillers, the quantitative proportion of the medium tiller exhibited relative stability across any N rates. In 2014 and 2015, the differences between the maximum and minimum quantitative proportion of medium tiller in LY287 were 9.5% and 4.7%, while in FYY299, these values were 11.7% and 8.9%, respectively. Likewise, in terms of yield contribution, the superior and inferior tillers exhibited similar trends to quantitative proportion with increasing N rates, while the yield contribution of the medium tiller remained stable. Under the highest N rates (247.5 kg N ha^{-1}), the quantitative proportion of the superior tiller was less than 30%; however, its yield contribution was almost 40% of the whole population. In contrast, the quantitative proportion of the inferior tiller was over 30% at the highest N rate, but its yield contribution attained only ~20%.

Table 3. The quantitative proportions and yield contributions of different types of tillers under different N applications in 2014 and 2015.

Variety	N rate (kg N ha^{-1})	Quantitative proportion (%)			Yield contribution (%)		
		S	M	I	S	M	I
2014							
LY287	0	43.5 ^{a}	35.1 ^{b}	21.4 ^{c}	55.1 ^{a}	34.2 ^{a}	10.7 ^{b}
	82.5	28.6 ^{b}	42.8 ^{a}	28.6 ^{bc}	40.8 ^{b}	43.7 ^{a}	15.5 ^{ab}
	165	21.6 ^{b}	44.6 ^{a}	33.8 ^{ab}	34.3 ^{b}	47.6 ^{a}	18.1 ^{ab}
	247.5	23.2 ^{b}	34.7 ^{b}	42.1 ^{a}	39.5 ^{b}	37.3 ^{a}	23.2 ^{a}
FYY299	0	53.7 ^{a}	34.7 ^{b}	11.6 ^{c}	61.7 ^{a}	31.8 ^{a}	6.5 ^{b}
	82.5	37.6 ^{ab}	46.4 ^{a}	16.0 ^{bc}	48.8 ^{b}	42.1 ^{a}	9.1 ^{ab}
	165	40.2 ^{ab}	36.2 ^{ab}	23.6 ^{ab}	49.1 ^{ab}	40.1 ^{a}	10.8 ^{ab}
	247.5	28.7 ^{b}	39.9 ^{ab}	31.4 ^{a}	45.9 ^{b}	41.5 ^{a}	12.6 ^{a}
2015							
LY287	0	43.3 ^{a}	33.5 ^{a}	23.2 ^{b}	51.9 ^{a}	34.2 ^{a}	13.9 ^{b}
	82.5	37.9 ^{ab}	34.3 ^{a}	24.9 ^{ab}	48.1 ^{ab}	36.1 ^{a}	15.8 ^{ab}
	165	35.4 ^{ab}	35.3 ^{a}	29.3 ^{ab}	46.7 ^{ab}	36.3 ^{a}	16.9 ^{ab}
	247.5	27.2 ^{b}	38.2 ^{a}	34.6 ^{a}	40.9 ^{b}	39.9 ^{a}	19.3 ^{a}
FYY299	0	48.1 ^{a}	40.7 ^{a}	11.1 ^{c}	58.9 ^{a}	33.7 ^{a}	7.4 ^{b}
	82.5	39.4 ^{a}	39.4 ^{a}	27.3 ^{bc}	49.7 ^{ab}	35.0 ^{a}	15.3 ^{ab}
	165	27.3 ^{b}	31.8 ^{a}	40.9 ^{a}	39.9 ^{bc}	35.6 ^{a}	24.5 ^{a}
	247.5	25.0 ^{b}	37.5 ^{a}	37.5 ^{ab}	37.9 ^{c}	39.1 ^{a}	22.8 ^{a}

S, superior tiller; M, medium tiller; I, inferior tiller.

LY287, early rice variety Liangyou 287; FYY299, late rice variety Fengyuanyou 299.

Means followed by different letters in a column represent significant difference ($P < 0.05$) for the different N levels.

Responses of yield components to nitrogen application

Published studies during 1995-2016 were collected to investigate the yield and yield component responses to N fertilizer applications (Figure 2). Compared with no-N fertilizer treatment, the rice yields and number of panicles were increased by 56.0% (95% confidence intervals = 19.9%−150.0%) and 40.6% (95% confidence intervals = 9.7%−112.5%), respectively under sufficient N fertilization. This result indicated that the appropriate application of N fertilizer may improve rice yields and panicles by varying degrees. Apart from yields and panicle numbers, the spikelets per panicle, grain filling percentage and grain weights might reduced following the application of N fertilizer. Spikelet numbers per panicle were increased by 13.9% (95% confidence intervals = -5.6%−41.0%) under sufficiently supply of N, with an only 4.4% probability of having equivalence to the N_0 treatment. The mean rates of increase in grain filling and grain weight were -2.3% and 0.9%, respectively; nearly 66.7% of grain filling and 36.4% of grain weight observations showed reductions in these attributes after N application. Grain filling was the parameter that was most likely to be decreased when sufficient N fertilizer was provided.

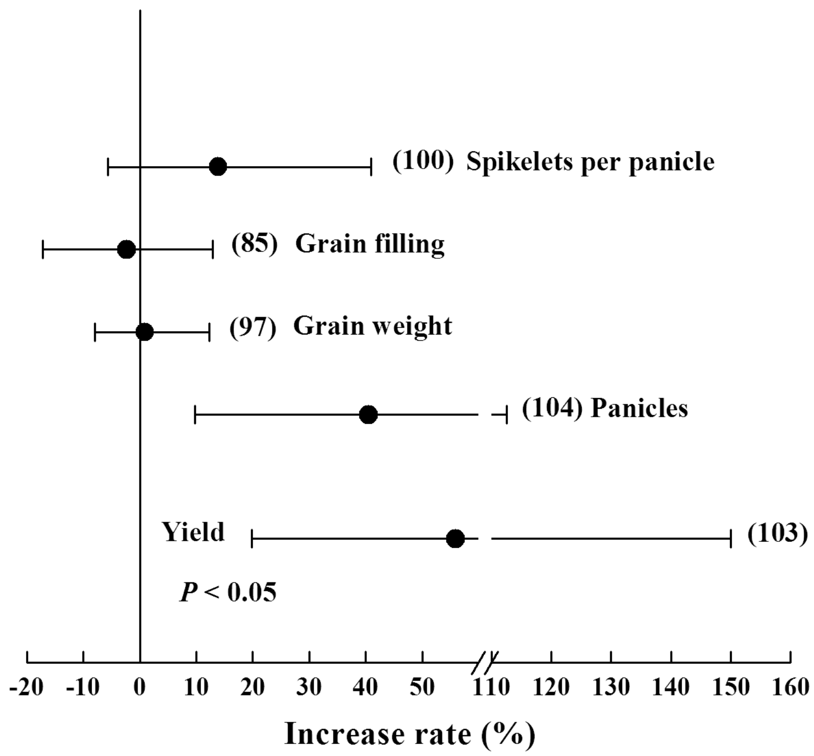

Figure 2. Changes in yields and yield components following the application of N fertilizer from 1995-2016. The number within the brackets indicates the number of observations employed for the analysis.

Yield components of different types of tiller

The yield components of different types of tillers were measured to analyze the variations in population yield-related characteristics under different N application rates (Figure 3). Compared with N_0, the spikelets of LY287 in all three types of tillers were increased following the application of N fertilizer in both years. Hence, the population spikelets were gradually increased under higher N rates. Likewise for FYY299, the spikelets of superior and medium tillers were increased after N fertilizer application. However, a decrease in spikelets of inferior tiller was observed following the addition of N fertilizer over both years. The increase in spikelets of the superior tillers and decrease in spikelets of the inferior tiller cumulatively led to the stable population of spikelets among different N fertilizer application. For rice variety LY287, differences for grain filling were not apparent between the superior and medium tillers at various N levels, except for the medium tillers under $N_{247.5}$ treatment in 2014. A sharp decline in the grain filling of the inferior tillers at high N rates (N_{165} and $N_{247.5}$) was the primary cause for the reduction of the population grain filling. Similar to LY287, the population grain filling of FYY299 was reduced with increasing N rates. The grain filling percentages of medium and inferior tillers were decreased when the N supply was increased; however, no significant differences were observed in the superior tiller at different N applications. Furthermore, the grain filling percentage of the superior tiller was close to that of the medium tillers, which were more abundant than that of the inferior tillers following the application of N fertilizer. Effect of N application on population grain weight was less apparent, however, a distinct decline in the grain weight of the inferior tillers was observed under sufficient N (N_{165} and $N_{247.5}$) treatments for both rice varieties.

Increased rate of yield components for different types of tillers

Increased rate in the population yield components was observed when the N supply was increased from N_0 to $N_{82.5}$, N_{165} or $N_{247.5}$; where the sum of the increased rate for the three types of tillers was equivalent to the population increase rate (Figure 4). The increase rate of inferior tiller was negative, which indicated that the inferior tillers reduced the population yield components following the application of N fertilizer. The combined spikelet increase rate for the superior and medium tillers of LY287 was higher than the decrease rate of the inferior tillers in 2014 and 2015; hence, the population of spikelets per panicle was increased with the application of N fertilizer. However, for FYY299, the increase rate of superior tillers on the population of spikelets per panicle was equal to the decreased rate of the inferior tillers, while the increase rate in the medium tillers was very low. Therefore, no significant differences were observed between the N_0 and other N application treatments regarding population of spikelets per panicle. In addition, the increased population of spikelets in the medium tiller was increased under higher N fertilizer rates.

The population grain filling percentage was reduced under the increasing application of N fertilizer, except for FYY299 under $N_{82.5}$ treatment in 2015 (Figure 4). The rate of grain filling across all three types of tillers was decreased with increasing N supply; the most significant decreases were associated with the inferior tiller. Grain weights of each rice variety varied considerably with N application in both years (Figure 4). The grain weights of the superior and medium tillers were decreased with increasing N supply, except for FYY299 in 2014. As the increase rate of the inferior tiller was less than, or equal to zero, the grain plumpness of the superior and medium tillers largely determined the population grain weight.

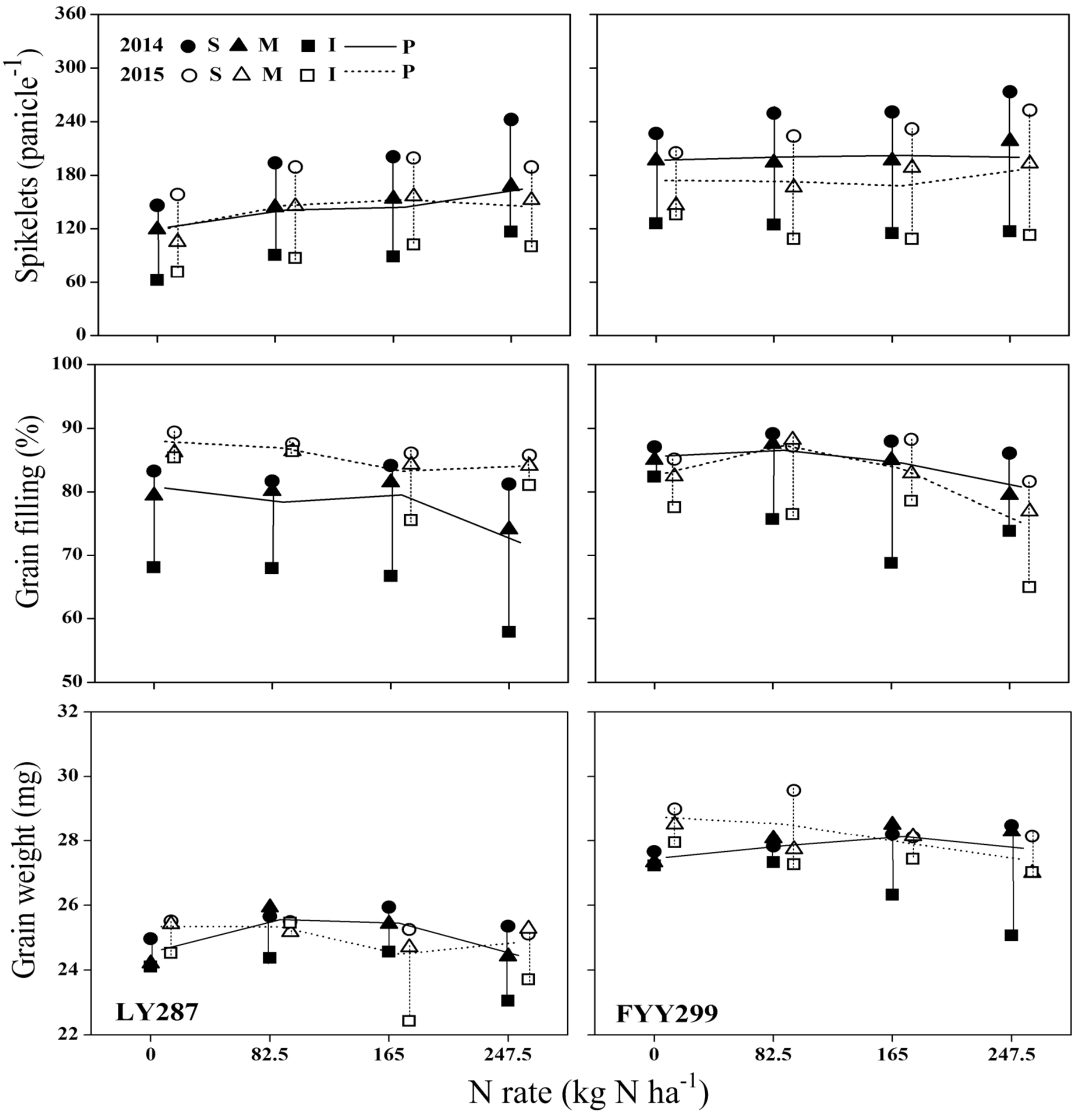

Figure 3. Yield components of different types of tillers as affected by N levels in 2014 and 2015. S, superior tiller, M, medium tiller, I, inferior tiller, P, population. LY287, early rice variety Liangyou 287; FYY299, late rice variety Fengyuanyou 299.

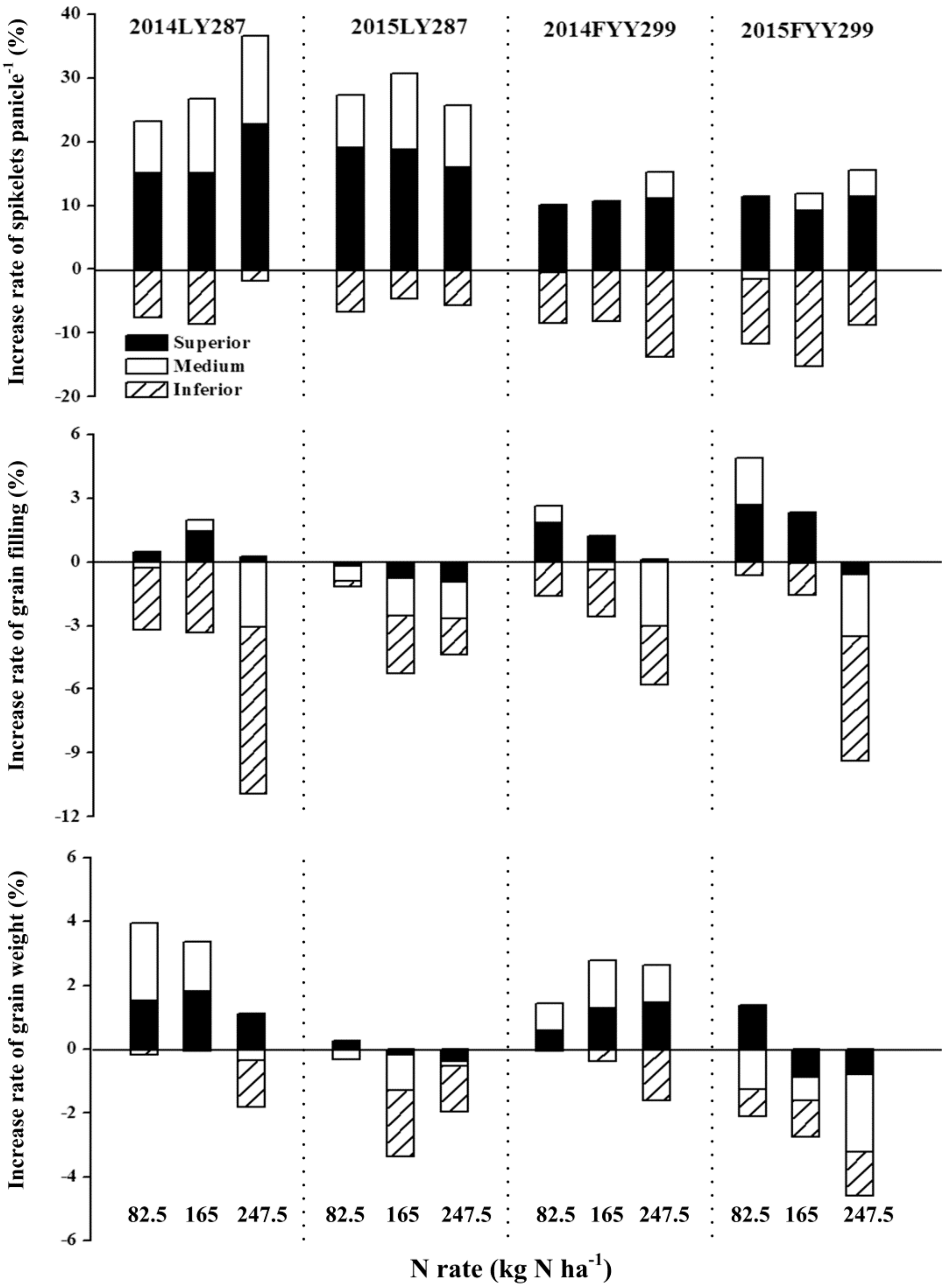

Figure 4. The increase rate on yield components of different types of tillers under different N applications in 2014 and 2015. LY287, early rice variety Liangyou 287; FYY299, late rice variety Fengyuanyou 299.

Discussion

Significance of tiller classification to facilitate the study of yield component variations

Among rice tillers, the panicle development pattern is hierarchical and grain yields decrease for each successive tiller (Sahu et al., 2004). The application of N fertilizer may increase the number of tillers per unit area; however, the quantity of late emerging tillers had a lower contribution to grain yields (Wang et al., 2007). In the present study on the population, the mean tiller grain yield was basically equivalent among different

N fertilization levels (Figure 1). However, for individual tillers, the maximum tiller yield was increased; while the minimum tiller yield was reduced under increasing N fertilization rates (Figure 1). In addition, increases in the range and coefficient of variations of tiller grain yields indicated that heterogeneity increased with N fertilizer applications (Table 2). Significant variations in rice tiller yields were observed under high N supply which indicated that variations might be in single or multiple yield-related parameters. Nevertheless, the 'smoothed' average value effectively blanketed over significant data that was relative to yield formation.

In order to minimize the disturbance of heterogeneity, all tillers under the same N treatment were divided into three types based on their productivity. The quantitative proportions of the superior and inferior tillers exhibited opposite trends under increasing N supply (Table 3). These results suggested that high plant N content boosted the emergence of tillers; however, approximately one-third of the tillers possessed low productivity. Unproductive and inferior tillers competed with other tillers for assimilates, solar energy and mineral nutrients particularly N (Nuruzzaman et al., 2000). Concurrently, low N use efficiency was found in the rice inferior tillers, as their vegetative organs fixed less carbon per unit N (Wang et al., 2016). In order to overcome the issue of low productivity tillers, some researchers have proposed new plant type (NPT) rice with low-tillering and large panicle size (Khush, 1995). Under sufficient N supply, the yield contribution of inferior tillers may attain up to ~20% (Table 3). In China, some farmers transplant rice at wide spacing due to labor shortage and high transplanting expenses; therefore, they typically apply N fertilizers to enhance the population of tillers (Zhang et al., 2013; Yousaf et al., 2016). In such circumstances, the yield contribution of the inferior tillers could not be ignored, because they possess high productivity potential in theory, as the totipotency of rice coleoptile tissues (Oinam and Kothari, 1995). If the limiting factors between the inferior and superior tillers could be reduced, or even removed, the yields of the inferior tillers might be dramatically improved. In addition, high-tillering rice varieties possess a good capacity for functional compensation and late emerging tillers may suitably compensate for yield losses when nascent tillers are subjected to environmental stresses (Wei and Li, 2013). Therefore, fine low-tillering and high-tillering rice varieties should be bred and conserved toward addressing diverse demands. Further, the quantitative proportion and yield contribution of the medium tillers were properly stable, which might comprise a key factor for yield stability of rice.

Response of yield components of different types of tiller to N supply

In comparison with N_0, the yields and panicles per unit area were increased in N fertilized treatments; however, variable trends were observed for the spikelets per panicle, grain filling and grain weight under different N levels (Figure 2). Previous studies have indicated various sources for different rice species responsible for their variable behavior to N fertilizer applications (Jian et al., 2015; Djaman et al., 2016). In the present study, the increased quantity of spikelets per panicle in the superior and medium tillers dominated the variation in population of spikelets. Once the increased rate of medium tillers was significantly dropped, the population of spikelets per panicle could potentially be reduced following N fertilizer application (Figure 4). Thus, the number of spikelets in the medium tillers (accounting for 40 percent of the population number) determined the changing trends of the population of spikelets per panicle.

Regarding grain filling, the rate of increase for the three types of tillers was decreased with higher N supply, particularly for the inferior tillers (Figure 4). The addition of N promoted a sink capacity (the number of spikelets per panicle) while it reduced the dry matter translocation rate (from source to sink), which cumulatively resulted in lower grain filling for the superior and medium tillers (Cheng et al., 2010; Puteh et al., 2014). The inferior tillers possessed short culm lengths and growth periods (Wang et al., 2016); hence, apart from source limitations, shading and premature senescence might also be the critical factors to further reduce the grain filling percentage of the inferior tillers (Mo et al., 2015; Kariali et al., 2012). Previous researchers have indicated that grain weight was the most stable yield component, which was a highly heritable characteristic that was less affected by environmental factors (Guo et al., 2009). To investigate the response of grain weight to N concentrations, 114 genotypes of rice were planted under different N fertilizer conditions, where response characteristics were shown to be variable across varieties (Ye et al., 2005). In the present study, the sum of the increase rate of grain weights for the superior and medium tillers dominated the population grain weight and the increase rate of grain weight was likely to be observed in superior or medium tillers under $N_{82.5}$ and N_{165} treatments (Figure 4). Hull lengths may be extended when grown under the condition of low N concentrations in hydroponic culture; hence, the grain weight of superior and medium tillers might be increased following the application of low N fertilizer. However, an application of N that is too high will shorten the rice hull length and width (Yang et al., 2002). In addition, the low grain weight of rice might be due to metabolic disorders involving carbon and N in plants that are over-crowded and stressed (Jiang et al., 2016).

Regulating yield components to enhance yield potential

In field conditions, the grains in late emerging tillers were “greener” than the early emerging tillers at the harvest stage, particularly under excess N supply. It is still poorly understood whether waiting for the ripening of these tillers (when the grains turn “yellow”) is valuable for grain production. In the present study, the superior and medium tillers played major roles in increasing the yields under the application of N fertilizer, their yield related parameters were higher than that in inferior tillers (Figure 3). High leaf malonaldehyde accumulation and low grain sucrose synthetase enzyme activity resulted in insufficient yield potential in inferior tillers at plant maturity (Wang et al., 2017). Additionally, delaying the harvest time increases the shattering risk of mature grains in superior and medium tillers. With the increase in N fertilizer, individual superior tiller production gradually attained its maximum value; however, large quantities of inferior tillers still possessed a significant yield potential (Wang et al., 2016). In the present study, grain filling and the grain weight of inferior tillers were declined considerably with increasing N concentrations (Figure 3). Late emergence resulted in a shortage of light and growth duration in the inferior tillers, which led to low production (Mohapatra and Kariali, 2008). Shading during the grain filling period severely impeded grain pollination and the accumulation of dry weight (Kobata et al., 2000). Appropriate sparse planting and the use of reflective films might serve as effective measures to increase the leaf intercepted light of inferior tillers (Glenn and Puterka, 2007). In addition, the foliar application of plant growth regulators such as gibberellin and cytokinin may reduce the grain sterility of inferior tillers (Kariali and

Mohapatra, 2007). The increased application of N fertilizer reduced the K content within the rice plants via the ‘dilution effect’ (Yu et al., 2013), where K was a key element in the promotion of non-structural carbohydrate (NSC) transfer to grains. High NSC/spikelets might enhance the physiological activity of grains in the early filling period (Yang et al., 2010). The interaction of nutrients occurs within rice tillers; the superior tillers typically got benefit when the nutrient supply was restricted (Altaf, 1962). Hence, it is necessary to provide K fertilizer in order to increase the sink capacity of the inferior tillers at the jointing stage.

Conclusions

Heterogeneity in tiller yields was increased with increasing supply of N fertilizer. At higher N rates, the quantitative proportions and yield contributions were decreased in superior tillers increased in the inferior tillers, while remained stable in the medium tillers. Spikelets per panicle, grain filling percentages and grain weights of the three types of tillers responded differently to the application of N fertilizer. The superior tillers possessed a higher increase rate of spikelets per panicle under all N applications levels; however, a high quantitative proportion and lower number of spikelets per panicle of the inferior tillers might have resulted in low production of population spikelets per panicle. The rates of grain filling percentages and grain weights were decreased for medium and inferior tillers under higher N applications, which led to decrease in the population grain filling and grain weights. In future, more accurate yield component data, in the perspective of rice tillers, will be valuable for finding the limiting factors in further improving grain yield of rice.

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References

Altaf, A.A.H.M., 1962. Studies on the translocation of nutrients in rice plant by radio-isotope. Jpn. J. Crop Sci. 30, 169-178. (In Japanese with English abstract)

Azizian, A., Sepaskhah, A.R., 2014. Maize response to water, salinity and nitrogen levels: physiological growth parameters and gas exchange. Int. J. Plant Prod. 8, 131-162.

Cheng, J.F., Jiang, H.Y., Pan, X.Y., Dai, T.B., Cao, W.X., 2010. Effects of nitrogen rates on post-anthesis accumulation and transfer of dry matter and nitrogen in rice with differential nitrogen nutrition efficiency. Chinese Agr. Sci. Bull. 26, 150-156. (In Chinese with English abstract)

Djaman, K., Bado, V.B., Mel, V., 2016. Yield and nitrogen use efficiency of aromatic rice varieties in response to nitrogen fertilizer. Emir. J. Food Agr. 28, 126-135.

Glenn, D.M., Puterka, G.J., 2007. The use of plastic films and sprayable reflective particle films to increase light penetration in apple canopies and improve apple color and weight. HortScience 42, 91-96.

Guo, L.B., Ma, L.L., Jiang, H., Zeng, D.L., Hu, J., Wu, L.W., Gao, Z.Y., Zhang, G.H., Qian, Q., 2009. Genetic analysis and fine mapping of two genes for grain shape and weight in rice. J. Integr. Plant Biol. 51, 45-51.

Jiang, Q., Du, Y.L., Tian, X.Y., Wang, Q.S., Xiong, R.H., Xu, G.C., Chuan, Y., Ding, Y.F., 2016. Effect of panicle nitrogen on grain filling characteristics of high-yielding rice cultivars. Eur. J. Agron. 74, 185-192.

Jian, Z.P., Wang, F., Li, Z.Z., Chen, Y.T., Ma, X.C., Nie, L.X., Cui, K.H., Peng, S.B., Lin, Y.J., Song, H.Z., Li, Y., Huang J.L., 2014. Grain yield and nitrogen use efficiency responses to N application in Bt (Cry1Ab/Ac) transgenic two-line hybrid rice. Field Crops Res. 155, 184-191.

Kariali, E., Mohapatra, P.K., 2007. Hormonal regulation of tiller dynamics in differentially-tillering rice cultivars. Plant Growth Regul. 53, 215-223.

Kariali, E., Sarangi, S., Panigrahi, R., Panda, B.B., Mohapatra, P.K., 2012. Variation in senescence pattern of different classes of rice tillers and its effect on panicle biomass growth and grain yield. Am. J. Plant Sci. 3, 1047-1057.

Khush, G.S., 1995. Modern varieties-their real contribution to food supply and equity. GeoJournal. 35, 275-284.

Kobata, T., Sugawara, M., Takatu, S., 2000. Shading during the early grain filling period does not affect potential grain dry matter increase in rice. Agron. J. 92, 411-417.

Kobayashi, K., Horie, T., 1994. The effect of plant nitrogen condition during reproductive stage on the differentiation of spikelets and rachis-branches in rice. Jpn. J. Crop Sci. 63, 193-199. (In Japanese with English abstract)

Li, G.H., Zhang, J., Yang, C.D., Song, Y.P., Zheng, C.Y., Liu, Z.H., Wang, S.H., Tang, S., Ding, Y.F., 2014. Yield and yield components of hybrid rice as influenced by nitrogen fertilization at different eco-sites. J. Plant Nutr. 37, 244-258.

Liu, M.J., Lin, S., Michael, D., Tao, Y.Y., Gustavo, S., Zuo, Q., Sebastian, S., Wei, J.J., Cao, J., Cai, X.Z., Klaus, B., 2013. Do water-saving ground cover rice production systems increase grain yields at regional scales? Field Crops Res. 150, 19-28.

Liu, Y., Ding, Y.F., Wang, Q.S., Meng, D.X., Wang, S.H., 2011. Effects of nitrogen and 6-benzylaminopurine on rice tiller bud growth and changes in endogenous hormones and nitrogen. Crop Sci. 51, 786-792.

Mohapatra, P.K., Kariali, E., 2008. Time of emergence determines the pattern of dominance of rice tillers. Aust. J. Crop Sci. 1, 52-63.

Mo, Z.W., Li, W., Pan, S.G., Timothy, L.F., Xiao, F., Tang, Y.J., Wang, Y.L., Duan, M.Y., Tian, H., Tang, X.R., 2015. Shading during the grain filling period increases 2-acetyl-1-pyrroline content in fragrant rice. Rice. 8, 1-10.

Nuruzzaman, M., Yamamoto, Y., Nitta, Y., Yoshida, T., Miyazaki, A., 2000. Varietal differences in tillering ability of fourteen japonica and indica rice varieties. Soil Sci. Plant Nutr. 46, 381-391.

Oinam, G.S., Kothari, S.L., 1995. Totipotency of coleoptile tissue in indica rice (*Oryza sativa* L. cv. ch 1039). Plant Cell Rep. 14, 245-248.

Puteh, A.B., Mondal, M.M.A., Ismail, M.R., Latif, M.A., 2014. Grain sterility in relation to dry mass production and distribution in rice (*Oryza sativa* L.). Biomed Res. Int. 2014, 175-185.

Qiao, J., Yang, L.Z., Yan, T.M., Xue, F., Zhao, D., 2013. Rice dry matter and nitrogen accumulation, soil mineral N around root and N leaching, with increasing application rates of fertilizer. Eur. J. Agron. 49, 93-103.

Sahu, K.C., Kariali, E., Mohapatra, P.K., 2004. Tiller dominance in rice is dependent on assimilate concentration of the panicle during grain filling. Ind. J. Plant Physiol. 9, 402-406.

Sandhu, S.S., Mahal, S.S., Vashist, K.K., Buttar, G.S., Brar, A.S., Singh, M., 2012. Crop and water productivity of bed transplanted rice as influenced by various levels of nitrogen and irrigation in northwest India. Agr. Water Manag. 104, 32-39.

Tadahiko, M., 1997. Physiological nitrogen efficiency in rice: nitrogen utilization, photosynthesis and yield potential. Plant Soil, 196, 201-210.

Tong, H.H., Chen, L., Li, W.P., Mei, H.W., Xing, Y.Z., Yu, X.Q., Xu, X.Y., Zhang, S.Q., Luo, L.J., 2011. Identification and characterization of quantitative trait loci for grain yield and its components under different nitrogen fertilization levels in rice (*Oryza sativa* L.). Mol. Breeding. 28, 495-509.

Wang, F., Cheng, F.M., Zhang, G.P., 2007. Difference in grain yield and quality among tillers in rice genotypes differing in tillering capacity. Rice Sci. 14, 135-140.

Wang, W.N., Lu, J.W., Ren, T., Li, X.K., Su, W., Lu, M.X., 2012. Evaluating regional mean optimal nitrogen rates in combination with indigenous nitrogen supply for rice production. Field Crops Res. 137, 37-48.

Wang, Y., Ren, T., Lu, J.W., Ming, R., Li, P.F., Saddam, H., Li, X.K., 2016. Heterogeneity in rice tillers yield associated with tillers formation and nitrogen fertilizer. Agron. J. 108, 1717-1725.

Wang, Y., Lu, J.W., Ren, T., Saddam, H., Guo, C., Wang, S., Cong, R.H., Li, X.K., 2017. Effects of nitrogen and tiller type on grain yield and physiological responses in rice. Aob Plants. 9, plx012.

Wei, M., Li, D.X., 2013. The compensation capacity of tillering and production of main stem nodes in rice. Acta Ecol. Sin. 33, 7098-7107. (In Chinese with English abstract)

Yang, J.C., 2010. Mechanism and regulation in the filling of inferior spikelets of rice. Acta Agron. Sin. 36, 2011-2019. (In Chinese with English abstract)

Yang, L.X., Wang, Y.L., Dong, G.C., Huang, J.Y., Zhang, Y.J., Cai, H.R., 2002. Effects of nitrogen on hull traits and its causes in Yangdao 6. Agr. Sci. China. 1, 738-744.

Yoshida, S., 1981. Climatic environment and its influence. In fundamentals of rice crop science. The International Rice Research Institute, Los Banos, Philippines.

Ye, Q.B., Zhang, H.C., Xia, K., Wei, H.Y., Wang, B.F., Zhang, Y., Huo, Z.Y., Dai, Q.G., Xu, K., 2005. Genotypic difference and the classification in response of grain weight to nitrogen in rice. Acta Agron. Sin. 31, 1021-1028. (In Chinese with English abstract)

Yousaf, M., Li, X., Zhang, Z., Ren, T., Cong, R., Ata-Ul-Karim, S.T., Fahad, S., Shah, A,N., Lu, J., 2016. Nitrogen fertilizer management for enhancing crop productivity and nitrogen use efficiency in a rice-oilseed rape rotation system in China. Front. Plant Sci. 7, 1496.

Yu, Q.G., Ye, J., Fu, J.R., Ma, J.W., Sun, W.C., Jiang, L.N., Wang, Q., 2013. Effects of nitrogen application level on rice nutrient uptake and ammonia volatilization. Rice Sci. 20, 139-147.

Zhang, Z.J., Chu, G., Liu, L.J., Wang, Z.Q., Wang, X.M., Zhang, H., Yang, J.C., Zhang, J.H., 2013. Mid-season nitrogen application strategies for rice varieties differing in panicle size. Field Crops Res. 150, 9-18.