INTER-ANNUAL CLIMATE VARIABILITY CONSTRAINS RICE GENETIC IMPROVEMENT IN CHINA

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Abstract
Yield potential has been significantly increased through hybrid rice breeding in the past, however, the genetic gain in grain yield is becoming marginal in recent years, especially in farmers’ field. The increase in climate variability is one potential reason for the stagnant rice grain yield. Moreover, overuse of nitrogen fertilizer and poor grain quality of hybrid rice reduce its advantage over inbred rice. The present study evaluated seventy-eight elite hybrid varieties in 2014–2018 aiming to determine the climate variability and its influences on grain yield, nitrogen use efficiency (NUE), and grain protein content of the newly bred rice hybrid varieties simultaneously. It was found that daily maximum and minimum temperature, daily radiation varied significantly across planting years. The extreme differences for $T_{\text{max}}$, $T_{\text{min}}$, and radiation were 2.0°C, 1.5°C, and 3.6 MJ m$^{-2}$ d$^{-1}$, respectively. Overall, grain yield of 22 varieties was significantly increased in comparison to that of the control cultivar Yangliangyou6 (YLY6), which was closely dependent on the planting year. Grain yield of these elite varieties ranged from 9.69 to 11.97 t ha$^{-1}$, and NUE for grain production (NUEg) from 47.3 to 60.9 kg kg$^{-1}$. The inter-annual variation in grain yield, NUEg, and grain protein content was significantly related to the average daily minimum temperature ($T_{\text{min}}$), due to its effects on grain filling percentage and harvest index. Moreover, these three properties are mutually correlated for all varieties across five years: grain yield positively correlated with NUEg ($R^2 = 0.46$) and negatively correlated with protein content ($R^2 = 0.32$), whereas NUEg negatively related to protein content ($R^2 = 0.49$). These results suggest that enhancing the adaptation to climate variability in hybrid rice breeding is essential and urgent for sustainable rice production in China.

KEYWORDS
grain yield, Green super rice, nighttime temperature, NUE
Global demand for crop production in 2050 will increase by 100–110% because of the growth in population and dietary shifts toward a larger percentage of meat due to the higher income (Tilman et al., 2011). The challenge is reinforced by an urgent demand for sustainability in agricultural production under an increasingly changing climate (Cassman et al., 2003; Tilman et al., 2011). Rice is one of the major crops providing food for over half of the world population (Tao et al., 2014). China occupied 18.6% of global rice planting area and produced 27.9% of total rice production in 2014 (FAOSTAT, 2018). Due to the pressures from large population and limited arable land area, increasing yield potential and closing yield gap have been the major targets in rice research in China (Peng et al., 2008).

Yield potential is defined as the yield of a cultivar when grown in environments to which it is adapted, with nutrients and water non-limiting and with pests, diseases, weeds, lodging, and other stresses effectively controlled (Evans & Fischer, 1999). For irrigated rice in China, the Green Revolution, namely by development of semi-dwarf varieties nearly doubled the grain yield (Peng et al., 2008), and utilization of heterosis further increased grain yield by over 10% (Yuan et al., 1994). Through the incorporation of intersubspecific heterosis and ideotype approach, China’s super hybrid rice is developed with yield potential of more than 15 t ha\(^{-1}\) (Wang & Peng, 2017). Due to the diminishing returns as the actual yield approaching yield potential and the uncertainty in climate (such as high temperature, rainfall, and other weather extremes), 75–80% of yield potential is taken as the exploitable yield (van Ittersum et al., 2013). Yield gap is usually defined as the difference between this exploitable yield potential and farmers’ yields. Current national farm yield for single rice in China was 72% of the potential yield, which is very close to the 75–80% yield potential threshold, especially in Central China (Deng et al., 2019). Therefore, to further increase rice production, it is necessary to explore the possibility of closing yield gap beyond 80% of yield potential through breeding climate-resilient varieties (Bailey-Serres et al., 2019).

Globally, around 32% of the variability in rice yield is explained by climate variability depending on latitude and growth durations (Ray et al., 2015), and high temperature has been regarded as one of the major factors that will result in significant yield penalty (Lobell & Burke, 2008). Projections using climate models suggest that both the long-term global warming and the occurrence of extreme seasonal heat will cause significant damage to rice production (Lobell & Burke, 2008; Tao & Zhang, 2013; Zhao et al., 2017). Furthermore, rapid increases in night temperature than day temperature is frequently demonstrated in global warming, and posed significant challenges to rice production (Donat & Alexander, 2012; Impa et al., 2021; Ling et al., 2019; Peng et al., 2004). The physiological mechanisms underlying the reduction in grain yield resulted from high night temperature has been investigated mainly in growth chambers, which includes (1) higher respiration that leads to lower dry matter accumulation (Laza et al., 2015; Peraudeau et al., 2015), (2) the increase in spikelet degeneration due to the reduction in cytokinin biosynthesis (Shi et al., 2016; Wu, Cui, et al., 2016), (3) lower pollen fertility due to the lower content of IAA and GA\(_4\) (Mohammed et al., 2013; Wu, Cui, et al., 2016), (4) decrease in grain weight because of the reduction in grain filling rate and endosperm cell size (Morita et al., 2005; Shi et al., 2016; Wu, Cui, et al., 2016), and (5) decrease in the translocation of non-structural carbohydrates from the stem to grains (Shi et al., 2013). Impa et al., (2021) demonstrated that results from controlled environments where most of the previous studies were conducted were significantly different to that in field conditions. So evaluation on the performance of newly bred rice varieties across years with different climate conditions is meaningful.

High night temperature significantly affects rice grain quality, resulting in reduced grain length and width, reduced starch content but increased protein content, and the occurrence of chalkiness. Expression of starch-synthesis genes was downregulated, while the starch-degrading enzymes, such as α-amylase was increased (Impa et al., 2021). Despite the large amount of physiological and modeling studies about the response to climate change (especially on high temperature) in rice, the progress of climate-resilient rice breeding and the performance of the newly bred rice varieties in response to climate variability are unknown for Chinese hybrids. In addition, rice production in China facing many additional challenges, including the severely overuse of fertilizers and the poor rice grain quality of hybrid rice (Zhang, 2007). To overcome these challenges, the Ministry of Science and Technology of China launched a mega project (the 863 Program) to develop Green Super Rice (GSR) varieties, which entered its second phase in 2014 (Wang & Peng, 2017). The GSR concept includes the development of insect and disease resistance, N- and P-use efficiency, drought resistance, high grain yield, and superior quality (Zhang, 2007). Therefore, in present study, seventy-eight elite GSR candidate varieties from fourteen Provinces in South China were planted in field experiments in 2014–2018. The objectives were to (1) determine the inter-annual variability in climate conditions in Central China, (2) analyze the relationship among grain yield, N-use efficiency (NUE), and grain protein content for these varieties across different growth years at a moderate N fertilizer rate, (3) examine the climatic factors contributing to the inter-annual variability in grain yield, and its physiological mechanisms.
2 | MATERIALS AND METHODS

2.1 | Experimental materials

A set of seventy-eight rice varieties were used in the study from 2014 to 2018, and 15–25 varieties were used in each year (Table S1), which included indica and japonica inbred varieties, and indica and intersubspecific hybrid varieties. These varieties were selected as the GSR candidate varieties by each rice breeding institute, because they were new varieties developed recently and showed good performance in local cultivar tests in grain yield, grain quality, and nitrogen use efficiency. One super hybrid cultivar (YLY6) was used as the control cultivar in the five years, as this variety was one of the most widely planted super hybrid rice varieties. The release year, breeding institute, subspecies, and variety type of these varieties were shown in Table S1.

2.2 | Experimental design and crop managements

Five-year field experiments were performed in farmer’s fields (29°51′N, 115°53′E) at Dajin Township, Hubei Province in 2014–2018. The upper 20 cm soil was sampled, and the chemical properties were measured for the experimental field. Experiments were in two nearby fields in 2014 and 2015–2018, respectively. In 2014, the soil was clay loam with pH 5.60, 27.18 g kg\(^{-1}\) organic matter, 1.83 g kg\(^{-1}\) total N, 4.91 mg kg\(^{-1}\) available P, and 105.8 mg kg\(^{-1}\) available K. In 2015 to 2018, the soil had pH 5.20, 26.69 g kg\(^{-1}\) organic matter, 1.88 g kg\(^{-1}\) total N, 22.56 mg kg\(^{-1}\) available P, and 159.17 mg kg\(^{-1}\) available K.

Fifteen to twenty-five varieties were laid out in a complete randomized block design, and 3 to 4 replications were arranged in each year’s experiment. The plot size was 30 m\(^2\) (5 m × 6 m). Pre-germinated seeds were sown in seedbeds on 20 May, and transplanting of the seedling to the field was finished after 25–30 days. Hill spacing was set at 16.7 cm × 26.7 cm, and each hill had two seedlings. In present study, a moderate N fertilizer rate (100 kg N ha\(^{-1}\)) was used, which was around 44% lower than the national average value of 180 kg N ha\(^{-1}\) in China (Huang et al., 2018; Peng et al., 2002). The N fertilizer was applied in three growth stages, namely 40% as basal fertilizer, 30% on 7–10 days after transplanting, and 30% at panicle initiation stage. All P fertilizer (40 kg P ha\(^{-1}\)) was incorporated into the field when conducting field preparation at one day before transplanting. Half of the K fertilizer (50 kg K ha\(^{-1}\)) was applied with the basal N and P fertilizers when preparing the field, and the other 50 kg K ha\(^{-1}\) K fertilizer was applied at panicle initiation stage. Water management of the experimental fields was continuous flooding during the whole growth duration, except for two periods. About 20 days, after transplanting water was drained from the field for around one week to control tillering, and on 10 days before maturity water drainage was conducted again to ensure dry field when harvesting. Yield loss due to pests, pathogens, and weeds was avoided by intensive control.

2.3 | Measurements

2.3.1 | Climate data

Climate data used in present study were taken from the nearby weather station. The weather station collected data including temperature and solar radiation, locating within 2 km from our experimental field. Daily maximum temperature (\(T_{\text{max}}\)) was used as the daytime maximum temperature, while daily minimum temperature (\(T_{\text{min}}\)) as the nighttime minimum temperature.

2.3.2 | Yield and yield components

At maturity, plants of 5 m\(^2\) area in the center of each plot were sampled and threshed to determine grain yield. Water content was also measured to adjust the grain yield to a standard moisture content of 14%. Meanwhile, 12 hills were taken in each plot to determine the aboveground dry weight, harvest index (HI), and yield components. Tiller number of the 12 hills was counted to calculate panicle number per m\(^2\), and then separate the plants into straw and panicles. Spikelets were divided from the rachis by hand threshing, and then filled and unfilled spikelets were separated by submerging all the spikelets in tap water. The number of spikelets per m\(^2\) was determined by counting three filled spikelets subsamples of around 30 g and three unfilled spikelets subsamples of around 2 g. Grain filling percentage was the ratio of filled spikelets over total spikelets. The dry weights of each parts of the 12 plants were determined after oven drying at 80°C to a constant weight, and then, these dry weights were summed to calculate total dry weight (TDW). Harvest index was calculated as the percentage of grain yield to the aboveground total biomass.

2.3.3 | Nitrogen uptake and nitrogen use efficiency

At maturity, N concentration was measured for each plant part including stem plus leaf (straw), filled grains, and unfilled grains plus rachis with Elementar vario MAX CNS/CN (Elementar Trading Co., Ltd). The N content in each plant part was calculated as the product of N concentration and
dry weight, which was summed to calculate the total aboveground N uptake. Protein content in grain was calculated as the product of N concentration in the grain multiplying a coefficient of 5.95 (Shi et al., 2019). Nitrogen use efficiency for grain production was calculated as the following formula: NUEg = grain yield/total aboveground N uptake.

2.4 | Data analysis

Analysis of variance (ANOVA) was performed to assess the inter-annual variability in grain yield, total aboveground N uptake, NUEg, and protein content using the Statistix 9 software (Analytical Software). SigmaPlot 12.5 (Systat Software Inc.) was used to perform linear regression analysis in order to test the correlations between the measured parameters using.

3 | RESULTS

3.1 | Temperature and radiation

The $T_{\text{max}}$ and $T_{\text{min}}$, and daily radiation over the growing season of these varieties were calculated from 2014 to 2018 (Figure 1). Across the five years, $T_{\text{max}}$ ranged from 30.0°C to 32.0°C, $T_{\text{min}}$ was from 21.9°C to 23.4°C, and radiation was from 12.1 MJ m$^{-2}$ d$^{-1}$ to 15.7 MJ m$^{-2}$ d$^{-1}$. There was no significant correlation between the three climate parameters within the five years (Figure S1).

3.2 | Grain yield, NUE, and protein content

There were significant differences in the mean value of grain yield, N uptake, nitrogen use efficiency for grain production (NUEg), and protein content for all the varieties from 2014 to 2018 (Figure 2). The average grain yield was highest in 2015 (10.2 t ha$^{-1}$), and lowest in 2016 (8.6 t ha$^{-1}$). N uptake ranged from 157.8 kg ha$^{-1}$ in 2014 to 201.3 kg ha$^{-1}$ in 2017. An opposite trend was found in the average NUEg, with the highest value of 56.1 kg kg$^{-1}$ in 2014 and the lowest value of 41.2 kg kg$^{-1}$ in 2017. The average protein content ranged from 7.4% in 2015 to 8.1% in 2017.

In each year, difference in grain yield among the varieties was less than 1 t ha$^{-1}$, for example, 11 out of 15 varieties had a grain yield of 9–10 t ha$^{-1}$ in 2014 (Table S2), while grain yield of 15 out of 19 varieties was from 9.6 to 10.6 t ha$^{-1}$ in 2015 (Table S3). Totally, twenty-two elite varieties with significantly higher grain yield than the control cultivar of YLY6 were identified. HY549 had a grain yield of 9.26–10.99 t ha$^{-1}$ from 2014 to 2016, which were 6.2%–14.4% higher than YLY6. Grain yield of YY4913 was 11.97 t ha$^{-1}$, 33.3% higher compared to YLY6 (Table S6).

22.68% higher than that of YLY6 (Table S3). XY5013 had a grain yield of 10.18 and 10.61 t ha$^{-1}$ in 2017 and 2018, which was 8.1% and 18.2% higher than YLY6, respectively (Table S5 and S6). Grain yield of XY4913 (11.97 t ha$^{-1}$) was 33.3% higher compared to YLY6 (Table S6).

Genotypic variation within each year in N uptake (CV of 4.6%–8.8%) was smaller than that of NUEg (CV of
7.1%–13.5%) from 2014 to 2018 (Tables S2–S6). N uptake for most of the varieties was not significantly different compared to that of YLY6 in each year. The yield advantage of HY549 over YLY6 was accounted for by the coordination of N uptake and NUEg. The intersubspecific hybrids, such as YY4949, XY5013, and XY4913, tended to have higher NUEg than YLY6. NUEg of XY5013 and XY4913 in 2018 were 53.6 and 53.1 kg kg⁻¹, which were 23.2% and 24.4% higher than that of YLY6, respectively. Protein content in grain had a CV of 3.6%–6.2%. Most of the varieties had a protein content higher than 7%.

3.3 | Correlation between climate factors and grain yield, grain filling percentage, and protein content

Grain yield was significantly correlated with $T_{\text{min}}$ with $R^2 = 0.85$ ($p < 0.05$, Figure 3a), which was mainly due to the significantly negative correlation between grain filling percentage and $T_{\text{min}}$ ($R^2 = 0.94$, $p < 0.01$; Figure 3d). In addition, protein content in grain significantly and positively correlated with $T_{\text{min}}$ ($R^2 = 0.74$, $p = 0.06$; Figure 3g). Both $T_{\text{max}}$ and daily average radiation did not correlate with grain yield, grain filling percentage, and protein content (Figure 3).

3.4 | Correlations between grain yield and N uptake, NUEg, and protein content

For all the varieties across the five years, grain yield was more significantly correlated with NUEg ($R^2 = 0.46$, $p < 0.001$; Figure 4b) compared with N uptake ($R^2 = 0.04$, $p = 0.05$; Figure 4a). Protein content significantly and negatively correlated with grain yield ($R^2 = 0.32$, $p < 0.001$; Figure 4c) and NUEg ($R^2 = 0.49$, $p < 0.001$; Figure 4d), respectively.

3.5 | Physiological causes for the genotypic variation in grain yield and NUEg

Among the yield components, the variation in grain yield among the varieties was mainly related to grain filling percentage ($R^2 = 0.59$, $p < 0.001$; Figure S2a). Both total dry weight and harvest index significantly contributed to the difference in grain yield among the varieties, but the latter had a higher $R^2$ (0.31 vs 0.47; Figure S2b and S2c). Crop growth rate only slightly correlated with grain yield with $R^2$ of 0.16 (Figure S2d). NUEg significantly correlated with harvest index ($R^2 = 0.75$, $p < 0.0001$; Figure 5).

4 | DISCUSSION

In order to maintain food security in China in a sustainable way, development of Green Super Rice (GSR) varieties with high yield, high NUE, and superior grain quality was advocated a decade ago (Zhang, 2007) and made significant progresses (Wing et al., 2018). For example, several intersubspecific hybrid varieties with a high NUE gene of NRT1.1B were released in 2018, including XY7113 and XY4913 (Hu et al., 2015; Table S1). In present study, twenty-two varieties of 78 elite candidate varieties produced significantly higher grain yield than YLY6 under moderate N supply condition, and these varieties could be designated as GSR varieties (Tables S2–S6). Previous studies have demonstrated that rice breeding for higher grain yield is accompanied by an increase in NUE (Huang et al., 2018; Zhu et al., 2016). Here, 18 of the
22 genotypes produced a grain yield higher than 10 t ha\(^{-1}\) at a moderate N rate, indicating that it is possible to achieve high grain yield with reduced N input (Huang et al., 2019; Wu, Yuan, et al., 2016).

However, it is noteworthy that the performance of the newly bred varieties was significantly influenced by the climatic conditions in each planting year (Figures 1 and 2; Satapathy et al., 2014). The year with suitable climates facilitated the new varieties to express their yield advantages at a moderate N fertilizer condition. But in 2017 with the highest \(T_{\text{min}}\), the average grain yield was the lowest and none of the new varieties had significantly higher grain yield than YLY6 (Table S5). XY7113 produced a grain yield of 11.46 t ha\(^{-1}\) in 2018 (Table S6), but only 10.15 t ha\(^{-1}\) in 2017 (Table S5). The inter-annual variability in crop yield including rice was projected to increase due to the climate change in the future (Challinor et al., 2014; Iizumi & Ramankutty, 2016; Ray et al., 2015; Urban et al., 2012).

Climate variability, especially temperature, significantly contributed to the inter-annual variability in crop yield (Iizumi & Ramankutty, 2016; Ray et al., 2015). In rice, annual yield of double-season rice is significantly different between tropical and subtropical environments, which was mainly due to the difference in temperature (Wang et al., 2016). In present study, the inter-annual variation in grain yield was mainly related to the seasonal \(T_{\text{min}}\) due to its effect on grain filling (Figure 3).

Since Peng et al., (2004) found that rice grain yield declined by 10% for each 1°C increase in growing-season minimum temperature, effect of long-term global warming on crop production has been extensively investigated in global and regional scale through the use of statistical models (Gourdji et al., 2013; Lobell et al., 2011; Schaubberger et al., 2017; Tao et al., 2013; Zhang & Huang, 2011; Zhao et al., 2017). The present study emphasizes again the significant hidden costs of moderate inter-annual variation in
nighttime temperature on grain yield of newly bred varieties, on which urgent research efforts in rice breeding should focus (Sadok & Jagadish, 2020). The elite varieties identified in present study including HY549, HLY630, XY4913, and XY5013 all showed no yield advantage compared with YLY6 in 2016 and 2017 when nighttime temperature was high (Tables S2–S6). In maize, the historical cultivar improvement in yield was accompanied by greater sensitivity to drought (Lobell et al., 2014). The importance of crop-level adaptations to alleviate the negative impacts of climate variability has been pointed out in a global study, which could increase simulated crop yields by an average 7–15% in a changing climate (Challinor et al., 2014). In double rice regions of China, the reduction in growth duration and grain yield due to global warming has been partially mitigated by planting new varieties (Qiu et al., 2019). Therefore, modern crop breeding should further improve the stress tolerance of new varieties.

In the context of global climate change, increasing grain yield together with reducing nitrogen inputs has emerged as a key research target (Tester & Langridge, 2010). For all the varieties across the five years, variation in grain yield was mainly related to NUEg instead of N uptake (Figure 4a,b), which was possibly associated with the sensitivity of harvest index to climate variability across years (Figure 5). The result was consistent with that reduction in non-structural carbohydrate (NSC) translocation and harvest index contributed to the lower grain yield at high night temperature in rice (Xu et al., 2021). Two genes including one MADS transcription factor and a UDP-glycosyltransferase were identified as candidate genes orchestrating stem NSC remobilization. Moreover, increase in night respiration was also related to the decrease in spikelet number per panicle and grain yield at high night temperature (Xu et al., 2021). Only a few studies have investigated the effects of high temperature on N absorption and utilization in rice (Ito et al., 2009; Kanno et al., 2009; Liu et al., 2019). Generally, high temperature did not affect total aboveground N accumulation at maturity, but decreased the translocation and allocation of nitrogen to panicle, which led to lower grain N concentration (Ito et al., 2009; Liu et al., 2019). Since translocation of non-structural carbohydrates to
grain is significantly reduced at high night temperature (Shi et al., 2013), it is obscure whether low grain filling percentage at high night temperature is also related to the reduction in N translocation to grain.

Protein is the most abundant storage substance besides of starch in rice grain, and reducing the protein concentration has been a breeding and management target for better rice eating quality in Japan for several decades (Matsue et al., 1997 and Matsue et al., 2015), and in China only recently (Shi et al., 2019). It is generally accepted that protein content higher than 7% would cause reduction in eating quality (Matsue et al., 2015; Shi et al., 2019). In present study, most of the varieties has protein content higher than 7%, and three varieties with the best performance in grain yield including HY549, XY4913, and XY7113 had protein content less than 7%. Moreover, high nighttime temperature could potentially deteriorate the eating quality of rice, because of the significantly positive correlation between nighttime temperature and protein concentration in grain (Figure 3c). Inconsistently results have been observed about the effect of high temperature on grain protein content, which was significantly increased in some studies (Cao et al., 2012, 2017; Kwak et al., 2018; Liang et al., 2010; Liu et al., 2013), but remained stable in other studies (Ma et al., 2008; Ohdaira et al., 2010). Joint analysis of metabolome and transcriptome indicated that starch metabolism was inhibited, while amino acid accumulation was induced, both of which resulted in high protein content in grain at high temperature (Yamakawa & Hakata, 2010). However, only few studies have been focused on the effect of high night temperature on protein content in rice grain compared to starch accumulation (reviewed by Impa et al., 2021). Furthermore, developing climate-resilient rice varieties with superior grain quality suited for high-temperature stress has not been put into practice (Sreenivasulu et al., 2015). Here, significant and negative correlation between grain protein concentration and NUEg were observed across the five years (Figure 5d), indicating these two traits could be concomitantly improved in the context of climate variability.

In conclusion, twenty-two elite varieties produced significantly higher grain yield than YLY6 at a moderate N input. Most of these varieties could produce a grain yield of higher than 10 t ha⁻¹ and NUEg of higher than 50 kg kg⁻¹ when climate conditions were suitable. However, inter-annual variability in climate, especially nighttime temperature, constrained the fulfillment of their yield advantage mainly due to the effect on grain filling percentage and harvest index. This further led to lower NUEg and higher grain protein content. However, the present study used different varieties in different years. Although these varieties were all elite varieties from each breeding institute in China, genotypic effects on the inter-annual variation in grain yield, NUE, and protein content could not be fully eliminated. Therefore, further studies should be conducted in field conditions using the same representative varieties for several years or across several locations.

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**SUPPORTING INFORMATION**

Additional supporting information may be found online in the Supporting Information section.