agriculture

MDPI

Article

Plant Photosynthetic and Respiration Rates Are Key Populational Traits to Improve Yield and Quality for Good-Tasting Double-Cropped Rice

Shan Huang †, Jiaojiao Wu †, Yongjun Zeng and Guanjun Huang *

Key Laboratory of Crop Physiology, Ecology and Genetic Breeding, Ministry of Education, School of Agricultural Sciences, Jiangxi Agricultural University, Nanchang 330045, China; ecohs@126.com (S.H.); 14780041576@163.com (J.W.); zengyj2002@163.com (Y.Z.)

* Correspondence: guanjunhuang@jxau.edu.cn

† These authors contributed equally to this work.

Abstract: Improving the yield and quality for tasty rice varieties is a great challenge. In the present study, different nitrogen rates and plant density were utilized to form differential rice populational structures, which were determined to clarify key traits determining grain yield and quality for tasty rice varieties in a double-cropped rice system in subtropical China. The present results showed that the plant photosynthetic rate, leaf area index and plant respiration rate had important and significant impacts on the grain yields of both early and late rice, though the late rice yield was also significantly affected by the canopy temperature. In addition, among the studied populational traits, plant photosynthetic and/or respiration rates had significant effects on all quality traits. Consistently, grain yield and quality were significantly improved with the increasing plant photosynthetic and respiration rates through correlative analysis, which was also observed in principal components analysis. Overall, the present study suggests that both the grain yield and milling and appearance qualities could be improved through the optimal management of nitrogen and plant density through increasing plant photosynthetic and respiration rates.

Keywords: rice yield; rice quality; plant photosynthetic rate; plant respiration rate

check for updates

Citation: Huang, S.; Wu, J.; Zeng, Y.; Huang, G. Plant Photosynthetic and Respiration Rates Are Key Populational Traits to Improve Yield and Quality for Good-Tasting Double-Cropped Rice. *Agriculture* **2024**, *14*, 1861. https://doi.org/10.3390/agriculture14111861

Academic Editor: Daniel Tan

Received: 4 September 2024
Revised: 19 October 2024
Accepted: 20 October 2024
Published: 23 October 2024

Copyright: © 2024 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (https://creativecommons.org/licenses/by/4.0/).

1. Introduction

As the most important staple food crop around the world [1], rice feeds more than half of the global population [2]. Therefore, rice production is of great importance for global food demand and security. It has been reported that an increase rate of 2.4% per year for cereal crops yield is required to meet the demands of our ever-increasing population globally by 2050; however, the current increase rate of the rice yield is only 1.0% per year, which is far below what is expected [3]. Therefore, in the past few decades, most attention has been paid to improving the rice yield alone [4]. However, with improvements in people's living standards, grain quality has also received more and more interest in recent years [5,6], which is important for both rice farmers and consumers [7]. Therefore, how to achieve both high yield and quality is critical for future rice production.

Among the grain quality traits, milling and appearance qualities are the most important physical characteristics defining rice market value because these traits are absolutely obvious to consumers [7]. Therefore, if both high yield and great milling and appearance qualities are achieved in tasty rice varieties, then not only food demands but also high market value could be satisfied in rice production. However, to what extent both high yield, great milling and appearance qualities can be realized in tasty rice varieties is still not known. Recently, Huang et al. [8] carefully analyzed grain yield and quality for 224 early indica rice varieties released from 2000 to 2020 in Southern China, and they suggest that, though the grain yield has been significantly increased from 2000 to 2020, milling and

appearance quality has not, which indicates that rice yield and quality may be difficult to improve through conventional breeding. In fact, contrary responses of rice yield and quality to nitrogen (N) have been frequently observed in previous studies [9,10]. For instance, Zhu et al. [10] suggest that though grain yield and milling quality are significantly improved with increasing N application, the appearance quality is significantly deteriorated. Therefore, future research is needed to clarify the possible approaches for improving rice yield and quality coordinately.

It is acknowledged that rice yield and quality are highly dependent on populational traits, such as photosynthetic and respiration processes, leaf area index, grain leaf area ratio, temperature and relative humidity of canopy, especially at the post-heading stage [1,11–14]. For example, Zhou et al. [14] indicate that a higher canopy photosynthetic rate is associated with the accelerated crop growth rate during the flowering phase, which results in a larger harvest index and, thus, a greater grain yield in rice. In addition, significant impacts of canopy temperature and relative humidity on the rice yield and quality have also been reported in previous studies [12,15]. However, though these populational traits have been confirmed as key regulators for rice yield and quality, it still remains largely unknown whether the rice yield and quality could be improved through manipulations of a few key traits, such as plant photosynthetic and respiration rates, which are key factors determining the yield formation and grain filling process. For these purposes, a field experiment was conducted with different N and density treatments using two tasty (with low amylose and protein contents and high gel consistency) rice varieties in a double-cropped rice system to investigate the key populational traits at the post-heading stage that determines the rice yield and milling and appearance qualities, which should be informative and helpful for future rice production with both a high yield and quality.

2. Materials and Methods

2.1. Site Description

The experiment was conducted in 2023 in Shanggao county (28°31′ N, 115°09′ E) of Jiangxi province, China, which belongs to double rice cropping area and has a typical subtropical climate. Daily mean temperature and solar radiation during experiment were measured using a Vantage Pro2 automatic weather station (Davis Instruments Corp., Hayward, CA, USA). Generally, the average temperature and solar radiation for early rice were 25.5 °C and 14.7 MJ m^{-2}, respectively, while those for late rice were 26.5 °C and 15.3 MJ m^{-2}, respectively (Figure 1). The topsoil (0–15 cm) properties before the experiment in 2023 were as follows: soil pH of 5.5, soil organic matter content of 34.7 g kg^{-1}, soil total nitrogen content of 1.8 g kg^{-1}, alkaline hydrolysable nitrogen content of 163.1 mg kg^{-1}, available phosphorus content of 56.9 mg kg^{-1} and available potassium content of 183.1 mg kg^{-1}.

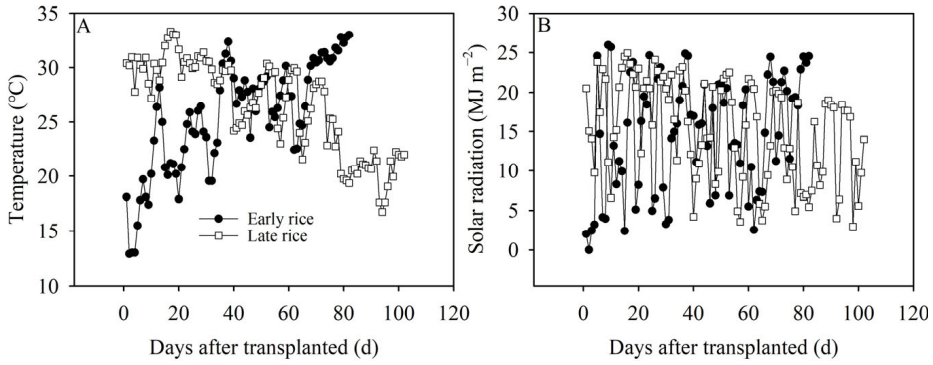


Figure 1. Daily mean temperature (**A**) and solar radiation (**B**) during the experiment for early and late rice.

2.2. Experiment Design

The experiment was arranged in a blocked split-plot design with nitrogen treatment as the main factor and plant spacing as the subplot treatment, with three replicates in a completely randomized block design. Two inbred indica cultivars, Songyazao 1 and Meixiangzhan 2, were used for early and late season, respectively. Each subplot was 4 m wide × 9 m long. Nitrogen treatment consisted of 0, 90, 120 and 150 kg ha^{-1} for early rice and 0, 120, 150 and 180 kg ha^{-1} for late rice, respectively, while plant spacing treatment consisted of 10, 12 (farmers' practice) and 14 cm for early rice and 12, 14 (farmers' practice) and 16 cm for late rice, respectively. Therefore, there were totally 4 N × 3 density treatments for both early and late rice (Figure S1).

2.3. Crop Management

Pre-germinated seeds of early and late rice were sown on 20 March and 25 June, respectively. Then, early and late rice seedlings were manually transplanted on 21 April and 19 July, respectively. Both early and late rice was transplanted with 4 seedlings per hill with a row spacing of 25 cm. Urea, phosphorus pentoxide and potassium oxide were used as N, P (60 kg ha^{-1}) and K (75 kg ha^{-1}) fertilizers, respectively, for both early and late rice. N fertilizer was applied in three splits for both early and late rice, with basal/tillering/panicle = 5:3:2. In addition, P fertilizer in both seasons was applied as basal fertilizer, while K fertilizer in both seasons was applied with basal/panicle = 1:1. The field was kept flooded with a water depth of 2–3 cm from transplanting to mid-season drainage and was then intermittently irrigated until maturity. Weeds, insects, and diseases were controlled by chemical spraying according to the recommendations by the local department of plant protection. Early and late rice was harvested on 12 July and 29 October, respectively.

2.4. Biomass, Yield and Quality

At the maturity stage of rice, rice plants in the middle of each plot (5 m^2) were harvested to determine the grain yield; then, aboveground crop residues were oven dried at 105 °C for 30 min followed by 75 °C to a constant weight. The rice grains were stored at room temperature for 3 months before determining the quality of the grains; the national standard for rice quality evaluation [16] was used to determine head rice rate, chalky rice rate and chalkiness degree.

2.5. Leaf Area Index and Spikelet to Leaf Ratio

At heading stage, panicles and leaves of rice plants in each plot were harvested to count spikelet number and measure total leaf area; then, spikelet to leaf ratio, a proxy of grain leaf area ratio, was calculated as total spikelet number divided by total leaf area. At 15 days after heading, leaves of rice plants were harvested in the middle of each plot (1 m^2), and leaf length and width were measured using rulers. The single leaf area was calculated as leaf length × leaf width × 0.75 [17], and the leaf area index was estimated as total leaf area divided by harvested area.

2.6. Plant Photosynthetic and Respiration Rates

At 15 days after heading, static-chamber method was used to measure plant photosynthetic and respiration rates from 9:00 to 12:00 following Zhou et al. [14]. Polyvinyl chloride (PVC) plates were used to make an assimilation chamber with dimensions of 0.5 m × 0.5 m × 1 m. Before measurements, 3 transparent and 3 dark PVC plates, respectively, were inserted into the soil with 6 hills inside them in each plot, and the steel sampling chamber was wrapped with a heat-insulating layer and equipped with a fan inside the top to blend gases. Gas samples were collected at 5 min intervals for a total of 15 min. After collection using an injection syringe, the gas sample was transferred immediately into a vacuum bag for analysis. CO_2 concentrations were measured using an Agilent 7890 A gas

chromatograph (Agilent Technologies, Santa Clara, CA, USA). Then, plant photosynthetic and respiration rates could be estimated with following equation:

$$A_{\text{plant}} = \rho \times h \times \frac{dc}{dt} \times \frac{273}{273 + T} \quad (1)$$

where A_{plant} represents plant photosynthetic rate or respiration rate, ρ is CO_2 gas density (1.964 kg m^{-3}), h is the height of chamber used to collect gas samples, dc/dt is the rate of change in CO_2 concentration inside chamber per unit time and T is the average temperature (°C) inside chamber during gas samples collection, which was monitored through a thermometer inserted into the top of the chamber. It should be noted that transparent and dark PVC plates were used to estimate plant photosynthetic rate and respiration rate, respectively.

2.7. Canopy Temperature and Relative Humidity

At 15 days after heading, canopy temperature and relative humidity were measured using hygrothermograph (Taishi, Taiwan, TES-1360A), which was placed 10 cm below the canopy.

2.8. Statistical Analysis

One-way and two-way analyses of variance were conducted using SPSS 27 software (SPSS Inc., Chicago, IL, USA) to examine the impacts of nitrogen, density and their interactions on the studied traits. It should be noted that when examining the impact of N on the studied traits, values of different density treatments were averaged for a single N treatment; similarly, when examining the impact of density on the studied traits, values of different N treatments were averaged for a single density treatment. Multiple comparisons were performed using the least significant difference test at $p < 0.05$ level.

Pearson's correlative analysis was used to detect the relationships between plant photosynthetic rate, plant respiration rate and yield and quality traits, which was conducted using Sigmaplot 15 (SPSS Inc., Chicago, IL, USA). In order to investigate which populational traits are key factors determining the rice yield and quality, relative importances of populational traits to rice yield and quality were further assessed through random forest analysis using R package *rfPermute*. In addition, principal components analysis was conducted using R packages *factoMineR* and *factoextra* to test the relationships among the studied yield, quality and populational traits.

3. Results

3.1. Effects of Nitrogen and Plant Density on Biomass, Yield and Quality of Rice

Nitrogen and plant density (D) had significant impacts on biomass, grain yield and quality of both early and late rice (Table 1). Compared with N_0 treatment, biomass, grain yield and quality were significantly improved under N_{90}, N_{120} and N_{150} treatments, while no significant differences of biomass, grain yield and quality were observed among these three high-N treatments in early rice (Table 1). Similar to early rice, the biomass and grain yield of late rice were significantly increased, while the chalky rice rate was significantly decreased under N_{120}, N_{150} and N_{180} treatments relative to N_0 treatment (Table 1). However, an improved head rice rate was only observed under N_{150} treatment, and a decreased chalkiness degree was only found under N_{150} and N180 treatments when compared with N_0 treatment in late rice (Table 1).

In early rice, biomass, grain yield and quality were first improved with increased plant spacing from 10 to 12 cm and then decreased when plant spacing was further increased to 14 cm. Overall, among different D treatments, early rice had the highest grain yield and best quality under D_{12} treatment (Table 1). In addition, significant interactive effects of N and D on grain yield were observed in early rice (Table 1). Compared with D_{12} treatment, the grain yield and head rice rate were increased, while the chalky rice rate and chalkiness degree were decreased under D_{14} treatment in late rice; however, a further increase in plant

spacing to 16 cm did not significantly affect the grain yield and quality of late rice but significantly decreased biomass (Table 1). In general, plant spacing at 14 cm is better for late rice to obtain both high yield and quality. In addition, significantly interactive effects of N and D on the grain yield and appearance quality were observed for early and late rice, respectively (Table 1, Figures S2 and S3).

Table 1. Biomass, grain yield (GY), head rice rate (HRR), chalky rice rate (CRR) and chalkiness degree (CD) of early and late rice.

Season	Treatment	Biomass (t ha^{-1})	GY (t ha^{-1})	HRR (%)	CRR (%)	CD (%)
Early	N					
	N_0	13.16 b	5.55 b	46.5 b	15.2 a	4.8 a
	N_{90}	17.37 a	7.70 a	51.4 a	11.5 b	3.3 b
	N_{120}	17.38 a	8.26 a	53.6 a	9.3 b	2.8 b
	N_{150}	18.37 a	7.94 a	52.3 a	9.8 b	2.9 b
	D					
	D_{10}	16.52 ab	7.14 b	50.9 ab	12.0 a	3.7 a
	D_{12}	17.47 a	7.53 a	52.7 a	10.4 b	3.1 b
	D_{14}	15.73 b	7.42 a	49.2 b	11.9 a	3.5 a
	F values					
	N	51.58 **	40.23 **	8.60 *	16.26 **	10.84 **
	D	6.02 *	8.14 **	3.79 *	9.16 **	10.20 **
	N × D	0.46	12.40 **	0.51	0.42	0.97
Late	N					
	N_0	10.93 c	4.71 b	53.2 b	11.0 a	3.5 a
	N_{120}	14.20 b	7.22 a	53.5 b	8.9 b	2.7 ab
	N_{150}	16.19 a	7.56 a	58.0 a	7.4 b	2.2 b
	N_{180}	15.27 ab	7.54 a	55.8 ab	7.5 b	2.3 b
	D					
	D_{12}	13.92 ab	6.59 b	54.2 b	9.1 a	2.9 a
	D_{14}	14.85 a	7.01 a	56.6 a	8.3 b	2.5 b
	D_{16}	13.67 b	6.67 a	54.5 ab	8.6 ab	2.5 b
	F values					
	N	21.55 **	67.82 **	6.20 *	18.89 **	6.55 *
	D	3.68 *	4.22 *	5.44 *	3.74 *	4.25 *
	N × D	0.59	1.28	0.81	6.52 **	3.00 *

Note: N and D represented nitrogen and density, respectively, N_0, N_{90}, N_{120}, N_{150} and N_{180} represented nitrogen input at 0, 90, 120, 150 and 180 kg ha^{-1}, respectively, D_{10}, D_{12}, D_{14} and D_{16} represented plant spacing at 10, 12, 14 and 16 cm, respectively. Different lowercase letters represent significant difference among different N or D treatments. * and ** represented significant differences at $p < 0.05$ and $p < 0.01$ levels, respectively. There were 3 replications for each trait.

3.2. Effects of Nitrogen and Plant Density on Rice Populational Traits

Generally, plant photosynthetic and respiration rates, leaf area index and spikelet to leaf ratio showed increasing trends with increasing N inputs for both early and late rice (Table 2). However, for early rice, plant photosynthetic and respiration rates were increased first when the plant spacing increased from 10 to 12 cm and then decreased when plant spacing was further increased to 14 cm, while the leaf area index continuously declined with

increasing plant spacing, though the spikelet to leaf ratio showed no significant response to plant spacing (Table 2). For late rice, the plant photosynthetic and respiration rates and spikelet to leaf ratio significantly increased, while the leaf area index significantly decreased under D_{14} treatment when compared with D_{12} treatment; however, further increasing plant spacing from 14 to 16 cm had no significant effect on rice populational traits, except for the plant respiration rate, which was significantly reduced under D_{16} treatment (Table 2). Additionally, significant interactive effects of N and D on the plant respiration rate were observed for early rice, while those for the plant photosynthetic and respiration rates were found for late rice (Table 2, Figures S4 and S5).

Table 2. Plant photosynthetic and respiration rates, leaf area index and spikelet to leaf ratio of early and late rice.

Season	Treatment	Plant Photosynthetic Rate (mg m^{-2} h^{-1})	Plant Respiration Rate (mg m^{-2} h^{-1})	Leaf Area Index	Spikelet to Leaf Ratio (cm^{-2})
Early	N				
	N_0	361.1 c	537.7 d	3.26 b	1.01 c
	N_{90}	430.4 b	555.9 c	4.45 a	1.15 bc
	N_{120}	526.3 a	626.5 b	4.74 a	1.28 ab
	N_{150}	521.4 a	640.3 a	4.93 a	1.37 a
	D				
	D_{10}	450.7 c	574.6 c	5.00 a	1.21 a
	D_{12}	467.9 a	602.5 a	4.32 b	1.25 a
	D_{14}	460.7 b	593.3 b	3.72 c	1.15 a
	F values				
	N	60.4 **	86.02 **	13.25 **	9.69 *
	D	13.25 **	93.48 **	16.74 **	1.82
	N × D	1.842	32.44 **	1.66	0.16
Late	N				
	N_0	305.7 c	445.0 c	4.91 b	0.66 b
	N_{120}	354.2 b	533.5 b	7.92 a	0.68 b
	N_{150}	506.5 a	600.8 a	8.07 a	1.02 a
	N_{180}	498.6 a	595.8 a	8.47 a	1.00 a
	D				
	D_{12}	394.6 b	525.6 c	7.76 a	0.79 b
	D_{14}	428.7 a	563.6 a	7.23 b	0.87 a
	D_{16}	425.5 a	542.1 b	7.03 b	0.85 ab
	F values				
	N	28.15 **	56.24 **	19.96 **	59.68 **
	D	14.84 **	29.56 **	6.80 **	3.92 *
	N × D	4.91 **	6.86 **	1.16	2.71

Note: N and D represented nitrogen and density, respectively, N_0, N_{90}, N_{120}, N_{150} and N_{180} represented nitrogen input at 0, 90, 120, 150 and 180 kg ha^{-1}, respectively, D_{10}, D_{12}, D_{14} and D_{16} represented plant spacing at 10, 12, 14 and 16 cm, respectively. Different lowercase letters represented significant difference among different N or D treatments. * and ** represented significant differences at $p < 0.05$ and $p < 0.01$ levels, respectively. There were 3 replications for each trait.

Additionally, N and D also had significant impacts on canopy micro-environments, including canopy temperature and relative humidity (Table S1). In general, the canopy

temperature decreased, while the canopy relative humidity increased with increasing N inputs for both early and late rice (Table S1). For early rice, the canopy temperature was significantly decreased under D_{12} treatment when compared with D_{10} treatment, and further increasing the plant spacing had no significant impact on canopy temperature; however, canopy relative humidity was not significantly affected by plant spacing (Table S1). Similar to early rice, the canopy temperature of late rice increased first when the plant spacing increased from 12 to 14 cm and then remained unchanged when the plant spacing was further increased from 14 to 16 cm; however, different from early rice, the canopy relative humidity of late rice increased first under D_{14} treatment when compared with D_{12} treatment and then decreased when the plant spacing was further increased to 16 cm (Table S1).

3.3. Relative Importance of Populational Traits in Determining Rice Yield and Quality

Random forest analysis suggested that the plant photosynthetic rate, leaf area index and plant respiration rate are the three important and significant factors affecting early rice yield (Figure 2A), while the leaf area index, plant respiration rate, plant photosynthetic rate and canopy temperature significantly affected the late rice yield (Figure 2B).

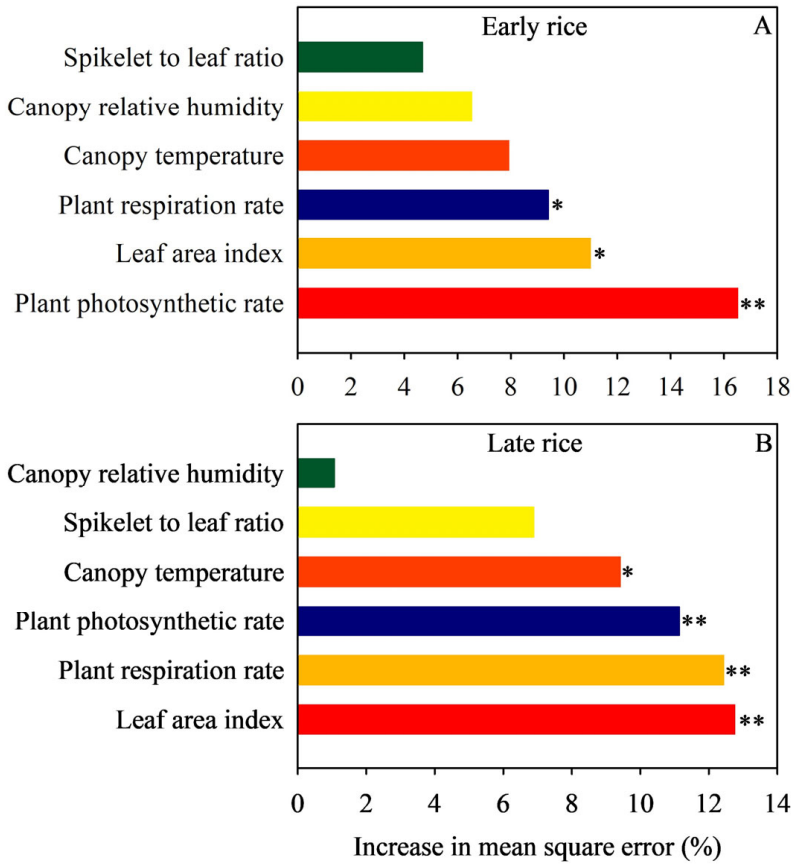


Figure 2. Relative importance of populational traits to the yield of early (**A**) and late rice (**B**). ** and * represented significant at $p < 0.01$ and $p < 0.05$ levels, respectively. Populational traits with larger increased mean square error indicated more important to rice yield.

As for rice quality, the spikelet to leaf ratio and plant photosynthetic rate are significant factors affecting the head rice rate of both early and late rice; additionally, the head rice rate of late rice is also significantly impacted by the plant respiration rate and canopy relative humidity (Figure 3A,B). Interestingly, the plant photosynthetic and respiration rates had significant impacts on the chalky rice rate and chalkiness degree of both early and late rice, while the chalky rice rate of early rice and chalkiness degree of early and late rice were

additionally affected by the leaf area index, canopy relative humidity and spikelet to leaf ratio, respectively (Figure 3C–F). Overall, plant photosynthetic and respiration rates are key factors modulating rice yield and quality (Figures 2 and 3).

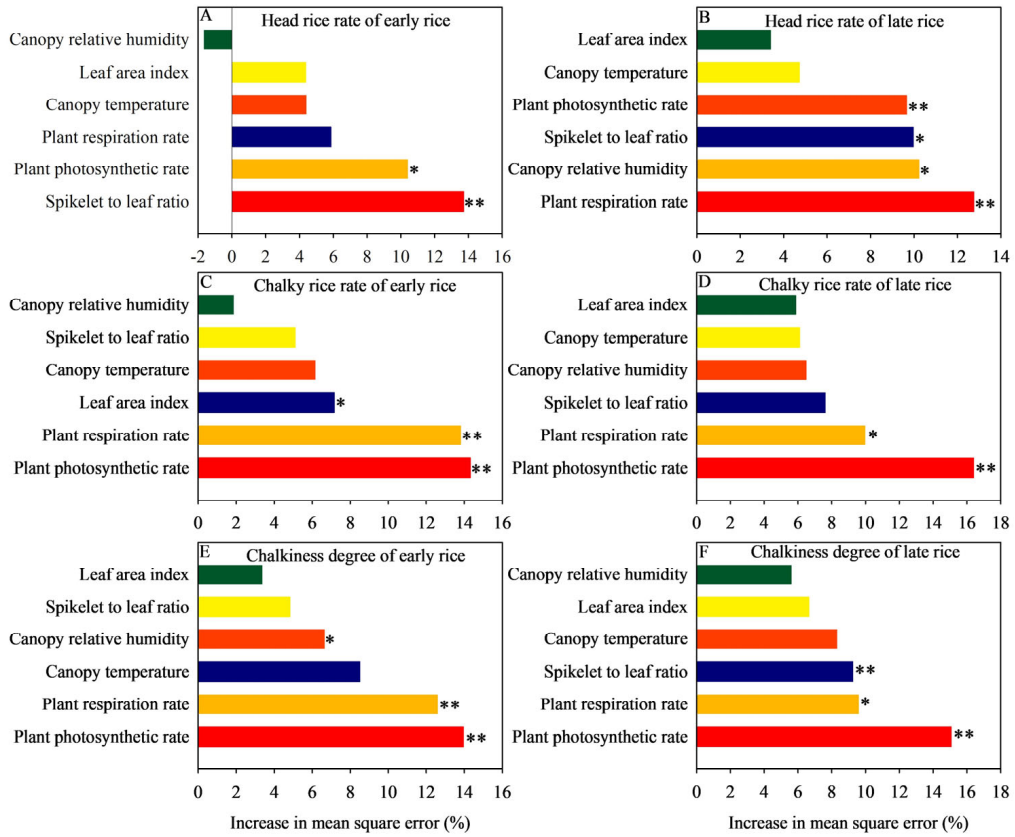


Figure 3. Relative importance of populational traits to head rice rate ((**A**,**B**) for early and late rice, respectively), chalky rice rate ((**C**,**D**) for early and late rice, respectively) and chalkiness degree ((**E**,**F**) for early and late rice, respectively). ** and * represented significant at $p < 0.01$ and $p < 0.05$ levels, respectively. Populational traits with larger increased mean square error indicated more important to rice quality.

3.4. Relationships Between Populational Traits and Grain Yield and Quality

Further correlation analysis revealed that plant photosynthetic and respiration rates were significantly and positively associated with the plant biomass and grain yield for both early and late rice (Figures 4 and S6). Additionally, the leaf area index also had positive relationships with the grain yield of both early and late rice, while the canopy temperature was negatively related to the yield of late rice (Figure S7).

Our results suggested that plant photosynthetic and respiration rates were positively correlated with the head rice rate and negatively associated with the chalky rice rate and chalkiness degree for both early and late rice (Figure 5). In addition, a larger spikelet to leaf ratio was found to be related to the higher head rice rate of early and late rice; moreover, a positive relationship between the canopy relative humidity and head rice rate was also observed for late rice (Figure S8A–C). As for the appearance quality, the leaf area index was negatively correlated with the chalky rice rate and chalkiness degree in early rice, while the chalkiness degree of late rice was negatively correlated with the spikelet to leaf ratio (Figure S8D–F). Consistently, principal component analysis suggested that plant photosynthetic and respiration rates were positively related to the grain yield and head rice rate but negatively associated with the chalky rice rate and chalkiness degree for both early and late rice, and the first two major axes (Dim1 and Dim2) explained 76.4% and 77.5% of the total variation for early and late rice, respectively (Figure 6).

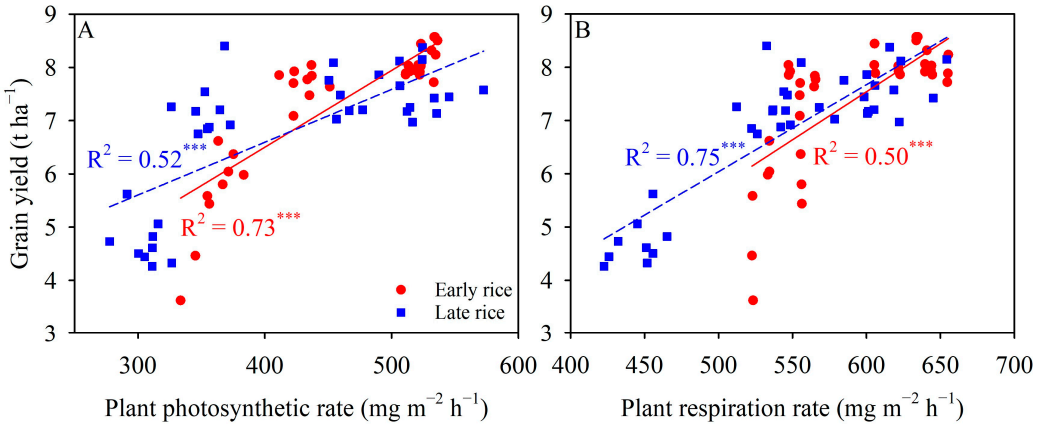


Figure 4. Pearson's relationships between grain yield and plant photosynthetic (**A**) and respiration rates (**B**) in early and late rice. *** represents significant at $p < 0.001$ level and there were 36 paired observations used for correlative analysis.

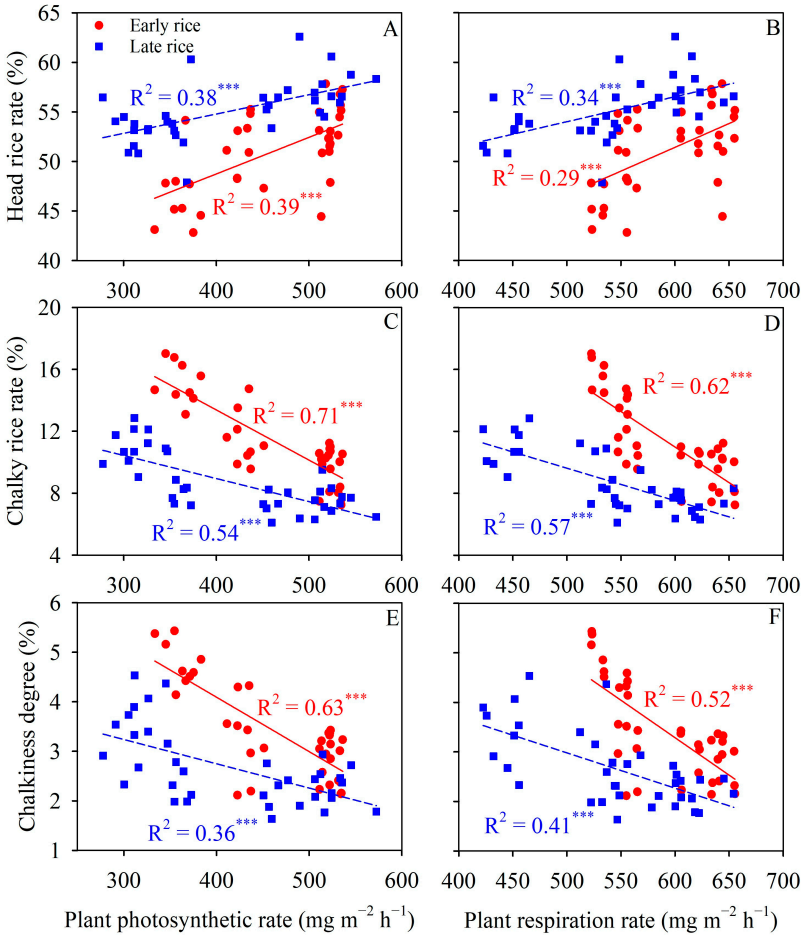


Figure 5. Pearson's relationships between plant photosynthetic and respiration rates and head rice rate ((**A**) for early rice and (**B**) for late rice, respectively), chalky rice rate ((**C**) for early rice and (**D**) for late rice, respectively) and chalkiness degree ((**E**) for early rice and (**F**) for late rice, respectively). *** represents significant at $p < 0.001$ level and there were 36 paired observations used for correlative analysis.

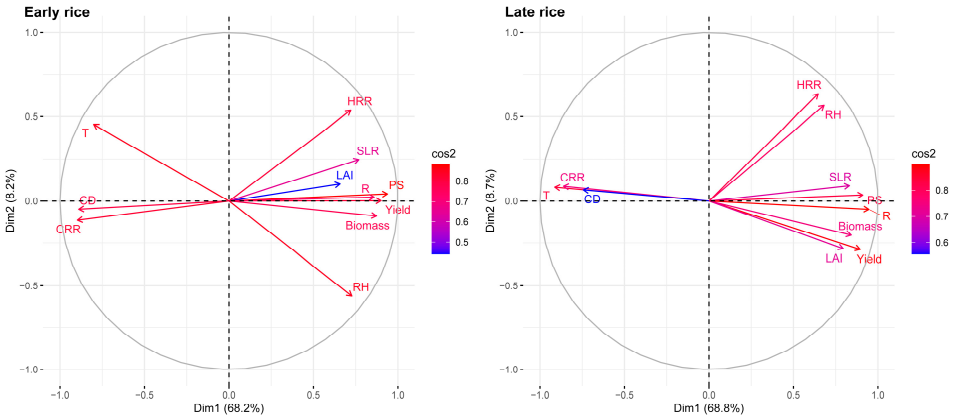


Figure 6. Principal components analysis's biplot showing major axes of variations in biomass, yield, quality and populational traits among different nitrogen and plant density treatments for early and late rice. The arrows were vectors showing the correlation between a trait and the Dims, and the quality of representation of the variables on the factor map (cos2) was indicated in different colors. A higher cos2 indicated a good representation of the variable on the principal component. CD, chalkiness degree; CRR, chalky rice rate; HRR, head rice rate, LAI, leaf area index; PS, plant photosynthetic rate; R, plant respiration rate; RH, canopy relative humidity; SLR, spikelet to leaf ratio; T, canopy temperature.

4. Discussion

4.1. Effects of Nitrogen and Plant Density on Grain Yield, Milling and Appearance Qualities of Tasty Double-Cropped Rice

Our present study suggests that N rates of 90 and 120 kg ha^{-1} are enough for early and late rice to obtain a high yield, respectively (Table 1). However, these results were somewhat different from a previous study, where an N rate of 180 kg ha^{-1} was suggested for both early and late rice when the highest yield is obtained [18]. These differences likely resulted from the different plant densities used between our present study and the research of Xu et al. [18], which is supported by the findings that the nitrogen response of the rice yield is highly dependent on plant density [19]. In fact, significant interactive effects of N and D on the grain yield were also observed for early rice in our present study (Table 1, Figure S2).

The increased grain yield with N inputs observed in early and late rice was consistent with previous studies due to the important roles of N in regulating plant growth [19]. However, when N inputs increased to a certain extent, further increasing N would result in null or even negative effects on grain yield, as reported in previous research [10,19,20] and observed in our present study (Table 1). For example, excess N application is suggested to cause decreased panicles and grains per panicle and, thus, reduce the rice yield [10]. Similarly, excess N inputs are also reported to result in suppressed grain filling of inferior grains, which leads to lower rice yield ultimately [20].

An improved head rice rate with N application observed in our present study was in line with previous studies [10,20], indicating that increased N application is conductive to the high milling quality of rice grains, which may be associated with the increased protein and/or gliadin contents in grains [10]. However, though our present results suggested that increasing N inputs would ameliorate the appearance quality of rice (Table 1), the findings regarding this in previous studies are mixed. For instance, consistent with our present study, increasing N application has also been suggested to result in a decreased chalky rice rate and chalkiness degree [20]. On the contrary, a previous study indicates that the chalky rice rate and chalkiness degree would increase with increasing N inputs [10]. Though the exact mechanisms underlying these different results still remain largely unknown, various N rates used among studies may take effect. In support of this assertion, our present results showed that, though increasing N rates from 0 to 120 kg ha^{-1} for early rice and from 0 to 150 kg ha^{-1} for late rice, respectively, could ameliorate the appearance quality, further increasing N inputs result in an increased chalky rice rate and chalkiness degree, though

there was no statistically significant difference (Table 1). Similarly, though increasing N application from 0 to 270 kg ha^{-1} could improve the appearance quality, further increasing the N rate to 345 kg ha^{-1} causes increasing trends of the chalky rice rate and chalkiness degree [20]. Therefore, it is possible that N application at low and/or moderate levels could improve the appearance quality, while high N inputs would deteriorate it.

In addition to the N rate, plant density also had significant impacts on grain yield and quality for both early and late rice, with an optimal density of 25 cm × 12 cm for early rice and 25 cm × 14 cm for late rice, respectively (Table 1). When plant spacing was increased from 10 to 12 cm in early rice and from 12 to 14 cm in late rice, respectively, the grain yield and quality were both improved (Table 1). These results were consistent with previous studies, in which decreased plant density is associated with enhanced rice yield and improved appearance quality [21]. However, when plant spacing was further increased, declining trends of yield and quality were noticed (Table 1), indicating that both high and low density are detrimental to the yield and quality formation. Consistently, in a previous study, when the plant density decreased from 27 × 104 to 15 × 104 hills ha^{-1}, the rice yield first increased and then followed a decreasing trend [19]. Overall, our results suggest that both high yield and great milling and appearance qualities of tasty double-cropped rice could be achieved through optimal managements of nitrogen and plant density.

4.2. High Plant Photosynthetic and Respiration Rates Are Conductive to High Rice Yield and Great Milling and Appearance Qualities

In the present study, the rice yield and quality were significantly improved with increasing photosynthetic and respiration rates (Figures 2–5). Consistent with our present results, a higher leaf photosynthetic rate after heading has been indicated as contributing to a higher crop growth rate and, thus, a larger biomass accumulation in rice [22], which suggests that photosynthetic capacity after heading should have considerable impacts on the biomass and yield formation of rice. In fact, positive relationships between photosynthetic capacity and rice yield are frequently reported in studies [23,24], and improving the photosynthetic capacity has been implied as the most promising approach to further increase the rice yield in the future [25]. However, the positive relationship between the plant respiration rate and grain yield observed in both early and late rice (Figure 3B) seems counterintuitive at first glance, as increased respiration is usually associated with reduced crop yields, caused by the growing consumption of accumulated carbohydrates, especially under high-temperature conditions [1]. For example, increased night temperature is suggested to be associated with the increased respiration rate in two rice genotypes, which results in decreased grain weight and yield consequently [1]. However, though an increase in the night temperature significantly increased the leaf respiration rate in rice plants, the biomass accumulation is not significantly affected, as reported in a previous study [26], which questions the assumption that an increased respiration rate should be responsible for the decreased rice biomass and yield under high-temperature conditions. Therefore, an increased respiration rate may not always be associated with reduced crop growth.

Generally, the plant respiration rate is highly dependent on the plant carbon substrate (mainly as carbohydrates) supply and energy demands. In the present study, the plant photosynthetic and respiration rates were positively correlated with each other in both early and late rice (Figure 6). These results are expected because a higher plant photosynthetic capacity is usually associated with enhanced carbohydrate accumulation [26,27], which could be further used in respiratory processes. Consistently, positive relationships between photosynthesis and respiration rates have been frequently observed at the leaf level [28], indicating that photosynthetic carbon reduction and respiratory metabolisms are highly correlated. Therefore, the positive correlations between the plant respiration rate and grain yield observed in our present study might be partly a result of the covariation between photosynthesis and respiration (Figures 4 and 6). In addition, another possible and important mechanism underlying the positive association between the plant respiration rate and grain yield is the large energy demands for phloem loading and unloading during

grain filling. For instance, by means of model analysis and experimental observations, Chang et al. [29] suggest that a higher grain respiration rate is correlated with a higher instantaneous grain filling rate in rice, which contributes to a higher grain yield ultimately. However, in the present study, the exact mechanism that may be responsible for the positive impacts of respiration on the grain yield is still not known. Further research is needed to examine the possible roles of respiration in regulating carbohydrate translocation, phloem loading and grain filling rate, which should give us more valuable information for achieving high yields in rice.

Importantly, the present study showed that higher plant photosynthetic and respiration rates were associated with a higher head rice rate but lower chalky rice rate and chalkiness degree in both early and late rice (Figure 5), indicating that maintaining high post-heading photosynthetic and respiration rates is crucial for rice to obtain excellent milling and appearance quality, which has been seldom reported in previous studies. It is suggested that the development of rice chalkiness is mainly related to the dry matter accumulation, grain filling rate and grain water content [30]. In the present study, a higher plant photosynthetic rate was correlated with larger plant biomass (Figure S6A), which could ensure the supply of carbohydrates from source to sink organs. Additionally, as discussed above, if an increased plant respiration rate was accompanied with an increased grain filling rate [29], then grains could be fully filled, thus leading to a low chalkiness appearance [30]. Moreover, decreased chalkiness could also contribute to an increased head rice rate due to the decreased friability during milling process [15]. Overall, our present results suggested that high photosynthetic and respiration rates after heading are key populational traits to achieve both a high yield and quality of rice, and more efforts should be devoted to the amelioration of plant photosynthesis and respiration processes after heading in field conditions.

4.3. Study Limitations and Future Outlooks

It should be noted that there were only two rice varieties used in our present study, and more rice varieties in different experimental sites across different years should be further examined. Further, in addition to the populational traits examined in this study, more populational traits should be further explored through new advancing techniques, such as 3D canopy modeling [31], which should give us more mechanistic understandings of the key processes affecting the rice yield and quality in the future.

5. Conclusions

The present study suggests that plant photosynthetic and respiration rates are key populational traits determining the rice yield and quality, and higher plant photosynthetic and respiration rates are conductive to a high grain yield and quality in both early and late rice.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/agriculture14111861/s1, Table S1: Canopy temperature and relative humidity of early and late rice; Figure S1: An example of plot layout of late rice; Figure S2: Grain yield of early rice under various N and D treatments; Figure S3: Chalky rice rate and chalkiness degree of late rice under various N and D treatments; Figure S4: Plant respiration rate of early rice under various N and D treatments; Figure S5: Plant photosyn-thetic (A) and respiration rates (B) of late rice under various N and D treatments; Figure S6: Rela-tionships between biomass and plant photosynthetic and respiration rates in early and late rice; Figure S7: Relationships between rice yield and populational traits in early and late rice; Figure S8: Relationships between rice quality and populational traits in early and late rice.

Author Contributions: Conceptualization, S.H. and G.H.; methodology, J.W.; software, G.H. and J.W.; validation, G.H. and J.W.; formal analysis, G.H. and J.W.; writing—original draft preparation, S.H., J.W. and G.H.; writing—review and editing, S.H., G.H. and Y.Z.; visualization, G.H.; supervision, G.H. and S.H.; project administration, S.H.; funding acquisition, S.H. and Y.Z. All authors have read and agreed to the published version of the manuscript.

Funding: This work was supported by the National Key R&D Program of China (2022YFD2300700), the Jiangxi Agriculture Research System (JXARS-02-03), and Jiangxi Provincial Key Laboratory of Crop Bio-breeding and High-Efficient Production (2024SSY04101).

Data Availability Statement: The data presented in this publication are available on request from the corresponding author.

Conflicts of Interest: The authors declare no conflicts of interest.

References

1. Bahuguna, R.N.; Solis, C.A.; Shi, W.; Jagadish, K.S. Post-flowering night respiration and altered sink activity account for high night temperature-induced grain yield and quality loss in rice (*Oryza sativa* L.). *Physiol. Plant.* **2017**, *159*, 59–73. [CrossRef] [PubMed]
2. Godfray, H.C.J.; Beddington, J.R.; Crute, I.R.; Haddad, L.; Lawrence, D.; Muir, J.F.; Pretty, J.; Robinson, S.; Thomas, S.M.; Toulmin, C. Food security: The challenge of feeding 9 billion people. *Science* **2010**, *327*, 812–818. [CrossRef] [PubMed]
3. Ray, D.K.; Mueller, N.D.; West, P.C.; Foley, J.A. Yield trends are insufficient to double global crop production by 2050. *PLoS ONE* **2013**, *8*, e66428. [CrossRef] [PubMed]
4. Wang, F.; Peng, S.B. Yield potential and nitrogen use efficiency of China's super rice. *J. Integr. Agric.* **2017**, *16*, 1000–1008. [CrossRef]
5. Yang, T.; Xiong, R.; Tan, X.; Huang, S.; Pan, X.; Guo, L.; Zeng, Y.; Zhang, J.; Zeng, Y. The impacts of post-anthesis warming on grain yield and quality of double-cropping high-quality indica rice in Jiangxi Province, China. *Eur. J. Agron.* **2022**, *139*, 126551. [CrossRef]
6. Wang, Y.; Yang, T.; Xiong, R.; Zeng, Y.; Zhang, J.; Tang, F.; Zeng, Y.; Huang, S. Effect of climate warming on the grain quality of early rice in a double-cropped rice field: A 3-year measurement. Front. Sustain. *Food Syst.* **2023**, *7*, 1133665. [CrossRef]
7. Fitzgerald, M.A.; McCouch, S.R.; Hall, R.D. Not just a grain of rice: The quest for quality. *Trends Plant Sci.* **2009**, *14*, 133–139. [CrossRef]
8. Huang, G.; Guo, L.; Zeng, Y.; Huang, S.; Zeng, Y.; Xie, X. Changes in the Grain Yield and Quality of Early Indica Rice from 2000 to 2020 in Southern China. *Agronomy* **2024**, *14*, 295. [CrossRef]
9. Gu, J.; Chen, J.; Chen, L.; Wang, Z.; Zhang, H.; Yang, J. Grain quality changes and responses to nitrogen fertilizer of japonica rice cultivars released in the Yangtze River Basin from the 1950s to 2000s. *Crop J.* **2015**, *3*, 285–297. [CrossRef]
10. Zhu, D.W.; Zhang, H.C.; Guo, B.W.; Ke, X.; Dai, Q.G.; Wei, H.Y.; Gao, H.; Hu, Y.J.; Cui, P.Y.; Huo, Z.Y. Effects of nitrogen level on yield and quality of japonica soft super rice. *J. Integr. Agric.* **2017**, *16*, 1018–1027. [CrossRef]
11. Fukai, S.; Mitchell, J. Role of canopy temperature depression in rice. *Crop Environ.* **2022**, *1*, 198–213. [CrossRef]
12. Chen, L.; Deng, X.; Duan, H.; Tan, X.; Xie, X.; Pan, X.; Guo, L.; Gao, H.; Wei, H.; Zhang, H.; et al. Water management can alleviate the deterioration of rice quality caused by high canopy humidity. *Agric. Water Manag.* **2023**, *289*, 108567. [CrossRef]
13. Huang, X.; Yang, J.; Zhou, W.; Zhang, G.; Liao, B.; Wahab, A.; Yi, Z.; Tu, N. Comparison of the Source–Sink Characteristics between Main Season and Ratooning in Rice (*Oryza sativa* L.). *Agronomy* **2023**, *13*, 1731. [CrossRef]
14. Zhou, Z.; Struik, P.C.; Gu, J.; van der Putten, P.E.; Wang, Z.; Yin, X.; Yang, J. Leaf-colour modification affects canopy photosynthesis, dry-matter accumulation and yield traits in rice. *Field Crop. Res.* **2023**, *290*, 108746. [CrossRef]
15. Dou, Z.; Tang, S.; Chen, W.; Zhang, H.; Li, G.; Liu, Z.; Ding, C.; Chen, L.; Wang, S.; Zhang, H.; et al. Effects of open-field warming during grain-filling stage on grain quality of two japonica rice cultivars in lower reaches of Yangtze River delta. *J. Cereal Sci.* **2018**, *81*, 118–126. [CrossRef]
16. *GB/T 1354-2018*; National Standards of the People's Republic of China, High Quality Paddy. National Standards of the People's Republic of China: Beijing, China, 2017.
17. Palaniswamy, K.M.; Gomez, K.A. Length-width method for estimating leaf area of rice. *Agron. J.* **1974**, *66*, 430–433. [CrossRef]
18. Xu, X.P.; Zhou, W.; Liang, G.Q.; Sun, J.W.; Wang, X.B.; He, P.; Xu, F.S.; Yu, X.C. Effects of nitrogen and density interactions on grain yield and nitrogen use efficiency of double-rice systems. *J. Plant Nutr. Fertil.* **2015**, *21*, 763–772.
19. Hou, W.; Khan, M.R.; Zhang, J.; Lu, J.; Ren, T.; Cong, R.; Li, X. Nitrogen rate and plant density interaction enhances radiation interception, yield and nitrogen use efficiency of mechanically transplanted rice. *Agric. Ecosyst. Environ.* **2019**, *269*, 183–192. [CrossRef]
20. Zhao, C.; Liu, G.; Chen, Y.; Jiang, Y.; Shi, Y.; Zhao, L.; Liao, P.; Wang, W.; Xu, K.; Dai, Q.; et al. Excessive nitrogen application leads to lower rice yield and grain quality by inhibiting the grain filling of inferior grains. *Agriculture* **2022**, *12*, 962. [CrossRef]
21. Zhou, C.; Huang, Y.; Jia, B.; Wang, Y.; Wang, Y.; Xu, Q.; Li, R.; Wang, S.; Dou, F. Effects of cultivar, nitrogen rate, and planting density on rice-grain quality. *Agronomy* **2018**, *8*, 246. [CrossRef]
22. Honda, S.; Ohkubo, S.; San, N.S.; Nakkasame, A.; Tomisawa, K.; Katsura, K.; Ookawa, T.; Nagano, A.J.; Adachi, S. Maintaining higher leaf photosynthesis after heading stage could promote biomass accumulation in rice. *Sci. Rep.* **2021**, *11*, 7579. [CrossRef] [PubMed]
23. Chen, J.; Cao, F.; Li, H.; Shan, S.; Tao, Z.; Lei, T.; Liu, Y.; Xiao, Z.; Zou, Y.; Abou-Elwafa, S.F.; et al. Genotypic variation in the grain photosynthetic contribution to grain filling in rice. *J. Plant Physiol.* **2020**, *253*, 153269. [CrossRef] [PubMed]
24. Shi, Y.; Guo, E.; Cheng, X.; Wang, L.; Jiang, S.; Yang, X.; Ma, H.; Zhang, T.; Li, T.; Yang, X. Effects of chilling at different growth stages on rice photosynthesis, plant growth, and yield. *Environ. Exp. Bot.* **2022**, *203*, 105045. [CrossRef]
25. Xiong, D. Perspectives of improving rice photosynthesis for higher grain yield. *Crop Environ.* **2024**, *3*, 123–137. [CrossRef]

26. Peraudeau, S.; Roques, S.; Quiñones, C.O.; Fabre, D.; Van Rie, J.; Ouwerkerk, P.B.; Jagadish, K.S.; Dingkuhn, M.; Lafarge, T. Increase in night temperature in rice enhances respiration rate without significant impact on biomass accumulation. *Field Crop. Res.* **2015**, *171*, 67–78. [CrossRef]
27. Yang, X.; Liu, R.; Jing, M.; Zhang, N.; Liu, C.; Yan, J. Variation of root soluble sugar and starch response to drought stress in foxtail millet. *Agronomy* **2023**, *13*, 359. [CrossRef]
28. Faber, A.H.; Griffin, K.L.; Tjoelker, M.G.; Pagter, M.; Yang, J.; Bruhn, D. Consistent diurnal pattern of leaf respiration in the light among contrasting species and climates. *New Phytol.* **2022**, *236*, 71–85. [CrossRef]
29. Chang, T.G.; Wei, Z.W.; Shi, Z.; Xiao, Y.; Zhao, H.; Chang, S.Q.; Qu, M.; Song, Q.; Chen, F.; Zhu, X.G.; et al. Bridging photosynthesis and crop yield formation with a mechanistic model of whole-plant carbon–nitrogen interaction. *Silico Plants* **2023**, *5*, 1–19. [CrossRef]
30. Fan, P.; Xu, J.; Wei, H.; Liu, G.; Zhang, Z.; Tian, J.; Zhang, H. Recent research advances in the development of chalkiness and transparency in rice. *Agriculture* **2022**, *12*, 1123. [CrossRef]
31. Song, Q.; Liu, F.; Bu, H.; Zhu, X.G. Quantifying contributions of different factors to canopy photosynthesis in 2 maize varieties: Development of a novel 3D canopy modeling pipeline. *Plant Phenomics* **2023**, *5*, 75. [CrossRef]

Disclaimer/Publisher's Note: The statements, opinions and data contained in all publications are solely those of the individual author(s) and contributor(s) and not of MDPI and/or the editor(s). MDPI and/or the editor(s) disclaim responsibility for any injury to people or property resulting from any ideas, methods, instructions or products referred to in the content.