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Effect of climate warming on the grain quality of early rice in a double-cropped rice field: A 3-year measurement

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Introduction: The threat of climate warming to global rice production has been widely addressed, but little is known about its influence on the quality of rice grains.

Methods: A free-air temperature increase (FATI) facility with two widely-planted high-quality cultivars was used to explore the impact of warming on the grain quality of early rice in subtropical China over 3 consecutive years.

Results: Compared with the control, FATI increased diurnal canopy temperature by 1.5°, and thus, rice growth duration was shortened by 4.0 d under warming. We found that warming significantly reduced both the milled rice and head rice rates relative to the control, thereby leading to a decrease in the milled rice and head rice yield by 3.9 and 8.3%, respectively. The chalky grain rate and chalkiness were increased by 19.1 and 22.2% under warming compared with the control, respectively. The content of protein, essential amino acids, and non-essential amino acids were increased by 4.1, 5.4, and 4.9% under warming, respectively. Warming reduced the amylose content and setback by 2.0 and 47.5% but increasing peak viscosity, trough viscosity, breakdown, and final viscosity by 9.5, 13.6, 5.7, and 6.0%, respectively.

Conclusion: Our results suggest that the deteriorated milling and appearance quality induced by warming may be an upcoming challenge for high-quality early rice production in the future.

KEYWORDS

experimental warming, amylose, chalkiness, protein, amino acids, eating quality

1. Introduction

The global surface temperature has increased by 1.1°C in 2011–2020 compared with that in 1850–1900 and is predicted to rise by 1.2–1.9°C in the near term (2021–2040) (IPCC, 2021). Climate warming has raised serious concerns over crop production and food quality (Seck et al., 2012; Zhao et al., 2017). Rice (*Oryza sativa* L.) is the staple food for >50% of the world's population (Food FAO Agriculture Organization of the United Nations, 2019). Although a large deal of research has shown that climate change affects rice yield, few studies have examined how warming alters rice grain quality (Lyman et al., 2013; Deng et al., 2015; Wang et al., 2018). As most rice is directly consumed as grains, different grades of milling (i.e., milled rice and head rice) significantly affect food availability, while the nutritional quality has important implications for human health (Lyman et al., 2013). In addition, the appearance and eating quality determine consumers' preferences, thus affecting rice marketability and farmers'

income (Anang et al., 2011). Therefore, there is an urgent need to examine the influence of climate warming on the quality of rice grains.

The quality of rice grains is generally evaluated by their milling, appearance, nutritional, and eating characteristics (Liu et al., 2013). Temperature increase can affect the physiological processes of rice that are associated with grain quality such as assimilate accumulation and transport, grain filling, and starch synthesis (Yamakawa and Hakata, 2010; Chen et al., 2017). Previous investigations have demonstrated that temperature increase reduces the percentage of both milled rice and head rice but increases the chalky grain rate and chalkiness, thus leading to the degradation of rice milling and appearance quality (Dou et al., 2017). The nutritional quality of rice grains is evaluated by protein and amino acid contents. Growing evidence shows that warming could increase the content of proteins and amino acids in rice grains by promoting N uptake and transport (Tang et al., 2018; Yin et al., 2021). The amylose content and rapid viscosity analyzer (RVA) parameters are strongly relevant to the eating quality of cooked rice (Xuan et al., 2020). Several reports showed that warming reduced the amylose content in rice grains and significantly altered RVA parameters with higher peak viscosity, breakdown, and pasting temperature but lower setback values (Liu et al., 2013; Shi et al., 2016; Zhi et al., 2018). Nevertheless, most of these previous experiments regarding the influence of warming on rice quality were conducted under the controlled environment such as greenhouses and growth chambers, where micrometeorology (e.g., light, wind, and air humidity) is drastically altered compared with ambient conditions (Chen et al., 2017). The free-air temperature increase (FATI) facility, which applies infrared heaters to warm plant canopies under open-field conditions, is appealing and has been widely employed in climate warming research (Chen et al., 2020). In the last decade, several FATI facilities have been established to investigate the impact of increased temperature on rice quality (Zhi et al., 2018; Wang et al., 2019). For instance, Dou et al. (2017) showed that a temperature increase of 2.7°C during the grain-filling stage deteriorated rice milling and appearance quality but improved the nutritional quality. Wang et al. (2019) found that warming increased the protein and amino acid contents in rice grains. However, these studies were mainly performed in the single rice cropping system. As far as we know, no studies have reported the effect of climate warming on grain quality with FATI facilities in the double rice cropping system.

Double rice cropping accounts for approximately 34% of the total harvested rice area in China, thus playing an important role in food security (Ministry MOA of Agriculture of China, 2022). In addition, double rice cropping is mostly distributed in subtropics and tropics, where rice production has greater vulnerability and increasing risks of heat stress due to climate warming (Zhao et al., 2017). Particularly, grain filling occurs from June to July in the early rice growth season when warming has a large impact on both grain yield and quality due to high ambient air temperature (Cheng et al., 2019). Thus, we expected that climate warming may have dramatic impacts on the grain quality of early rice. To clarify the change in the grain quality of early rice under climate warming in the future, we conducted a 3-year field experiment using the FATI facility to examine the effect of warming on the milling,

appearance, nutritional, and eating quality of early rice grains in a double-cropped rice field of subtropical China.

2. Materials and methods

2.1. Site description

A warming experiment was carried out in a rice paddy field during the early rice cropping season from 2017 to 2019 in Shanggao of Jiangxi province, China (28°31' N, 115°09' E). This region has a typical subtropical monsoon climate, with June to August as the annual high-temperature season. The annual mean temperature was 18.7°C in 2017, 18.7°C in 2018, and 19.7°C in 2019. The annual precipitation was 1,983 mm in 2017, 1,458 mm in 2018, and 2,341 mm in 2019 (Supplementary Figure 1). Double-cropped rice with winter fallow has been cropped in the paddy field for over 30 years, with early rice planted from April to July and late rice from July to October. The soil from the upper 15 cm depth before initiating the experiment contained organic matter of 35.3 g kg⁻¹, total nitrogen of 2.0 g kg⁻¹, with a soil pH of 5.5.

2.2. Experimental design

The experiment was arranged in a blocked split-plot design with warming as the main factor and cultivars as the subplot treatment. There were three blocks with two 3.0 × 4.0 m main plots in each block, in which one plot was randomly assigned as the warming treatment and the other as the ambient control. Each main plot was divided into two 3.0 × 2.0 m subplots, in which two high-quality early rice cultivars, Xiangzaoxian 45 (XZX45) and Qiliangyou2012 (QLY2012), were randomly cropped. In each warmed subplot, a rectangular infrared heater (180 cm in length, 20 cm in width) was installed 75 cm above the rice canopy during the whole rice growing season, with the long side of the infrared heater perpendicular to the long side of the subplot. Each control subplot had a similar “dummy” heater to simulate shading by the heater. It was observed that each infrared heater produced uniform heating over a sampling area of 1.5 m × 1.8 m. Details about the FATI facility were reported by Yang et al. (2020).

2.3. Crop management

Pre-germinated seeds were manually sown on 29 March 2017, 17 March 2018, and 16 March 2019. We manually transplanted 30-day-old rice seedlings at a planting density of 38 hills m⁻² (20 × 13 cm), with three seedlings per hill. Mineral N fertilizer was applied in the form of urea at a rate of 165 kg N ha⁻¹, 50% of which was applied as basal fertilizer before transplanting, 20% at the tillering stage with the remaining 30% at the panicle initiation. All the P fertilizer was applied in the form of calcium magnesium phosphate as basal fertilizer at a rate of 35.9 kg P ha⁻¹. Mineral K fertilizer was applied in the form of potassium chloride at a rate of 123.3 kg K ha⁻¹, half of which was applied as basal fertilizer with the other half at the panicle initiation. The water regime followed local cultivation practices. The field was kept flooded with a water depth

of 3–10 cm due to transplanting until mid-season drainage and then was intermittently irrigated until 1 week before maturity. Weeds, diseases, and insects were intensively controlled by chemicals.

2.4. Sampling and measurements

Rice grains (~50 hills) were harvested manually, and then, the grain yield was measured and adjusted by a moisture content of 13.5%. The grain samples were stored at room temperature for 3 months before the determination of rice quality. Milling and appearance quality were determined according to the Chinese national standard for rice quality evaluation (GB/T 17891/2017) (National Standards of the People's Republic of China, 2017). In brief, 200 g of rice grain samples for each cultivar were de-hulled with a rice huller to calculate the brown rice rate, and then, brown rice was milled with a rice polisher to determine the milled rice rate. Head rice rate, chalky grain rate (i.e., the percentage of chalky rice grains in the total sample), and chalkiness (i.e., the percentage of chalky area to the total area of rice grains) for milled rice were measured with a grain quality inspector (ScanMaker i800 Plus, Zhongjin, China) and equipped with image analysis software (SC-E, Wanshen Technology Company, Hangzhou, China). The yield of brown rice, milled rice, and head rice was determined by grain yield multiplied by the rate of brown rice, milled rice, and head rice, respectively.

The amylose content in milled rice was determined by the iodine adsorption method, according to Man et al. (2012). The N content was analyzed by an N analyzer (Kjeltec 8400, FOSS, Denmark) after digesting with sulfuric acid and hydrogen peroxide. The protein content in milled rice was estimated by multiplying the N content with a conversion factor of 5.95 (Wang et al., 2018). The content of total amino acids in milled rice was determined using an amino acid analyzer (L-8900, Hitachi Corp, Japan) (Wang et al., 2019). The amino acids were classified into essential amino acids (EAAs) and non-essential amino acids (NEAAs), according to Wu (2009).

Rapid viscosity analyzer (RVA) parameters were measured by a rapid viscosity analyzer (RVA-Super4, Australia), following the standard procedure from the American Association of Cereal Chemists (AACC, 2000-61-02). In brief, 3 g of rice flour was mixed well with 25 g of ultra-pure water in an aluminum cylinder. The samples were heated at 50°C for 1 min and then heated from 50 to 95°C and cooled to 50°C at a rate of 12°C/min.

2.5. Statistical analysis

Analyses of variance (ANOVAs) were employed to examine the impacts of warming, cultivar, study year, and their interactions on rice quality parameters. Multiple comparisons were performed using the least significant difference test at $P \leq 0.05$. As the contents of EAAs and NEAAs were determined only in 2018, two-way ANOVAs were performed to explore the effects of warming, cultivar, and their interactions. All data were analyzed by JMP Pro 16 software (SAS, USA).

3. Results

3.1. Canopy temperature and growth duration

Compared to the control, the mean diurnal canopy temperature was increased by 1.3, 1.5, and 1.9°C in 2017, 2018, and 2019, respectively, under warming over the entire rice growth period (i.e., from transplanting to maturity) (Supplementary Figure 2). Daytime and nighttime canopy temperatures across the early rice season were increased by an average of 0.9 and 1.6°C in 2017, 1.0 and 2.0°C in 2018, and 1.1 and 2.6°C in 2019 under warming.

Specifically, warming increased diurnal canopy temperature by an average of 1.2, 1.5, and 1.9°C in 2017, 2018, and 2019, respectively, during the grain-filling period (i.e., from heading to maturity) (Table 1). On average, daytime and nighttime canopy temperatures during the grain-filling period were increased by 0.3 and 1.4°C in 2017, 1.0 and 2.0°C in 2018, and 1.3 and 2.5°C in 2019 under warming.

Warming shortened the entire growth duration of early rice by an average of 4.0 d compared to the control (Table 2). Specifically, the length of the pre-anthesis phase (i.e., from transplanting to heading) was shortened by an average of 2.9 d under warming, while the length of the grain-filling period was reduced by an average of 1.2 d.

3.2. Milling, appearance, and nutritional quality

Warming significantly reduced the milled rice rate and head rice rate relative to the control but did not affect the brown rice rate (Table 3). Consequently, the yield of milled rice and head rice was reduced by 4.0 and 8.4% under warming relative to the control, respectively, whereas the brown rice yield was not significantly affected by the increase in temperature. In addition, there was a significant interaction between warming and year in affecting the milled rice rate. Warming reduced the milled rice rate by 3.2% in 2019, whereas no significant effects were observed in 2017 and 2018 (Figure 1A).

Chalky grain rate and chalkiness were increased by 19.0 and 24.0% under warming relative to the control, respectively (Table 3). Significant interactive effects of warming and year on chalkiness were observed. Warming increased chalkiness by 38.2 and 37.6% in 2018 and 2019, respectively, but had no significant effect in 2017 (Figure 1B).

Protein content was increased by an average of 4.2% under warming compared to the control (Table 3). No interactions of warming, cultivar or warming, and year were found to affect protein content.

Rice grain quality varied with cultivars and experimental years. XZX45 had a higher brown rice rate, milled rice rate, chalky grain rate and chalkiness, and lower head rice rate and head rice yield than in QLY2012 (Table 3). Milled rice rate, chalky grain rate, and chalkiness were higher in 2017 than in 2018 and 2019.

TABLE 1 Mean diurnal, daytime, and nighttime temperature (°C) in rice canopy during the grain-filling period (from heading to maturity).

Cultivar	Year	Treatment	Diurnal	Daytime	Nighttime
XZX45	2017	Control	25.9	28.9	23.7
		Warming	27.2	29.4	25.3
	2018	Control	27.8	31.2	24.3
		Warming	29.3	32.2	26.3
	2019	Control	26.4	29.2	23.7
		Warming	28.4	30.6	26.3
QLY2012	2017	Control	26.0	29.3	24.1
		Warming	27.1	29.4	25.3
	2018	Control	28.2	31.7	24.6
		Warming	29.6	32.6	26.6
	2019	Control	26.4	29.2	23.6
		Warming	28.1	30.3	26.0

TABLE 2 Effect of warming on the growth duration (d) of early rice.

Cultivar	Year	Treatment	Transplanting to heading	Heading to maturity	Transplanting to maturity
XZX45	2017	Control	48	30	78
		Warming	46	29	75
	2018	Control	52	31	83
		Warming	49	30	79
	2019	Control	53	32	85
		Warming	50	31	81
QLY2012	2017	Control	53	28	81
		Warming	50	26	76
	2018	Control	54	31	85
		Warming	51	29	80
	2019	Control	56	32	88
		Warming	53	32	85

3.3. Essential amino acids and nonessential amino acids

In comparison to the control, warming increased the content of EAAs and NEAAs by 5.4% and 4.9%, respectively, while the EAAs-to-NEAAs ratio was not significantly affected (Table 4). XZX45 had higher contents of EAAs and NEAAs than in QLY2012. Warming interacted with cultivars to impact the content of NEAAs in rice grains. Warming led to an increase of 8.5% in the NEAAs content for QLY2012 but had no significant effects for XZX45 (Figure 1C).

For NEAAs, warming increased the content of glutamic acid, alanine, and cysteine by 24.7, 7.1, and 34.8% for QLY2012, respectively, whereas only the cysteine content was increased by 47.6% under warming for XZX45 (Supplementary Table 1). For EAAs, valine, methionine, leucine, and lysine contents were increased by 9.9, 18.0, 12.1, and 11.1% for QLY2012 under warming

relative to the control, respectively. On the contrary, warming did not significantly affect the content of any EAAs for XZX45.

3.4. Eating quality

In comparison to the control, warming decreased the content of amylose by 2.0% (Table 3). No interactions of warming, cultivar or warming, and year were observed to affect amylose content.

Relative to the control, warming increased the peak viscosity, trough viscosity, breakdown, and final viscosity of rice flour by 9.5, 13.6, 5.7, and 6.0%, respectively, whereas the setback was reduced by 47.5% under warming (Table 5). XZX45 had higher peak viscosity, trough viscosity, final viscosity, and setback than in QLY2012. Rice grains had higher peak viscosity, breakdown,

TABLE 3 Rice grain quality as affected by warming, cultivar, and study year.

	Brown rice rate (%)	Milled rice rate (%)	Head rice rate (%)	Brown rice yield (t ha ⁻¹)	Milled rice yield (t ha ⁻¹)	Head rice yield (t ha ⁻¹)	Chalky grain rate (%)	Chalkiness (%)	Amylose (g kg ⁻¹)	Protein (g kg ⁻¹)
Warming (W)^a										
Control	76.8 a	63.6 a	47.6 a	5.76 a	4.77 a	3.57 a	23.7 b	7.95 b	147.8 a	83.2 b
Warming	77.4 a	62.8 b	44.8 b	5.65 a	4.58 b	3.27 b	28.2 a	9.86 a	144.8 b	86.7 a
Cultivar (C)^b										
XZX45	77.9 a	63.9 a	44.9 b	5.65 a	4.63 a	3.26 b	27.0 a	9.82 a	151.7 a	85.0 a
QLY2012	76.2 b	62.5 b	47.4 a	5.76 a	4.72 a	3.58 a	24.8 b	7.99 b	140.9 b	84.9 a
Year (Y)^c										
2017	77.2 b	67.1 a	46.6 a	5.64 a	4.90 a	3.41 a	34.4 a	12.12 a	145.7 a	84.0 b
2018	75.3 c	62.2 b	45.1 b	5.78 a	4.78 a	3.47 a	22.5 b	7.27 b	145.8 a	81.8 c
2019	78.7 a	60.4 c	46.8 a	5.68 a	4.36 b	3.38 a	20.8 c	7.33 b	147.4 a	89.0 a
F-values										
W × C	3.76	1.46	0.46	0.13	0.04	0.47	0.10	0.01	0.61	0.01
W × Y	1.73	3.80*	1.52	1.24	0.02	0.81	1.00	6.41**	0.54	1.37
C × Y	13.26***	0.01	7.52**	7.22**	2.88	1.50	5.18*	16.25***	28.76***	32.21***
W × C × Y	0.33	1.85	1.86	0.73	0.90	2.77	12.13***	16.22***	0.49	6.80**

Different lowercase letters in the same column indicate significant differences in the main effect of warming, cultivar, or year.

Significant interactive effects are indicated by * (0.01 < P ≤ 0.05), ** (0.001 < P ≤ 0.01), or *** (P ≤ 0.001).

^aValues were averaged across cultivars and years.

^bValues were averaged across warming treatments and years.

^cValues were averaged across warming treatments and cultivars.

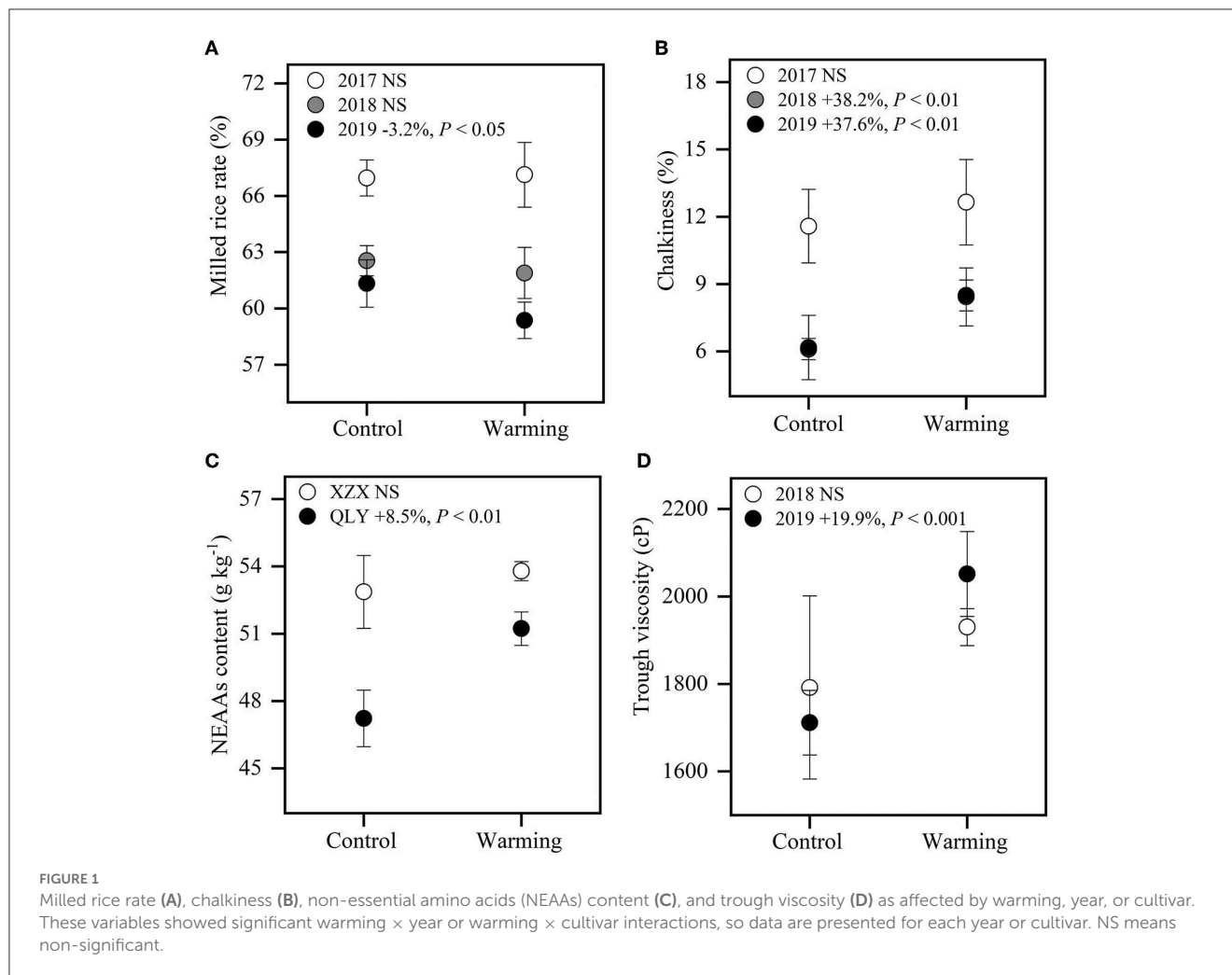


TABLE 4 The content of essential amino acids (EAAs) and non-essential amino acids (NEAAs) in milled rice as affected by warming and cultivar in 2018.

	EAAs (g kg ⁻¹)	NEAAs (g kg ⁻¹)	EAAs: NEAAs
Warming (W)^a			
Control	23.90 b	50.05 b	0.48 a
Warming	25.18 a	52.51 a	0.48 a
Cultivar (C)^b			
XZX45	25.64 a	53.33 a	0.48 a
QLY2012	23.44 b	49.23 b	0.48 a
F values			
W×C	3.14	4.78*	0.02

Different lowercase letters in the same column indicate significant differences in the main effect of warming or cultivar.

Significant interactive effects are indicated by * (0.01 < *P* ≤ 0.05), ** (0.001 < *P* ≤ 0.01), or *** (*P* ≤ 0.001).

^a Values were averaged across cultivars.

^b Values were averaged across warming treatments.

and final viscosity but a lower setback in 2018 than in 2019. No interactions of warming and cultivar were found to affect any of the RVA parameters. There was an interaction between warming

and year in affecting trough viscosity. Warming increased trough viscosity by 19.9% in 2019, whereas no significant effect was observed in 2018 (Figure 1D).

3.5. Correlation between rice canopy temperature and grain quality

No significant correlation between rice canopy temperature during the grain filling period and grain quality parameters was found, except for the negative relationship between the head rice rate and both mean diurnal and nighttime temperature (Supplementary Table 2).

4. Discussion

4.1. Effect of warming on the milling quality of early rice

Our previous study in the same field experiment showed that warming had no significant effect on the grain yield of early rice (Wang et al., 2022a). Consistent with grain yield, both rate and yield of brown rice were not significantly affected by warming. However,

TABLE 5 Rapid viscosity analyzer (RVA) parameters for milled rice as affected by warming, cultivar, and study year.

	Peak viscosity (cP)	Trough viscosity (cP)	Breakdown (cP)	Final viscosity (cP)	Setback (cP)
Warming (W)^a					
Control	3,410 b	1,752 b	1,650 b	3,125 b	−284.5 a
Warming	3,734 a	1,991 a	1,745 a	3,314 a	−419.5 b
Cultivar (C)^b					
XZX45	3,632 a	1,934 a	1,697 a	3,362 a	−269.9 a
QLY2012	3,511 b	1,808 b	1,699 a	3,077 b	−434.2 b
Year (Y)^c					
2018	3,966 a	1,861 a	2,100 a	3,434 a	−532.2 b
2019	3,177 b	1,882 a	1,296 b	3,005 b	−171.9 a
F-values					
W×C	0.30	2.28	1.69	0.06	0.07
W×Y	2.49	24.52***	4.18	2.44	0.00
C×Y	8.34*	12.39**	0.03	11.71**	0.21
W×C×Y	7.27*	48.37***	4.34	40.09***	10.41**

Different lowercase letters in the same column indicate significant differences in the main effect of warming, cultivar, or year.

Significant interactive effects are indicated by * ($0.01 < P \leq 0.05$), ** ($0.001 < P \leq 0.01$), or *** ($P \leq 0.001$).

^aValues were averaged across cultivars and years.

^bValues were averaged across warming treatments and years.

^cValues were averaged across warming treatments and cultivars.

warming reduced the milled rice and head rice rates of early rice, regardless of cultivars. Previous research also reported that temperature increase deteriorates the milling quality of rice grains (Zhi et al., 2018). First, several studies have found that both milled rice and head rice rates are negatively correlated with chalkiness that makes rice grains more fragile in processing (Ambardekar et al., 2011; Lanning et al., 2011; Shi et al., 2016). Indeed, our findings demonstrated that warming significantly increased both chalkiness and chalky grain rates. Thus, the decrease in the milled rice and head rice rates under warming may be attributed to more chalkiness (Lanning et al., 2011). In addition, a temperature increase may lead to the formation of loosely packed starch granules that reduce the strength of kernels and make chalky grains more brittle, thus deteriorating the milling quality of rice grains (Sreenivasulu et al., 2015).

Our findings indicated that warming caused a decrease in the yield of both milled rice and head rice due to the reduced milled and head rice rates. As rice is consumed mainly as intact grains, the decrease in head rice yield under warming will threaten food security in the future (Lyman et al., 2013; Shi et al., 2016). Moreover, the lower milled and head rice rates under climate warming will reduce the profit of rice processors, which, in turn, may lead to a higher price in the future and thus reduce rice accessibility for low-income people (Sreenivasulu et al., 2015).

In addition, we found that warming led to a decrease in the milled rice rate in 2019 but not in 2017 and 2018 (Figure 1A). Chen et al. (2017) demonstrated that the decrease in the milled rice rate was positively related to the increase in the temperature during the grain-filling period. In the present FATI facility, the magnitude of the increase in rice canopy temperature was higher in 2019 than in

2017 and 2018 (Table 1). Thus, the decrease in the milled rice rate in 2019 may be attributed to the higher temperature increase during the grain-filling period than in 2017 and 2018.

Our results showed that the cultivar XZX45 had a higher brown rice rate and milled rice rate than in QLY2012 but showed a lower head rice rate (Table 3). It is anticipated that the greater thickness of hull and bran in rice grains may contribute to the lower brown rice rate and milled rice rate for QLY2012 than in XZX45, while the underlying mechanisms need further examination (Liu et al., 2022). The head rice rate of XZX45 is lower mainly due to its high ratio of length and width of rice grains (3.4), which is greater than that of QLY2012 (3.0). It is well known that the larger the ratio of length and width of rice grains, the easier it is to break when processing (Zhou et al., 2015). In addition, the lower head rice rate of XZX45 than that of QLY2012 may be due to its higher chalky grain rate and chalkiness that makes rice grains more fragile in processing (Shi et al., 2016).

4.2. Effect of warming on the appearance quality of early rice

As described earlier, our study indicated that warming significantly increased both chalky grain rate and chalkiness and thus reduced rice appearance quality. A large deal of research has shown that temperature increase enhances rice chalkiness (Jing et al., 2016; Shi et al., 2016; Zhi et al., 2018). First, warming during the grain-filling stage could increase the grain-filling rate and reduce assimilate supply, thereby limiting endosperm development (Chen et al., 2017). Second, warming may promote the activity

of amylase but reduce the synthase activity for both soluble and granule-bound starch in rice grains, which increases the number of loose starch granules on the endosperm surface and thus enhances chalkiness formation (Dou et al., 2017). In addition, temperature increases during the early stage of grain filling may lower water content in the endosperm center, thereby constraining the development of amyloplasts and thus increasing the chalkiness (Ishimaru et al., 2009).

Chalkiness has a large impact on consumers' preferences and the marketing value of rice grains (Cheng et al., 2019). Rice consumers and producers generally lack interest in high chalky rice with poor appearance quality (Anang et al., 2011). Thus, the increase in chalkiness under warming will reduce the marketing price of rice grains in the future. In addition, the loose structure of starch granules in chalky grains may degrade the palatability of cooked rice (Chun et al., 2009). The present FATI study suggests that even a moderate temperature increase may promote the chalky grain rate and chalkiness of rice grains. As chalkiness is closely related to the milling, appearance, and eating quality of rice grains, more attention should be paid to alleviating chalkiness formation under climate warming (Cheng et al., 2019).

In addition, the present results showed that warming increased the chalkiness of rice grains in 2018 and 2019 but not in 2017. Many studies have indicated that rice chalkiness is positively correlated with the temperature during the grain-filling period (Ishimaru et al., 2009; Chen et al., 2017; Zhou et al., 2021). Therefore, as stated earlier, the higher increase in rice canopy temperature in 2018 and 2019 may lead to their stronger responses of rice chalkiness to warming than in 2017.

Our results showed that both chalky grain rate and chalkiness were lower in QLY2012 than that of ZZX45 (Table 3). It is acknowledged that rice chalkiness is controlled by quantitative trait loci and is influenced greatly by environmental conditions, particularly temperature (Li et al., 2003; Cheng et al., 2019). Thus, the lower chalky grain rate and chalkiness in QLY2012 may be due to both its genetic characteristics and higher heat tolerance compared to ZZX45 (Ishimaru et al., 2016).

4.3. Effect of warming on the nutritional quality of early rice

Our finding that warming significantly increased protein content in milled rice is consistent with previous reports (Tang et al., 2018; Wang et al., 2019). The increase in protein content in rice grains caused by warming can be explained by several reasons. First, our previous research showed that warming increased rice N uptake in the same field experiment, whereas neither grain yield nor biomass was significantly affected (Yang et al., 2019). Therefore, the increase in protein content in rice grains may be attributed to the greater N uptake by rice plants under warming. Second, warming raises leaf temperature and promotes the vapor pressure deficit, thereby increasing N translocation to grains (Wang et al., 2018). Third, warming may promote the assimilation of N in rice plants by increasing the activities of both glutamine and glutamate synthases, thus increasing protein content in grains (Tang et al., 2018). In addition, although warming had no significant effect

on the grain yield of early rice (Wang et al., 2022a), our results showed that the grain yield of early rice was negatively correlated with the protein content of grains (Supplementary Figure 3), which were consistent with previous studies (Wang et al., 2019; Yin et al., 2021). Thus, the mechanisms underlying the negative correlation between grain yield and the protein content of rice grains need further examination.

In addition, the present study found that warming increased both EAAs and NEAAs content in milled rice, whereas the EAAs-to-NEAAs ratio was not altered. As discussed earlier, warming promotes both rice N uptake and N translocation to grains, thereby providing more substrates for the synthesis of amino acids (Wang et al., 2018). Furthermore, Yamakawa and Hakata (2010) indicated that the expression of genes for amino acid transporters was relatively stable under warming. Thus, higher N supply and translocation combined with stable amino acid transporters contribute to the synthesis of more amino acids and their accumulation in rice grains under warming (Wang et al., 2018). In conclusion, the increase in protein and EAAs in rice grains under warming will benefit human nutrition in regions where rice is the main caloric source (Wu, 2009).

4.4. Effect of warming on the eating quality of early rice

It is generally acknowledged that the lower the amylose content, the better the taste of cooked rice (Xuan et al., 2020). Consistent with previous research, our results indicated that warming reduced amylose content in milled rice (Chen et al., 2017; Dou et al., 2017). Many reports have revealed that there is a trade-off between protein and amylose contents in rice grains because their syntheses consume common ATP and carbon skeleton (Gutiérrez et al., 2007; Tayefe et al., 2012; Gu et al., 2015). Thus, the increase in protein content under warming may lead to a decrease in amylose content in rice grains (Tayefe et al., 2012). In addition, temperature increases may limit the activity of granule-bound starch synthase that is involved in the synthesis of amylose, thus reducing the content of amylose (Yamakawa and Hakata, 2010).

The RVA parameters, particularly the peak viscosity, breakdown, and setback, are widely used for the rapid evaluation of rice texture (Xuan et al., 2020). The peak viscosity reflects the extent of swelling and disruption of starch granules. The breakdown is used to evaluate the stability of swollen starch granules such as hydration, swelling power, and shear resistance. Setback viscosity indicates the tendency of starch retrogradation (Shi et al., 2022). Previous studies have shown that larger peak viscosity and breakdown and smaller setbacks mean lower firmness and higher stickiness that both contribute to a better taste (Zhi et al., 2018; Xuan et al., 2020). We found that warming raised the peak viscosity and breakdown values and lowered the setback of cooked rice, thereby improving the eating quality of rice grains (Zhi et al., 2018). Previous research has reported that amylose content has a positive relationship with setback values and a negative relationship with peak viscosity and breakdown values (Tong et al., 2014; Xuan et al., 2020). Thus, the reduced amylose content induced by warming may contribute to the increase in peak

viscosity and breakdown values and the decline in the setback of cooked rice. Although the RVA parameters indicated that warming improved the eating quality of early rice grains, the increase in the content of protein may reduce the eating quality. Many studies have shown that high protein content limits water absorption when cooking, prevents the hydration of protein and starch, and reduces the viscosity and texture of cooked rice, thus reducing the eating quality of rice grains (Gu et al., 2015; Cheng et al., 2021; Shi et al., 2022). Furthermore, the golden rule for evaluating the eating quality of rice grains should be evaluated by human tasters (Kim et al., 2017). Thus, human tasting should be employed to evaluate the actual effect of warming on the eating quality of rice grains in the future. In addition, other parameters such as water uptake, volume expansion ratio, and a gel consistency should be measured in the future to clarify the effect of warming on the cooking quality of rice grains (Wang et al., 2022b). Moreover, as starch is the most important component of rice grains, its content, structure, and physicochemical properties should be determined to reveal the mechanisms underlying the response of grain quality to climate warming (Xiong et al., 2022).

In addition, we found that XZX45 had higher peak viscosity, trough viscosity, final viscosity, and setback than in QLY2012. As stated earlier, the high setback of XZX45 may be attributed to its high amylose content. The differences in peak viscosity, trough viscosity, final viscosity, and setback between the two rice cultivars are likely associated with the physicochemical properties of rice starch. Our previous results indicated that XZX45 had a higher average diameter of starch granules than in QLY2012, whereas the relative crystallinity of starch granules showed the opposite (Yang et al., 2020). In addition, the lower swelling power and higher water solubility of rice starch for XZX45 may contribute to its higher viscosity compared to QLY2012 (Yang et al., 2020).

Overall, we did not find significant correlations between rice canopy temperature (mean diurnal, daytime, and nighttime) during the grain-filling period and grain quality parameters, except for the negative relationship between the head rice rate, and both mean diurnal and nighttime temperature (Supplementary Table 2). In contrast, many studies show that mean temperature during the grain-filling period is positively correlated with the chalkiness of rice grains (Lanning et al., 2011; Cheng et al., 2019; Zhou et al., 2021), whereas it was not observed in the present study. Most of the previous studies employed ambient temperature variation across a large geographic area or manipulated large temperature increases in controlled conditions (Cheng et al., 2019; Zhou et al., 2021). We anticipated that the large variation in rice canopy temperature over different years and the relatively small magnitude of the temperature increase under FATI (Supplementary Figure 2) may mask the relationship between rice canopy temperature and grain quality parameters (Zhou et al., 2021).

In short, climate warming has adverse effects on the grain quality of early rice, particularly the milling and appearance quality. Climate-smart strategies including innovative crop management and breeding should be developed to alleviate the negative impact of warming on rice grain quality. For instance, previous studies have shown that optimizing the rate and timing of mineral N fertilizer, organic manure amendment, and selecting heat-tolerant cultivars could mitigate the adverse effects of temperature increase

on rice yield and quality (Dou et al., 2017; Yang et al., 2017, 2022; Zhu et al., 2022).

5. Conclusion

The 3-year field experiment showed that free-air temperature increase reduced the rate of both milled rice and head rice and led to a decrease in the yield of both milled rice and head rice. Temperature increases enhanced both the chalky grain rate and chalkiness of rice grains. Thus, climate warming would reduce the milling and appearance quality of early rice grains in the double-cropped rice systems in the future. In contrast, warming improved the nutritional and eating quality of rice grains due to the increase in the content of protein and the improvement in the RVA properties, respectively. Therefore, future research should focus on the trade-off between the positive and negative effects of warming on rice grain quality.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary material, further inquiries can be directed to the corresponding author.

Author contributions

YW conceived the idea and wrote the manuscript. TY and RX contributed to the writing of the manuscript. YaZ, YoZ, JZ, and FT contributed to the conception and design of the study. SH edited the manuscript. All authors contributed to the manuscript and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fsufs.2023.1133665/full#supplementary-material>

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