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The Effect of Organ Temperature on Total Yield of Transplanted and Direct-Seeded Rice (*Oryza sativa* L.)

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ABSTRACT

The canopy temperature of rice is an important index that directly reflects the growth and physiological state of rice, and affects the yield of rice plants to a great extent. The correlation between the temperatures of different rice organs and canopy in different growth stages and the grain yield is complex. The stability and universality of these correlations must be verified. We conducted a pot experiment using two rice varieties and two temperature treatments (high temperature treatment was carried out at the beginning of heading stage for 10 days). We measured rice organ temperature during seven stages of growth using a high-precision infrared thermal imager. Results showed that the optimal observation period for the rice canopy temperature was 13:00. Although the rice variety did not significantly impact the canopy or organ temperature ($p > 0.05$), the different organs and canopy exhibited significantly different temperatures ($p < 0.05$). The correlations between the leaf, stem, panicle, canopy–air temperature differences and seed setting rate, theoretical and actual yields were the strongest during the milk stage. Among them, the correlation coefficient between ΔT_s and theoretical and actual yields was the highest, the relationship between theoretical yield (Y) and ΔT_s (X) was $Y = -5.6965X + 27.778$, $R^2 = 0.9155$. Compared with ΔT_l , ΔT_p and ΔT_c , ΔT_s was closely related to the main traits of plants. ΔT_s could better reflect the growth characteristics of rice than ΔT_c , such as dry matter accumulation ($r = -0.931$), SPAD ($r = 0.699$), N concentration ($r = 0.714$), transpiration rate ($r = -0.722$). In conclusion, stem temperature was more important indicator than canopy temperature. Stem temperature is a better screening index for rice breeding and cultivation management in the future.

KEYWORDS

Planting method; canopy temperature; organ temperature; grain yield

Nomenclature

| | |
|--------------|-------------------------------------|
| ΔT_l | Leaf–air temperature differences |
| ΔT_s | Stem–air temperature differences |
| ΔT_p | Panicle–air temperature differences |
| ΔT_c | Canopy–air temperature differences |



1 Introduction

The canopy temperature of rice refers to the average surface temperature of the stems, leaves, and panicles, which is closely related to canopy function [1]. The canopy temperature of rice is also an important index that directly reflects the growth and physiological state of rice. It is of great significance to explore the biological basis and effect of canopy temperature formation for improving canopy function and promoting high-quality and high-yield cultivation. Canopy temperature provides a feasible and reliable method for the timely assessment of crop growth on land [2,3]. Canopy temperature is mainly composed of its thermal characteristics and physiological response to the environment. First, the energy transfer between plants and the surrounding environment is carried out through conduction, radiation, convection and latent heat evapotranspiration. For example, factors such as water in the environment [4,5], atmospheric temperature and nitrogen fertilizer [6] affect canopy temperature [7–9]. Second, heat transfer within tissues, such as leaf temperature, affects enzyme activity and leaf metabolism [10]. Among these environmental factors, air temperature has been the most synergistically reflected in plant body temperature, and air and plant temperatures have shown the same change rule. The difference between canopy and atmospheric temperature could produce heat convection and conduction [11]. Obviously, the magnitude of thermal convection and heat conduction is related to the temperature differences between the leaves, as well as to the thermal conductivity of the boundary layer of the heat exchange between the blade and environment.

Canopy temperature is difficult to measure directly, but can be measured indirectly by infrared thermal imaging [12,13]. In 1963, Tanner used an infrared thermometer to determine crop temperature [14]. With the development of agricultural thermal imaging technology, infrared thermal imaging system can quickly acquire the characteristics of crop temperature distribution, and can distinguish the temperature of different organs of crops through images. Therefore, infrared thermal imaging has also become the main tool for measuring plant temperature at present [15,16]. The infrared thermal imager could measure the temperature of crop organs and canopy accurately and quickly, and monitor the change of crop growth in real time, which provided an effective measurement method and technical basis in this study.

Canopy temperature is the result of the comprehensive reaction of growth environment and rice plant self-regulation. The external environment affects the growth and grain yield of rice by affecting canopy temperature [17–20]. The research on the relationship between rice canopy temperature and yield began in the 1990s. Garrity et al. reported that rice canopy temperature at flowering stage was significantly negatively correlated with rice seed setting rate and yield [21]. Melandri et al. found that canopy temperature was negatively correlated with grain yield within 2 weeks of drought stress at flowering stage. When the grain yield of rice was relatively high, the leaf temperature was relatively low. Moreover, canopy temperature was associated with significant genotypic differences and had a significant positive correlation with grain yield, which could be used as a reference index for breeding high-yield varieties. It shows that canopy temperature may be closely related to the internal metabolism of rice plants, which may directly affect the yield of plants to a large extent. In addition, it has been reported that the temperature of rice organs changes [22]. The canopy temperature of rice are not only depending on air temperature, air humidity, radiation and cultivation methods, but also influenced by the organ position, size, shape and surface area [17,23,24]. Zhang et al.'s results showed that heat stress of 40°C significantly decreased the spikelet fertility, while the photosynthesis in flag leaves had no significant effect, and the panicle temperature was about 4°C higher than flag leaves [25]. This indicated that the damage degree of rice organs varies with the change of organ temperature. Therefore, the correlation between the temperatures of different rice organs and canopy in different growth stages and the grain yield is complex. The stability and universality of these correlations must be verified.

Transplanting and direct seeding are two common rice sowing methods [26]. In transplanting, seedlings are usually raised in seedling tray for 2–3 weeks and then manually or mechanically transplanted into fields. In direct seeding, seeds can be sown directly on the soil surface under rainfed, deep water and irrigated

conditions [27]. It has been reported that direct-seeded rice can be used to maintain food security and crop resilience under adverse climatic conditions [10]. Direct-seeded rice significantly improves rice productivity and stress resistance. Compared to mechanical transplanting systems, the sowing time of the subsequent crop cycle is advanced by 15 days. The effects of direct-seeded and transplanting systems on the grain yield greatly vary in different regions and under different climatic conditions. In general, grain yields associated with single-cropping [28,29] and double-cropping [30] of transplanted rice are higher than that of direct-seeded rice. The results of previous studies also showed that, compared with traditional transplanted rice, yield loss could not be observed for direct-seeded rice [31–33]. Direct seeding can even lead to higher grain yields than transplanting [34]. Several researchers reported that the grain yield of wet direct-seeded rice is 10.8% higher than that of transplanted rice; the grain yields of dry direct-seeded rice and transplanted rice are similar [35]. Different planting measures can construct different population characteristics of rice [36], and appropriate planting measures can affect leaf area index, biomass, and regulate plant nitrogen, phosphorus, and potassium concentrations, thereby achieving higher grain yield [37].

The objectives were to (1) analyze the effects of different planting methods on canopy and organ temperatures during the whole growth period of rice, and to compare the difference between canopy temperature and organ temperature, (2) compare the relationship between canopy and organ temperatures and grain yield, (3) determine the growth factors affecting canopy and organ temperatures (such as dry matter accumulation, SPAD [soil plant analysis developme], N concentration, P concentration, K concentration, transpiration and photosynthesis).

2 Materials and Methods

2.1 Rice Materials

Experiments were carried out in the experimental field (119.42° east longitude, 32.39° north latitude) of the Agricultural College of Yangzhou University and in the artificial climate chamber of Yangzhou University in the Hanjiang District, Yangzhou City, China, in 2019, which has a subtropical monsoon climate. The late-maturing mid-japonica rice cultivar Nanjing 9108 (NJ-9108) and mid-maturing late japonica cultivar Nanjing 46 (NJ-46) bred at the Institute of Food Crops, Jiangsu Academy of Agricultural Sciences, China, were used as materials. The growth period of the two varieties differed by 15 d: the whole growth period of NJ-9108 was 150 d, while that of NJ-46 was 165 d. A potting soil culture (pot height 27 cm, inner diameter 31 cm, capacity 14 L) was utilized for the experiments. Artificial live seeding was carried out on June 15. The rice under the transplanting treatment was sown on May 28 and transplanted artificially on June 21. Three holes were inserted in each pot, and three seedlings were placed in each hole. Before transplanting, 2 g of urea and 0.5 g of potassium dihydrogen phosphate (KH_2PO_4) were applied as base fertilizer per pot. After 7 d of transplanting, 0.5 g of urea was applied to each pot. At panicle initiation, 0.6 g of urea was applied to each pot. Transplanting was performed until the effective tillering stage was reached, and the potted plants were maintained with shallow water irrigation. The potted soil used was sandy loam, and the soil's physical and chemical property indexes were 24.5 g kg^{-1} organic matter, 112.6 mg kg^{-1} total N, 58.0 mg kg^{-1} available P and 66.8 mg kg^{-1} available K. During the growth period of rice, diseases and insect pests were controlled. Bird nets were installed during the maturity period to avoid yield loss. Other management measures were uniformly implemented in accordance with conventional cultivation requirements [38,39].

2.2 Experimental Setup

We moved the rice plants that had been grown outdoors into the artificial climate room at Yangzhou University. The artificial climate room included two rooms with high and normal temperatures, each climate-controlled room contained direct-seeded and transplanted rice. The average daily temperature, high temperature, and minimum temperature for the normal temperature treatment were set with reference to the average temperature of the same day published by the Meteorological Bureau over the previous 10 years. There were 15 repetitions for each treatment and the heat stress treatment was 5°C higher than

the normal temperature setting (Table 1) [40–42]. Because the growth period of NJ-9108 and NJ-46 differed by 15 d, the time for high temperature treatment at the heading stage also differed. The temperature accuracy was $\pm 0.5^\circ\text{C}$, the constant humidity was 70%, the CO_2 concentration and illumination were consistent with those outside, and the wind speed was 0.5 m/s. The treatment time was 14 d in the initial heading stage when 10% of rice ears exhibited the sword leaf sheath. The temperature treatment time for NJ-9108 under transplantation mode was from August 23 to September 05. The temperature processing time for NJ-9108 under direct seeding mode was from August 29 to September 11; the temperature treatment time for NJ-46 under transplantation mode was from September 05 to September 18; the temperature processing time for NJ-46 under live broadcast mode was from September 11 to September 24. The plants were then moved outdoors at the end of the treatment period.

Table 1: The temperature treatment of the artificial climate chamber ($^\circ\text{C}$)

| Temperature treatment | Date (M-D) | 2:00–5:00 | 5:00–8:00 | 8:00–11:00 | 11:00–14:00 | 14:00–17:00 | 17:00–20:00 | 20:00–23:00 | 23:00–2:00 | Average temperature |
|-----------------------|-------------|-----------|-----------|------------|-------------|-------------|-------------|-------------|------------|---------------------|
| Normal temperature | 08.23~08.31 | 27.0 | 27.0 | 28.0 | 31.0 | 33.0 | 31.0 | 28.0 | 27.0 | 29.0 |
| | 09.01~09.05 | 26.0 | 26.0 | 27.0 | 30.0 | 32.0 | 30.0 | 27.0 | 26.0 | 28.0 |
| | 09.06~09.10 | 24.0 | 24.0 | 25.0 | 28.0 | 30.0 | 28.0 | 25.0 | 24.0 | 27.0 |
| | 09.11~09.16 | 23.0 | 23.0 | 24.0 | 28.0 | 30.0 | 27.0 | 25.0 | 24.0 | 25.5 |
| | 09.17~09.20 | 23.0 | 23.0 | 24.0 | 28.0 | 29.0 | 26.0 | 25.0 | 24.0 | 25.3 |
| 09.21~09.25 | 23.0 | 23.0 | 24.0 | 26.0 | 29.0 | 25.0 | 24.0 | 23.0 | 24.6 | |
| High temperature | 08.23~08.31 | 32.0 | 32.0 | 33.0 | 36.0 | 38.0 | 36.0 | 33.0 | 32.0 | 34.0 |
| | 09.01~09.05 | 31.0 | 31.0 | 32.0 | 35.0 | 37.0 | 35.0 | 32.0 | 31.0 | 33.0 |
| | 09.06~09.10 | 29.0 | 29.0 | 30.0 | 33.0 | 35.0 | 33.0 | 30.0 | 29.0 | 32.0 |
| | 09.11~09.16 | 28.0 | 28.0 | 29.0 | 33.0 | 35.0 | 32.0 | 30.0 | 29.0 | 30.5 |
| | 09.17~09.20 | 28.0 | 28.0 | 29.0 | 32.0 | 34.0 | 32.0 | 30.0 | 29.0 | 30.3 |
| 09.21~09.25 | 28.0 | 28.0 | 29.0 | 31.0 | 34.0 | 30.0 | 29.0 | 28.0 | 29.6 | |

2.3 Air Temperature and Thermal Imaging of Rice Organs

Using a FLIR E4 (FLIR Systems, USA) thermal imaging camera, thermal infrared and RGB (red, green, and blue) images were taken simultaneously. This thermal imaging camera could detect a temperature difference of $<0.15^\circ\text{C}$, with a FOL 7 mm lens, and an infrared resolution of 320×240 pixels. Moreover, the depression angle was set at 25° , and the emissivity was set to 0.95 [43]. A black cloth was used to minimize interference from other substances when recording the organ temperature. The thermal infrared image used to measure the plant and air temperature was taken at the original location. However, movement of the black cloth caused changes in the background temperature. To account for this, seven measurements were conducted at the rice tillering stage, jointing stage, booting stage, heading stage, filling stage, waxy stage, and full maturity stage. The potted plants under the high temperature and control treatments were moved outdoors during the thermal infrared measurements. The two rice varieties had different maturity dates, and temperature monitoring was performed at similar stages of plant development. The measurement in the tillering stage was performed from 8:00 to 19:00 and data were collected every 2 h. From the jointing to booting stages, the measurement was conducted from 00:00 for 24 h, and data were collected every hour. After the heading stage, the measurement was performed from 10:30 to 16:30 and data were collected every 3 h. We recorded three values from each panicle, stem, and leaf and used the averages as the final data while avoiding rainy weather during the sampling period. The rice organ temperature was analyzed using Flir® Tools software (version 6.2, FLIR Systems, Inc., USA)

[44]. The air temperature was measured using a Testo608-H1 thermal hygrometer, which was maintained at a constant height. The measurement duration was the same as that used for the infrared thermal imager.

2.4 Climatic Conditions

Daily average temperature, daily precipitation, and sunshine hour data were collected during the rice-growing season in 2019 at a weather station near Bonsai (Yangzhou, Jiangsu). The average temperature, average maximum temperature, average sunshine hour, and average precipitation were 23.6°C, 32.8°C, 5.5 h/day, and 2.9 mm/day, respectively (Fig. 1).

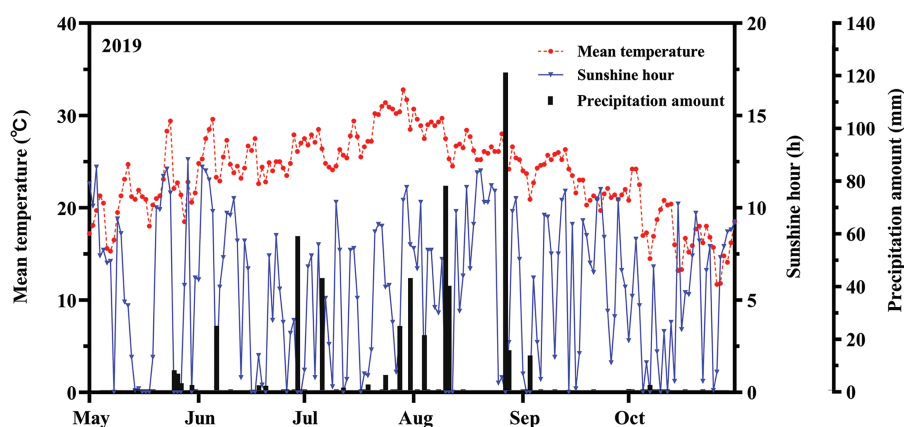


Figure 1: Diurnal variation of meteorological factors during the rice growth period in 2019. The red, blue, and black arrows represented the average temperature, sunshinehour, and precipitation, respectively

2.5 Sampling and Measurements

Three holes of rice were selected for each treatment, and the above-ground portion of rice was placed in an oven set at 105°C for 30 min and dried at 80°C to constant weight; the dry matter weight of the plants was measured.

In each treatment, ten holes of rice were selected to determine the SPAD value of the flag leaf using SPAD-502 chlorophyll meter produced by Minolta, Japan.

The plant samples, after grinding and drying, were boiled with $H_2SO_4-H_2O_2$. After distillation, the N, P, and K concentrations were determined. The total N concentration was determined with the micro-Kjedahl method; P was quantified by the vanadium–molybdenum yellow colorimetric method; K concentration was determined with a flame photometer.

The net photosynthetic rate, stomatal conductance, intercellular CO_2 concentration and transpiration rate were measured using an LI-6400 portable photosynthetic meter (LI-COR Inc. Lincoln, NE, USA). Sunny weather was selected for determination, during which the original state of the flag leaf was selected as far as possible, including position and angle. Each treatment was repeated for six leaves, and each leaf was measured ten times to obtain the average value.

During the maturity stage, three replicate values were measured for each treatment, and each replicate value contained three holes of rice using three holes from multiple pots. After natural air-drying, yield traits were measured including the number of spikelets, grains per panicle, 1000-grain weight, seed setting rate, and theoretical yield.

2.6 Data Analysis

Data were processed using Microsoft Excel 2010; GraphPad Prism 8 was employed for plotting, and ANOVA was performed using SPSS16.0. We had 2 cultivars \times 2 planting methods \times 7 growth periods \times 4 organs (leaf, spike, stem, canopy) per plant. We used a ONE-WAY analysis of variance to open the two-way significant interactions. The differences between treatments and varieties were compared using Tukey's least significant difference (LSD) at the 5% probability level. We used ONE-WAY ANOVA when we compared (1) organ temperature with atmospheric temperature, (2) yield and its components, and (3) biological characteristics.

3 Results

3.1 Effects of Two Planting Methods on the Organ Temperature from the Tillering to Grain-Filling Stages of Rice

The rice crop was found to have an intrinsic temperature. The temperature difference between the rice and surrounding environment was strongly pronounced in the thermal infrared image. Meanwhile, rice plants from the same cultivar and under the same treatment had almost the same crop temperature. Therefore, the canopy temperature of rice under the same treatment and variety was generally consistent (Fig. 2A). The canopy temperatures of "NJ-46" and "NJ-9108" showed a synergistic trend with the air temperature (Fig. 2B). Compared to the air temperature, the change in canopy temperature was relatively small. The canopy temperature was significantly lower than the air temperature during the day (11:00 to 17:00) and significantly higher than the air temperature at night (01:00 to 05:00). The ambient temperature changes in the jointing and booting stages were 28.30°C–37.00°C and 25.30°C–35.30°C, respectively. The canopy temperature changes were 30.23°C–35.67°C and 27.43°C–33.87°C, respectively (Fig. 2B). The order of the CV of the air and canopy temperatures was air temperature > transplanted rice, direct-seeded rice. At 13:00, the air and canopy temperatures reached the maxima. The best time to measure the canopy temperature was found to be 1 pm.

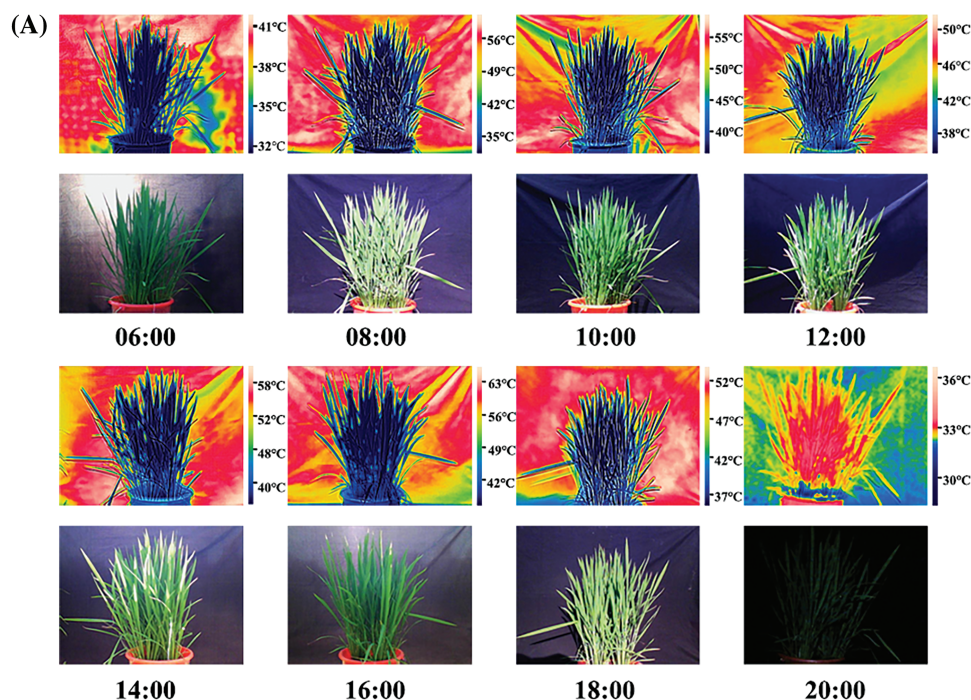


Figure 2: (Continued)

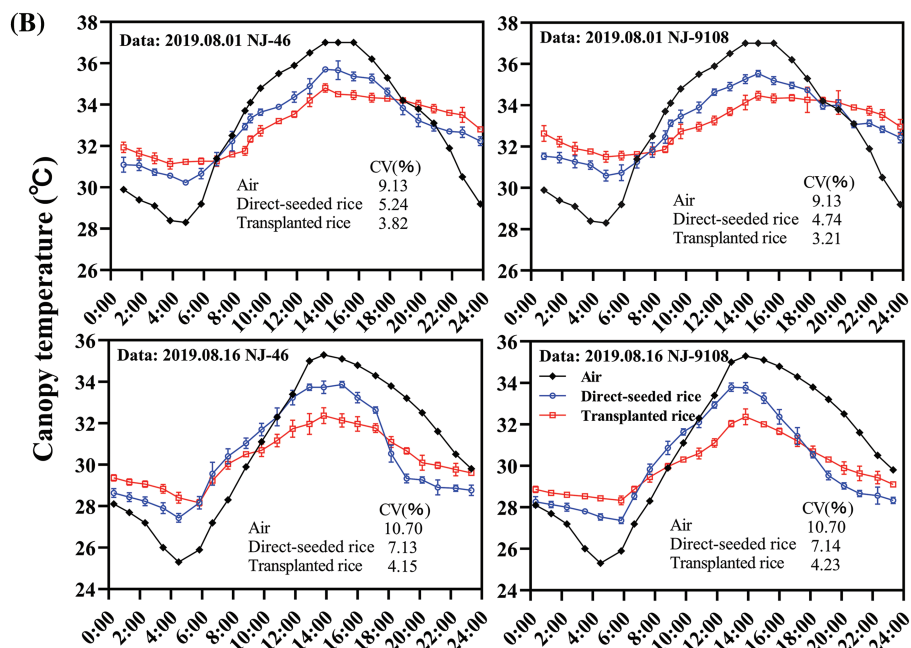


Figure 2: Diurnal variation in the rice canopy temperature. (A) Temperature change in rice variety “NJ-19108” throughout the day under transplanting mode (Date: 08/11/2019). The scale on the right of the thermal infrared image showed the environment temperature range and that of the plant. (B) Diurnal variations in the canopy temperatures of “NJ-46” and “NJ-9108” measured at ambient temperature, where CV represented the coefficient of variation (%)

In the seven key growth stages, the canopy temperature trends of the two varieties under different planting methods were consistent (Fig. 3). When the air temperature increased, the canopy temperature of “NJ-46” and “NJ-9108” also increased. When the air temperature decreased, the canopy temperature of “NJ-46” and “NJ-9108” also decreased. The coefficient of variation of air temperature was significantly higher than that of canopy temperature of direct-seeded and transplanted rice ($p < 0.05$). The variation trend of canopy temperature was similar to that of air temperature, and the coefficient of variation of air temperature was significantly greater than that of direct-seeded and transplanted rice during one day or seven key growth stages ($p < 0.05$). This indicated that canopy temperature was affected by air temperature.

In this experiment, the organ and canopy temperature was measured in the seven main rice growth periods. The analysis of variance (Tables 2 and 3) showed that the effects of atmospheric temperature and treatment on the temperature of rice organs and canopy were significant ($p > 0.05$). Different rice varieties had no significant effect on the temperature of canopy and organs ($p > 0.05$), but the temperature difference between different organs and canopy reached a significant level ($p < 0.05$). The interaction of atmospheric temperature, treatment, variety and different organs were observed to have a significant effect on the temperature of rice ($p < 0.05$).

In the interaction effect of air temperature \times organ, the effect caused by air temperature ($p < 0.05$) was higher than that caused by organ ($p < 0.05$). In the interaction effect of air temperature \times treatment, the effect caused by air temperature ($p < 0.05$) was higher than that caused by treatment ($p > 0.05$). Among the interaction effects of organ \times variety, the effect caused by organ ($p < 0.05$) was higher than that caused by variety ($p > 0.05$). Among the interaction effects of organ \times treatment, the effect caused by organ

($p < 0.05$) was higher than that caused by treatment ($p > 0.05$). Among the interaction effects of variety \times treatment, the effect caused by treatment ($p > 0.05$) was higher than that by variety ($p > 0.05$) (Table 2). In the interaction effect of air temperature \times organ, the effect caused by air temperature ($p < 0.05$) was higher than that caused by organ ($p > 0.05$). In the interaction effect of air temperature \times treatment, the effect caused by air temperature ($p < 0.05$) was higher than that caused by treatment ($p < 0.05$). Among the interaction effects of organ \times variety, the effect caused by organ ($p > 0.05$) was higher than that caused by variety ($p > 0.05$). Among the interaction effects of organ \times treatment, the effect caused by treatment ($p < 0.05$) was higher than that caused by organ ($p > 0.05$). Among the interaction effects of variety \times treatment, the effect caused by treatment ($p < 0.05$) was higher than that caused by variety ($p > 0.05$) (Table 3).

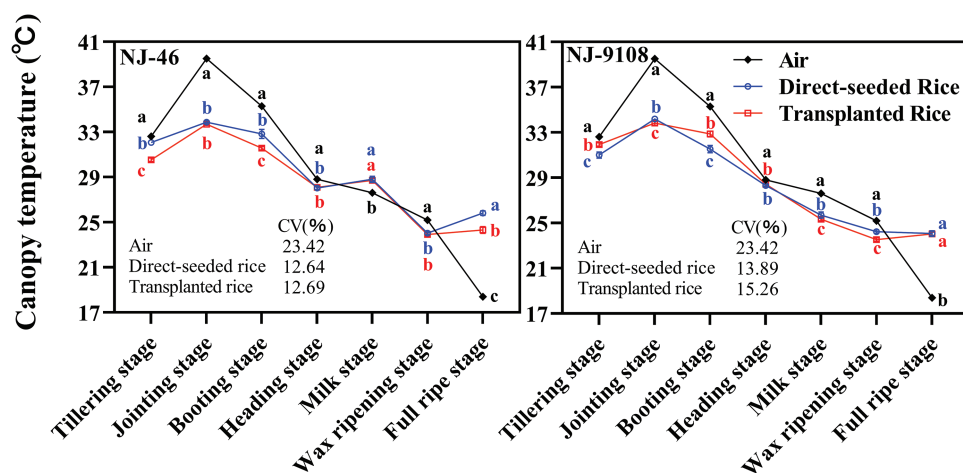


Figure 3: Based on the changes of air and canopy temperatures from tillering stage to full ripe stage of rice under two planting methods. Changes in the canopy temperature (13:00) of “NJ-46” and “NJ-9108” under natural conditions. Different lowercase letters close to each symbol compare canopy temperatures within each phenological stage. Each symbol is the mean of $n = 3$

Table 2: Variance analysis (F value) of organ temperature from tillering to heading stages among air temperatures, varieties, organs, and treatments

| Source of variation | df | MS | F |
|------------------------------------|----|---------|------------|
| Air temperature | 3 | 287.307 | 3822.632** |
| Organ | 2 | 63.965 | 851.059** |
| Variety | 1 | 0.002 | 0.033 |
| Treatment | 1 | 24.174 | 321.630** |
| Air temperature \times organ | 6 | 4.413 | 58.721** |
| Air temperature \times variety | 3 | 0.011 | 0.152 |
| Air temperature \times treatment | 3 | 0.296 | 3.936* |
| Organ \times variety | 2 | 0.394 | 5.247** |
| Organ \times treatment | 2 | 6.276 | 83.507** |
| Variety \times treatment | 1 | 0.588 | 7.820** |

(Continued)

| Table 2 (continued) | | | |
|---|----|-------|----------|
| Source of variation | df | MS | F |
| Air temperature × organ × variety | 6 | 0.203 | 2.701* |
| Air temperature × organ × treatment | 6 | 0.211 | 2.808* |
| Air temperature × variety × treatment | 3 | 0.574 | 7.638** |
| Organ × variety × treatment | 2 | 2.176 | 28.956** |
| Air temperature × organ × variety × treatment | 6 | 0.692 | 9.204** |

Note: * $p < 0.05$; ** $p < 0.01$.

Table 3: Analysis of variance (F value) of organ temperature at grain-filling stage among air temperatures, varieties, organs, and treatments

| Source of variation | df | MS | F |
|---|----|---------|------------|
| Air temperature | 2 | 653.503 | 9348.169** |
| Organ | 3 | 13.022 | 186.274** |
| Variety | 1 | 0.066 | 0.949 |
| Treatment | 3 | 25.188 | 360.300** |
| Air temperature × organ | 6 | 4.748 | 67.924** |
| Air temperature × variety | 2 | 0.002 | 0.035 |
| Air temperature × treatment | 6 | 40.185 | 574.828** |
| Organ × variety | 3 | 6.196 | 88.634** |
| Organ × treatment | 9 | 0.858 | 12.274** |
| Variety × treatment | 3 | 3.717 | 53.164** |
| Air temperature × organ × variety | 6 | 3.208 | 45.894** |
| Air temperature × organ × treatment | 18 | 0.483 | 6.904** |
| Air temperature × variety × treatment | 6 | 0.991 | 14.181** |
| Organ × variety × treatment | 9 | 0.209 | 2.983** |
| Air temperature × organ × variety × treatment | 18 | 0.349 | 4.993** |

Note: * $p < 0.05$; ** $p < 0.01$.

Because air temperature had a significant effect on organ and canopy temperatures, we used ΔT_1 , ΔT_s , ΔT_p , and ΔT_c to reduce the influence of air temperature factors. The effects of the direct-seeded and transplanting methods on the organ–air temperature differences varied in different growth stages. Under ambient temperature conditions, the ΔT_1 of direct-seeded rice was significantly higher than that of transplanted rice during the seven key growth periods ($p < 0.05$). The ΔT_s of direct-seeded rice was higher than that of transplanted rice during the seven key growth periods, and the difference reached a significant level from the tillering stage to the milking stage ($p < 0.05$). The ΔT_p of direct-seeded rice was significantly higher than that of transplanted rice during milk to wax ripening ($p < 0.05$). During the period from milk to wax ripening, the ΔT_c of direct-seeded rice was higher than that of transplanting rice, but the difference was not significant (Figs. 4A–4D) ($p > 0.05$). In the same growth period, the ΔT_1 , ΔT_s , ΔT_p , and ΔT_c of direct-seeded rice were smaller following high temperature treatment of “NJ-46” and “NJ-9108” than that of transplanted rice, with the difference reaching a significant level ($p < 0.05$).

(Figs. 4E and 4F). After treatment at ambient temperature, the organ–air temperature differences of the direct-seeded rice were larger than that of transplanted rice, as shown in the Fig. 5, the ΔT_i , ΔT_p , and ΔT_s increased by 0.57°C – 1.63°C ($p < 0.05$), 0.03°C – 1.23°C , and 0.03°C – 1.67°C , respectively.

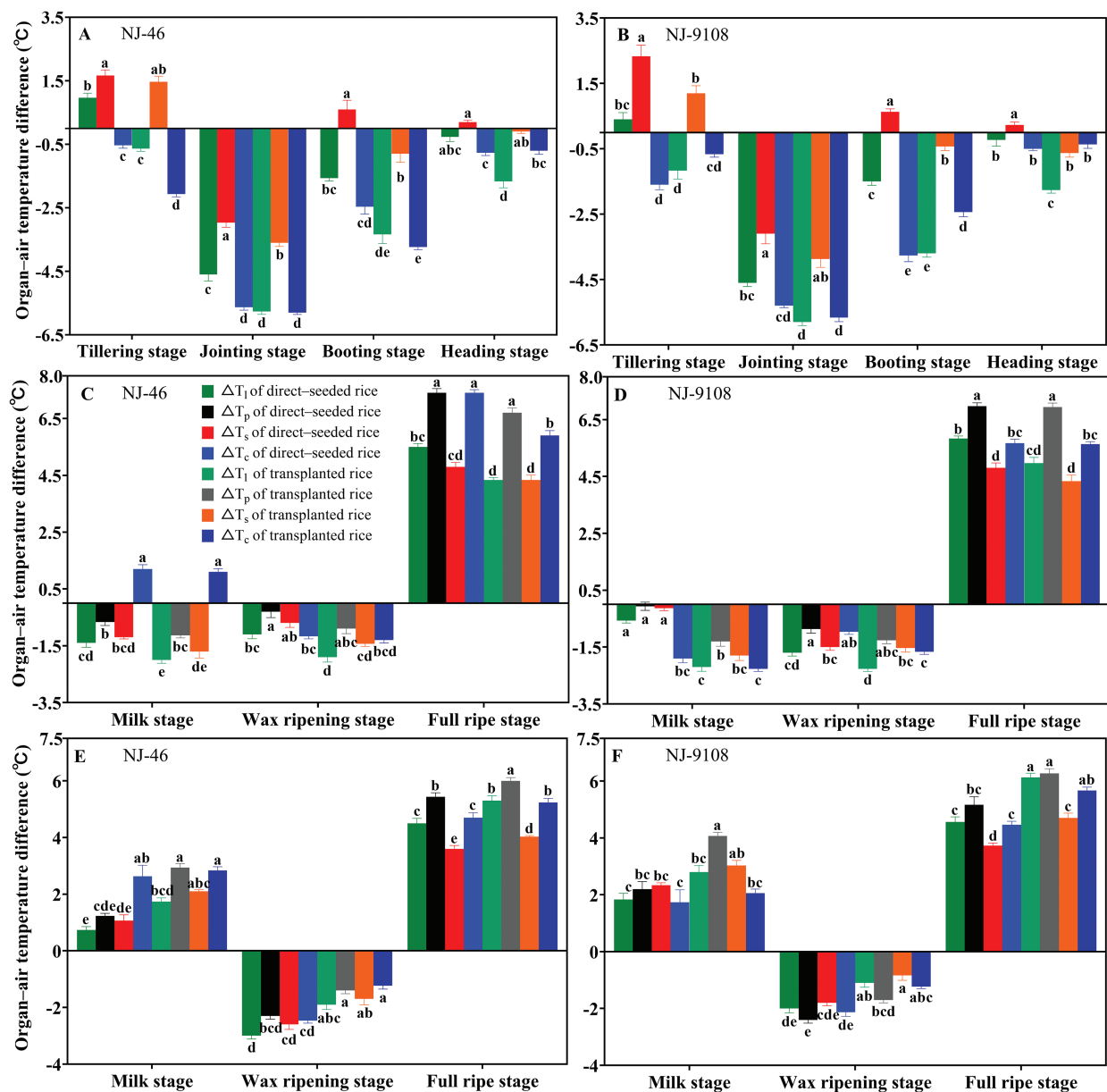


Figure 4: Based on the changes of organ–air temperature differences from the tillering stage to the full ripe stage of rice under two planting methods. Changes in the organ–air temperature differences (1 pm) of “NJ-46” and “NJ-9108” under natural conditions (A, B, C, D) and under high temperature conditions (E, F). Different letters indicated significant differences among treatments within each phenological stage for the same variety ($p < 0.05$)

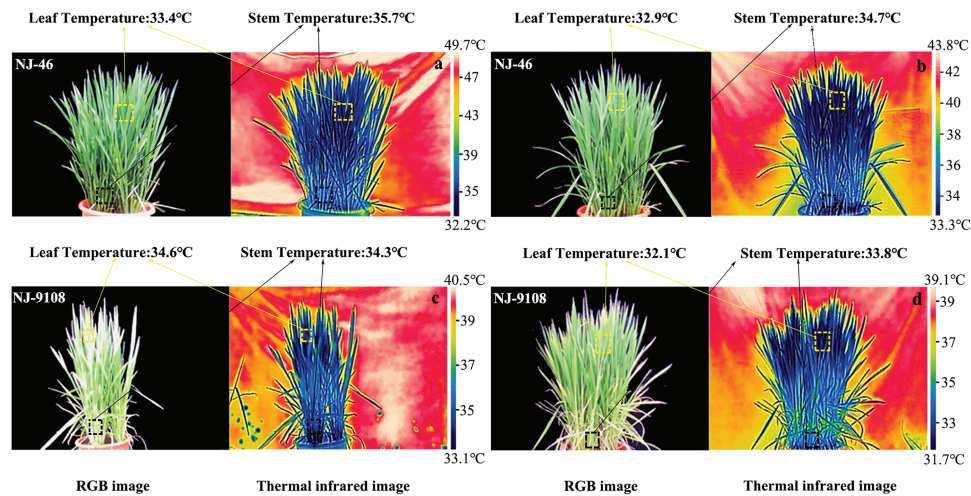


Figure 5: Thermal infrared images of rice based on two planting methods. The thermal and visible images were captured under natural sunlight at 00:30–13:30 in the booting stage. (a, c) Direct-seeded rice and (b, d) Transplanted rice

3.2 Correlation between Organ Temperature Differences and Rice Yield

Under the same planting method, the yields of “NJ-46” and “NJ-9108” decreased under heat stress (Table 4). After the treatment at ambient temperature, the theoretical and actual yields of “NJ-46” under the transplanting mode significantly increased by 20.01% and 16.03% compared with that based on the direct-seeded mode. The theoretical and actual yields of “NJ-9108” significantly increased by 25.02% and 19.33%, respectively. However, after heat stress, the theoretical yield of transplanted rice “NJ-46” and “NJ-9108” significantly decreased by 55.55% and 46.61%, and the actual yield decreased by 29.45% and 33.24%, respectively compared with direct-seeded rice.

Table 4: Effects of the two planting methods on grain yield and components after heat stress

| Variety | Treatment | No. of panicles/hole | Spikelet number per panicle | 1000-grain weight (g) | Filled grain percentage (%) | Theoretical yield (g)/hole | Actual yield (g)/hole |
|---------|----------------------------------|----------------------|-----------------------------|-----------------------|-----------------------------|----------------------------|-----------------------|
| NJ-46 | High temperature Direct seeded | 13.17ab | 127.55a | 21.60d | 0.71c | 25.76d | 26.38c |
| | High temperature Transplanted | 12.50abc | 117.37a | 25.12bc | 0.33e | 11.45f | 18.61e |
| | Normal temperature Direct seeded | 12.50abc | 124.14a | 27.02a | 0.88a | 36.14b | 30.69b |
| | Normal temperature Transplanted | 14.16a | 125.24a | 27.10a | 0.92a | 43.37a | 37.16a |
| NJ-9108 | High temperature Direct seeded | 11.33cd | 113.73a | 18.58e | 0.67d | 16.07e | 15.01f |
| | High temperature Transplanted | 11.33cd | 111.05a | 24.79c | 0.26f | 8.58f | 10.02g |
| | Normal temperature Direct seeded | 10.34d | 113.59a | 26.40ab | 0.83b | 26.06d | 22.96d |
| | Normal temperature Transplanted | 12.33bc | 113.19a | 26.11abc | 0.89a | 32.58c | 29.01bc |

After treatment at ambient temperature, there was no significant difference in seed setting rates between “NJ-46” and “NJ-9108” transplanted and direct-seeded rice ($p > 0.05$). After heat stress, the seed setting rate of transplanted rice was 53.52% and 61.19% significantly lower than that of direct-seeded rice, respectively ($p < 0.05$). After treatment at ambient temperature, the 1000-grain weight between transplanted and direct-seeded rice in “NJ-46” and “NJ-9108” insignificantly differed ($p > 0.05$). After heat stress, the 1000-grain weight of transplanted rice was 16.30% and 33.42% significantly higher than that of direct-seeded rice, respectively ($p < 0.05$). High temperature stress led to a significantly lower seed setting rate and 1000-grain weight of transplanted rice than direct-seeded rice ($p < 0.05$).

Analysis of variance (Table 5) showed that variety \times temperature treatment had significant effects on theoretical yield and actual yield ($p < 0.05$). In the interaction effect of variety \times temperature treatment, the effect caused by temperature treatment ($p < 0.05$) was higher than that caused by variety ($p < 0.05$). The variety \times planting method had significant effects on theoretical yield ($p < 0.05$). The effect of variety on theoretical yield was higher than that of planting method ($p < 0.01$). The temperature treatment \times planting method had significant effects on no. of panicles, 1000-grain weight, filled grain percentage, theoretical yield and actual yield ($p < 0.01$). The effect of planting method on no. of panicles was higher than that of temperature treatment ($p < 0.01$), and the effect of temperature treatment on 1000-grain weight, filled grain percentage, theoretical yield and actual yield was higher than that of planting method ($p < 0.01$).

Table 5: Variance analysis (F value) of grain yield and components among varieties, temperature treatments and planting methods

| Coefficient of variation | No. of panicles/hole | Spikelet number per panicle | 1000-grain weight (g) | Filled grain percentage (%) | Theoretical yield (g)/hole | Actual yield (g)/hole |
|--|----------------------|-----------------------------|-----------------------|-----------------------------|----------------------------|-----------------------|
| Variety | 6.901 | 7.802 | 9.687 | 110.149** | 561.703** | 738.034** |
| Temperature treatment | 1.345 | 0.635 | 550.972** | 7682.379** | 2924.034** | 1425.743** |
| Planting method | 12.024* | 2.250 | 182.832** | 1554.563** | 32.601** | 0.033 |
| Variety \times temperature treatment | 1.318 | 0.091 | 5.997 | 2.011 | 34.740** | 9.570* |
| Variety \times planting method | 1.345 | 0.546 | 10.800 | 0.080 | 18.727** | 3.202 |
| Temperature treatment \times planting method | 25.099** | 2.803 | 199.311** | 2578.011** | 634.835** | 367.107** |

Note: * $p < 0.05$; ** $p < 0.01$.

In the seven main growth stages, a significant negative correlation was observed between ΔT_1 and actual yield ($p < 0.05$), ΔT_s was significantly negatively correlated with seed setting rate ($p < 0.05$), theoretical and actual yields, ΔT_s and ΔT_p were less correlated with seed setting rate, theoretical and actual yields ($p > 0.05$). A significant negative correlation was observed between ΔT_1 , ΔT_s , ΔT_p , ΔT_c and 1000-grain weight, seed setting rate, theoretical and actual yields, respectively, at milk ripening stage ($p < 0.05$). Therefore, the milk stage was found to be the best stage to observe the rice organ and canopy temperatures, where the correlation coefficient between organ and canopy temperatures, yield and its components was found to be the highest (Table 6).

Table 6: Correlation between the organ–air temperature difference and grain yield and components in rice

| Organ–air temperature difference | No. of panicles/hole | Spikelet number per panicle | 1000-grain weight (g) | Filled grain percentage (%) | Theoretical yield (g)/hole | Actual yield (g)/hole |
|----------------------------------|----------------------|-----------------------------|-----------------------|-----------------------------|----------------------------|-----------------------|
| Tillering stage ΔT_1 | -0.802* | -0.276 | -0.212 | -0.848* | -0.748* | -0.771* |
| Jointing stage ΔT_1 | -0.742* | -0.200 | -0.080 | -0.829* | -0.675 | -0.722* |
| Booting stage ΔT_1 | -0.713* | -0.147 | -0.039 | -0.802* | -0.650 | -0.711* |
| Heading stage ΔT_1 | -0.808* | -0.336 | -0.182 | -0.875* | -0.750* | -0.771* |
| Filling stage ΔT_1 | -0.374 | -0.332 | -0.569* | -0.918* | -0.956* | -0.904* |
| Wax ripening stage ΔT_1 | -0.321 | -0.335 | -0.873* | -0.399 | -0.609* | -0.615* |
| Full ripe stage ΔT_1 | -0.331 | -0.341 | -0.64* | -0.884* | -0.927* | -0.870* |
| Tillering stage ΔT_s | -0.970* | -0.551 | -0.580 | -0.968* | -0.901* | -0.836* |
| Jointing stage ΔT_s | -0.910* | -0.444 | -0.377 | -0.962* | -0.867* | -0.864* |
| Booting stage ΔT_s | -0.797* | -0.250 | -0.181 | -0.871* | -0.742* | -0.784* |
| Heading stage ΔT_s | -0.834* | -0.407 | -0.364 | -0.848* | -0.837* | -0.867* |
| Filling stage ΔT_s | -0.392 | -0.338 | -0.608* | -0.898* | -0.957* | -0.914* |
| Wax ripening stage ΔT_s | -0.240 | -0.489 | -0.630* | -0.673* | -0.731* | -0.705* |
| Full ripe stage ΔT_s | -0.160 | -0.356 | -0.770* | -0.524* | -0.632* | -0.627* |
| Filling stage ΔT_p | -0.314 | -0.339 | -0.455 | -0.969* | -0.948* | -0.882* |
| Wax ripening stage ΔT_p | 0.026 | -0.189 | -0.843* | -0.384 | -0.489 | -0.448 |
| Full ripe stage ΔT_p | -0.003 | -0.232 | -0.822* | -0.491 | -0.573* | -0.517* |
| Tillering stage ΔT_c | -0.143 | -0.070 | -0.198 | 0.003 | -0.200 | -0.199 |
| Jointing stage ΔT_c | -0.104 | 0.438 | 0.596 | -0.313 | -0.100 | -0.332 |
| Booting stage ΔT_c | -0.241 | -0.545 | -0.514 | 0.004 | -0.409 | -0.299 |
| Heading stage ΔT_c | 0.502 | 0.272 | 0.325 | 0.370 | 0.664 | 0.705 |
| Filling stage ΔT_c | -0.545* | -0.041 | -0.684* | -0.618* | -0.836* | -0.834* |
| Wax ripening stage ΔT_c | -0.134 | -0.104 | 0.853 | -0.067 | 0.088 | 0.077 |
| Full ripe stage ΔT_c | 0.021 | 0.037 | 0.772 | 0.365 | 0.465 | 0.358 |

Note: * $p < 0.05$

Among them, the correlation coefficient between ΔT_s and theoretical and actual yields were the highest, the relationship between theoretical yield (Y) and ΔT_s (X) was $Y = -5.6965X + 27.778$, $R^2 = 0.9155$, the relationship between actual yield (Y) and ΔT_s (X) was $Y = -3.935X + 25.647$, $R^2 = 0.8357$, both of them showed a significant negative correlation (Fig. 6). The correlation coefficient between ΔT_c and theoretical and actual yields was the lowest ($R^2 = 0.6986$ and 0.6963 , respectively).

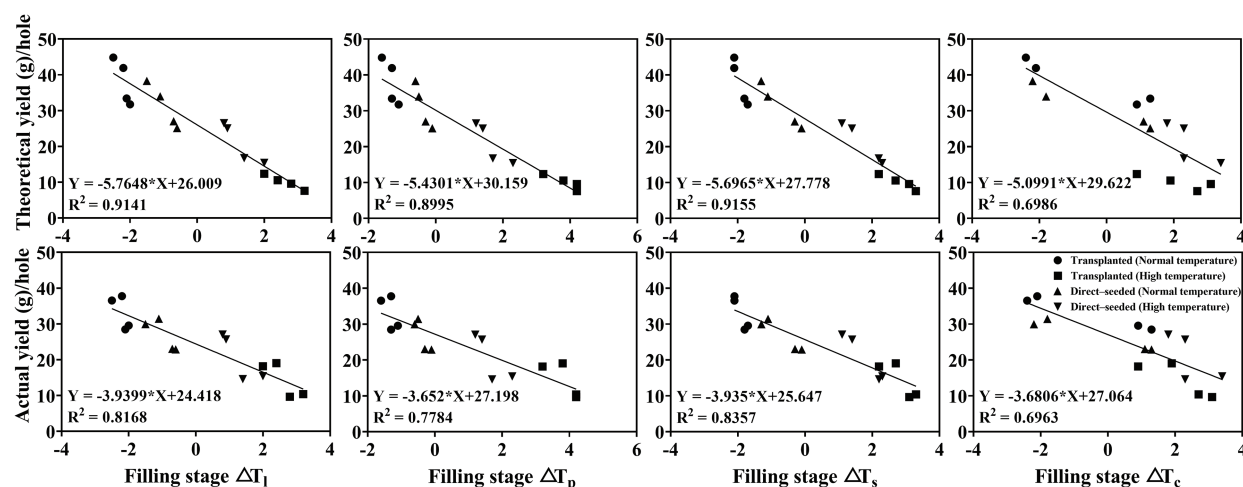


Figure 6: Correlation between yield, its constituent factors and rice organ–air temperature differences at the milk stage

3.3 Correlation between the Organ Temperature and Biological Characters in Rice during the Milk Stage

Under different planting methods, there were significant differences in the above–ground dry matter weight, N concentration, K concentration, SPAD, P_n, G_s, C_i and T_r of rice during milk stage ($p < 0.05$). Different planting methods had no significant effect on P concentration ($p > 0.05$) (Table 7).

Table 7: Effects of different planting methods on biological characteristics during milk stage after heat stress. P_n, G_s, C_i and T_r represented the net photosynthetic rate, stomatal conductance, intercellular CO₂ concentration, transpiration rate, respectively

| Variety | Treatment | Biomass weight (g)/hole | N concentration (mg/g) | P concentration (mg/g) | K concentration (mg/g) | SPAD | P _n (μmol CO ₂ m ⁻² s ⁻¹) | G _s (mol H ₂ O m ⁻² s ⁻¹) | C _i (μmol CO ₂ mol ⁻¹) | T _r (mmol H ₂ O m ⁻² s ⁻¹) |
|---------|----------------------------------|-------------------------|------------------------|------------------------|------------------------|---------|--|--|--|---|
| NJ-46 | High temperature Direct seeded | 50.20cd | 8.25abc | 3.64a | 11.32d | 47.25a | 15.92de | 0.27bcd | 314.89c | 3.31d |
| | High temperature Transplanted | 44.87cd | 8.10abc | 3.72a | 11.91cd | 46.95a | 17.52ab | 0.25cd | 293.37e | 2.56e |
| | Normal temperature Direct seeded | 54.46abc | 8.31abc | 3.76a | 12.12cd | 40.50cd | 16.59cd | 0.32a | 332.71b | 4.18a |
| | Normal temperature Transplanted | 63.06a | 7.69bcd | 3.82a | 12.56bc | 44.70b | 18.22a | 0.30ab | 315.45c | 3.73c |
| NJ-9108 | High temperature Direct seeded | 43.48cd | 8.50ab | 3.43a | 13.30ab | 46.35ab | 16.68cd | 0.24d | 304.72d | 3.54cd |
| | Normal temperature Transplanted | 40.18d | 8.81a | 3.29a | 12.78bc | 44.50b | 15.32e | 0.25cd | 333.77b | 2.63e |
| | Normal temperature Direct seeded | 51.45bc | 7.50cd | 3.38a | 14.41a | 40.95c | 17.01bc | 0.30ab | 327.49b | 4.14ab |
| | Transplanted | 61.71ab | 6.90d | 3.25a | 13.63ab | 38.55d | 16.56cd | 0.29abc | 342.48a | 3.76bc |

Among the biological indicators of rice, ΔT_i , ΔT_s , ΔT_p and ΔT_c were significantly negatively correlated with above–ground dry matter weight ($p < 0.05$). The coefficient of ΔT_s was the largest, which was -0.931 , and the coefficient of ΔT_c was the smallest, which was -0.668 . ΔT_i , ΔT_s , ΔT_p and ΔT_c were positively correlated with N concentration and SPAD, respectively. The correlation coefficient of ΔT_s reached the

highest (0.714 and 0.699), respectively, and the correlation coefficient of ΔT_c reached the lowest (0.299 and 0.512), respectively. The correlation coefficients between organ and canopy temperature and P and K concentration were not found to be significant ($p > 0.05$). In addition, SPAD and N concentration were significantly positively correlated ($p < 0.05$). ΔT_s could better reflect the growth characteristics of rice than ΔT_c (Fig. 7).

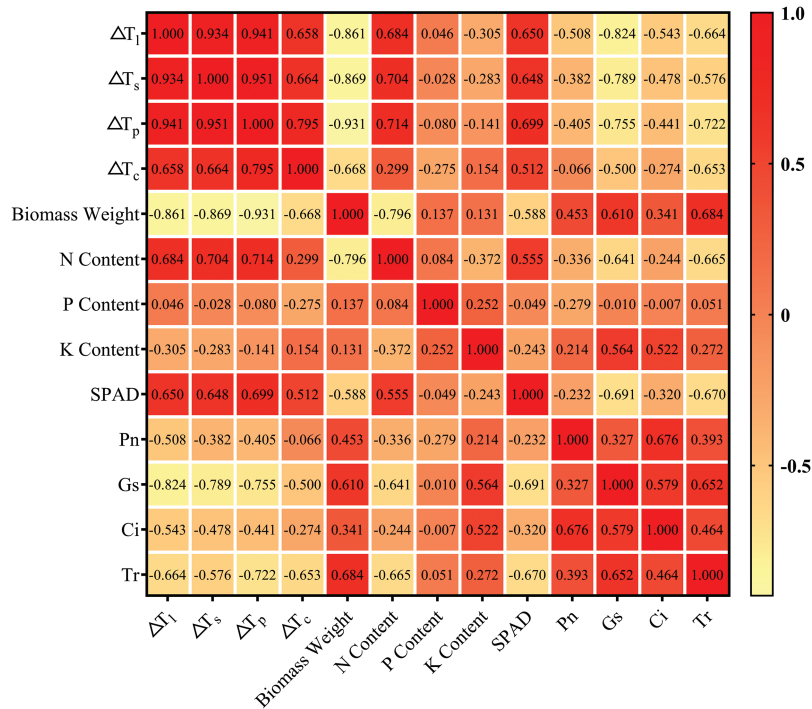


Figure 7: Correlation heat map between biological characters and rice organ-air temperature differences during the milk stage

Analysis of variance (Table 8) showed that variety \times temperature treatment had significant effects on N concentration and C_i ($p < 0.05$). In the interaction effect of variety \times temperature treatment, the effect caused by temperature treatment ($p < 0.05$) was higher than that caused by variety ($p < 0.05$). The variety \times planting method had significant effects on K concentration, P_n and C_i ($p < 0.01$). The effect of variety on K concentration, P_n and C_i was higher than that of planting method ($p < 0.01$). The temperature treatment \times planting method had significant effects on biomass weight, N concentration, SPAD, P_n , C_i and T_r ($p < 0.05$). The effect of temperature treatment on biomass weight, N concentration, SPAD, P_n , C_i and T_r was higher than that of planting method ($p < 0.05$).

Table 8: Variance analysis (F value) of biological characteristics during milk stage among varieties, temperature treatments and planting methods

| Coefficient of variation | Biomass weight (g)/hole | N concentration (mg/g) | P concentration (mg/g) | K concentration (mg/g) | SPAD | P_n ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) | G_s ($\text{mol H}_2\text{O m}^{-2} \text{ s}^{-1}$) | C_i ($\mu\text{mol CO}_2 \text{ mol}^{-1}$) | T_r ($\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$) |
|--------------------------|-------------------------|------------------------|------------------------|------------------------|-----------|--|--|---|---|
| Variety | 5.597 | 2.483 | 30.279** | 120.864** | 6.842 | 48.591** | 5.631 | 246.621** | 2.187 |
| Temperature treatment | 93.252** | 66.086** | 0.159 | 36.776** | 428.984** | 58.659** | 106.009** | 464.145** | 371.541** |
| Planting method | 3.612 | 7.030* | 0.220 | 0.247 | 0.127 | 13.819** | 5.108 | 2.515 | 162.519** |

(Continued)

Table 8 (continued)

| Coefficient of variation | Biomass weight (g)/hole | N concentration (mg/g) | P concentration (mg/g) | K concentration (mg/g) | SPAD | P _n (μmol CO ₂ m ⁻² s ⁻¹) | G _s (mol H ₂ O m ⁻² s ⁻¹) | C _i (μmol CO ₂ mol ⁻¹) | T _r (mmol H ₂ O m ⁻² s ⁻¹) |
|---|-------------------------|------------------------|------------------------|------------------------|----------|--|--|--|---|
| Variety × temperature treatment | 1.715 | 40.684** | 1.121 | 0.818 | 4.721 | 0.256 | 0.063 | 6.465* | 2.340 |
| Variety × planting method | 0.472 | 1.442 | 2.076 | 17.070** | 9.806 | 172.483** | 1.577 | 624.529** | 0.166 |
| Temperature treatment × planting method | 26.097** | 11.915* | 0.003 | 0.529 | 16.162** | 5.928* | 0.568 | 8.757* | 17.913** |

Note: * $p < 0.05$; ** $p < 0.01$.

Among the physiological indexes, P_n, G_s, C_i and T_r were negatively correlated with organ and canopy temperatures ($p < 0.05$), and ΔT_1 showed the highest correlation coefficient with P_n, G_s and C_i ($p < 0.05$), which were -0.508 , -0.824 and -0.543 , respectively. The correlation coefficient between ΔT_s and T_r was the highest, which was -0.722 . The correlation coefficients between ΔT_c and P_n, G_s, C_i and T_r were the lowest, which were -0.066 , -0.500 , -0.274 and -0.653 , respectively. In addition, the correlation coefficients of ΔT_1 and ΔT_s , ΔT_p and ΔT_c were 0.934, 0.941 and 0.658, respectively, showing significant positive correlation ($p < 0.05$) (Fig. 7). Compared with ΔT_c , ΔT_1 and ΔT_s could reflect the physiological characteristics of rice better.

4 Discussion

4.1 Effects of Different Planting Methods on Rice Organ and Canopy Temperature

The results of continuous 24 h thermal infrared monitoring showed that the canopy temperature differences was the most significant at 13:00, which was the best observation time. The environment of rice, such as temperature, light, water and wind speed, has affected its surface temperature [17]. Several researchers reported diurnal variations of the canopy and ambient temperatures of rice variety NJ-9108 under sunny conditions, the canopy temperature of rice variety NJ-9108 was lower and higher than the ambient temperature in the daytime and at night, respectively [44]. Zheng et al. continuously observed the diurnal variation of the canopy temperature and reported that the canopy temperature of rice was close to the maximum at 1 pm and thus the time period from 11 am to 3 pm was ideal for the identification of a potential water deficit of rice with the thermal imager [18]. Gao et al. suggested that the best period to analyze the effect of water stress on rice based on the canopy temperature was 1–3 pm [45]. The results of this study were similar to those of previous studies. At the highest temperature time of the day, the light intensity and air temperature were high. At this time, the physiological and biochemical reactions of the rice population were strong [46].

Rice canopy and organ temperatures is not only determined by ambient factors, but is also reflected by its own characteristic. Researchers have found differences in the temperature of different organs of rice, Fu et al. showed that the temperatures of superior rice spikelets were significantly higher than those of inferior ones regardless of the natural conditions or heat stress [23]. Zhang et al. applied moderate heat stress to N22 and GT937 at 40°C; the panicle temperature was 38°C and the flag leaf temperature was ~34°C [25]. We excluded the effect of the atmospheric temperature on the temperature of the rice organs and obtained the following conclusions. Under the same planting method, there were significant temperature differences between the rice canopy and various organs, and different planting methods could affect the growth of rice and cause changes in the temperature of the rice canopy and organs.

4.2 Correlation between the Rice Canopy and Organ Temperatures and Grain Yield

The Pearson correlation coefficients between the ΔT_1 , ΔT_s , ΔT_p , and ΔT_c , and the seed setting rate, theoretical yield, and actual yield were the highest during the milk stage. The seed setting rate, theoretical yield, and actual yield significantly increased with a decrease in the organ–air temperature differences during the milk stage. The correlations between ΔT_s and 1000-grain weight, theoretical yield, and actual yield were higher than ΔT_1 , ΔT_p and ΔT_c . Compared with ΔT_c and ΔT_s could be used as a more convenient and accurate index to reflect rice growth and predict rice yield. Several researchers also reported that an elevated canopy temperature has adverse effects on the grain yield. For example, Fu et al. subjected two rice plants to different heat tolerances to heat stress at 40°C at anthesis. The results showed that the fertility and kernel weight of superior and inferior spikelets decreased as the number of panicles per plant decreased under heat stress, accompanied by significantly increasing canopy temperatures [23]. Yan et al. conducted water stress treatments for seven days after the heading stage of rice. Under severe water stress, the canopy temperature of rice significantly increased, whereas the 1000-grain weight, seed setting rate, and yield decreased [22]. Based on the results of the above–mentioned studies and the data obtained in this study, the grain yield decreased with the increasing canopy and organ temperatures. However, the influence of different planting methods on the canopy and organs of rice was comprehensive, and it was necessary to further isolate the main factors affecting the temperature difference of rice stems.

4.3 Effect of Rice Biological Characteristics on Organ and Canopy Temperature

Rice canopy and organ temperatures are closely related to plant morphological structure, physiological and metabolic characteristics and organ structural characteristics [1,47]. Therefore, we further studied the external characters such as above-ground dry matter accumulation, SPAD, N, K and P concentrations, and the internal mechanism of photosynthesis and transpiration of flag leaves during milk stage. In this study, it was found that canopy and organ temperatures were significantly negatively correlated with dry matter accumulation, and canopy and organ temperatures were positively correlated with SPAD and N concentration, respectively. The correlation between ΔT_s and dry matter accumulation, SPAD and N concentration was higher than that of ΔT_1 , ΔT_p and ΔT_c . This indicated that canopy temperature had a great influence on nitrogen fertilizer [46] and rice dry matter accumulation [18,48], and the stem temperature differences could better reflect the growth characteristics of rice among different organ temperatures. The growth and development of rice population affected canopy and organ temperature. Appropriate planting density [49] can effectively improve the ventilation and light transmittance of paddy fields and maintain a relatively stable canopy microclimate [50].

This is because plant surface temperature changes are affected by environmental temperature changes [51]. It was found that Pn, Gs, Ci and Tr were negatively correlated with canopy and organ temperature, respectively. Compared with ΔT_s , ΔT_p and ΔT_c , ΔT_1 had higher correlation coefficient with Pn, Gs and Ci, respectively. The correlation coefficient between ΔT_s and Tr was higher than ΔT_1 , ΔT_p and ΔT_c , respectively. Canopy temperature affects the physiological and biochemical processes in rice plants. Plant surface temperature also affects leaf function, chlorophyll content, transpiration rate, photosynthetic capacity [52]. When the ambient temperature increased, the temperature of rice leaves increased, as well as stomatal conductance on rice leaves, thus accelerating the transpiration rate and inhibiting the increase in leaf temperature. Under extreme high temperature stress conditions, water rapidly passed through the leaf vessels, and the canopy temperature of rice was regulated by stomatal transpiration [53]. However, rapid transpiration led to the rapid loss of water in the plant. Simultaneously, stomatal conductance and net photosynthetic rate of rice flag leaves decreased, and the leaf temperature increased [54]. Since ΔT_1 and ΔT_s were significantly positively correlated, when the leaf photosynthetic rate decreased, ΔT_s also

decreased. In conclusion, stem temperature was more important indicator than canopy temperature. Stem temperature is a better screening index for rice breeding and cultivation management in the future.

5 Conclusions

This study emphasized the difference of canopy and organ temperatures and the relationship between canopy temperature and growth characteristics of rice under different planting methods. The results showed that the best observation time of the rice canopy temperature was 13:00. There were significant temperature differences between the rice canopy and various organs under the same planting method ($p < 0.05$). Compared with canopy temperature, the correlation between stem temperature and 1000-grain weight, actual yield, and theoretical yields during the milk stage were superior. Since the growth characteristics of rice were affected by canopy and organ temperatures, we also found that canopy and organ temperatures were significantly negatively correlated with dry matter accumulation during the milk stage ($p < 0.05$), and significantly positively correlated with nitrogen and SPAD ($p < 0.05$). The correlation between stem temperature and rice growth characteristics was higher than canopy, leaf and panicle temperature. Leaf internal physiological traits were closely related to leaf and stem temperature, while leaf and stem temperature were significantly positively correlated ($p < 0.05$). In conclusion, stem temperature was more important indicator than canopy temperature. Stem temperature is a better screening index for rice breeding and cultivation management in the future.

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Conflicts of Interest: The authors declare that they have no conflicts of interest to report regarding the present study.

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