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Abstract: Temperature thresholds during the rice ($Oryza \ sativa \ L$.) cycle development have been reported to affect plant metabolism. Therefore, this study aimed to evaluate the effects of the above-optimal temperature on photosynthetic and morphometric parameters in two contrasting irrigated rice genotypes (BRS Querência—sensitive and Nagina 22 (N22)—tolerant). Plants of both genotypes were grown in rhizotrons and always maintained under two temperature conditions: Out—under environmental temperature conditions, and In—rhizotrons inside a plastic structure, which increased the temperature about 3 °C to 5 °C above the external one. In the genotype N22, there was an increase (twofold higher) in CO₂ assimilation in plants cultivated under elevated temperature (In). In BRS Querência, the stomatal conductance (g_s) and transpiration rate (E) decreased upon high temperature. The rise in the temperature also negatively impacted in the modulated fluorescence parameters in both genotypes. Increases in root dry weight (RDW) and shoot dry weight (SDW) were also observed in the genotype N22 when compared to BRS Querência upon temperature rise. In general, the N22 genotype showed greater response to the above-optimal temperature due to its intrinsic thermotolerance traits over BRS Querência. Thus, N22 appeared as a potential donor of heat tolerance genes aiming to obtain new cultivar to face current global warming.

Key words: Oryza sativa L., heat, thermotolerance, photosynthesis, root system.

1. Introduction

Rice is the most important food crop cultivated worldwide due to its growth adaptability in a multitude of environments and has been considered a staple food for human consumption [1]. However, as an increase in growth population is expected [2], food production, such as annual cereal production, must increase over the next years [3]. To reach this demand, rice farmers will need to produce about 8-10 million tons more paddy per year without area expansion (productivity of rice per unit of land), requiring annual yield increase of about 1.2%-1.5% [1]. As rice yield increases have slowed about 0.8% in the last decades, mainly due to the negative impacts of increase in the temperature, a consequence of global warming, especially increases in night-time temperatures [4-6]. Thus, efforts are necessary to understand how above-optimal temperature affects critical cycle stages of rice, aiming to construct plants ideotypes to supply the global food requirement.

In this sense, forecasts estimated the rise in the average temperature from 2 °C to 5.4 °C, up to 2100 [6], with optimistic increases in the temperature in Brazil, up to 3.8 °C [7]. In the south of Brazil (mostly in the Rio Grande do Sul state), where the rice production reached 81.6% of the national productivity [8], it has been reported that an increase in the minimum average temperature (approximately 2 °C) in the summer season (Jan.-Mar.) may negatively

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impact on yield components and, consequently on grain yield and quality when exceeding the temperature threshold suitable for plant development.

Temperature rises can significantly influence photosynthetic mechanisms, such as increases in CO₂ assimilation via RuBisCO enzyme and ribulose 1.5-bisphosphate regeneration (RuBP) through Calvin-Benson cycle [9]. So far, studies of the authors' group have reported that increases in the temperature average above the optimal one lead to a decrease in CO₂ assimilation and consequently losses in rice productivity [10]. However, the temperature was above the optimal threshold for rice flowering [11] and, for most plant species, vegetative development usually has a higher optimum temperature than for reproductive development [12].

Rates of photosynthesis and respiration increase with an increase in temperature until a threshold at which maximum photosynthesis level is achieved. Generally, it is around 22-24 °C and remains that way, up to 30-35 °C [13], with biomass increasing up to 33 °C in rice [14]. The decline was observed between 40 °C and 43 °C, although assimilation rates at these temperatures remained positive, whereas steady-state fluorescence yield declined up to 41 °C and then increased moderately above it, implying drastically reduced effective quantum yields of photosystem II (PSII— Φ_{PSII}) [13].

The extent to which elevated temperature occurs in specific climatic zones is a complex issue. Plants can be damaged in diverse ways by either high day or high night temperatures and by either high air or high soil temperatures. Also, crop species and cultivars differ in their sensitivity to high temperatures, according to phenological stages [4, 11, 15, 16], which have been reported as plant-genotype specific [17], and to temperature thresholds [16].

In rice, when temperature increases from a base of 8 °C to 36-40 °C (the thermal threshold of survival), there is an increase in leaf appearance rate [18], biomass increases until temperatures reach 33 °C [14].

However, grain formation and yield are maximum at the optimum temperature of 25 °C [18]. Cheng et al. [19] found that high night temperatures increased living leaf N concentration and leaf area (LA), and caused higher photosynthetic capacity during the last stage of growth. Carbon assimilation also increases with higher night temperatures, and however, loss of carbon increases due to respiration.

The effect of elevated temperature on plant growth and development has not been extensively studied in rice, especially at early stages of development. As vegetative stage precedes reproductive one, increases in temperature above optimal one may lead to a progressive failure to produce filled grains caused by reduced pollen viability and pollen production [20]. Besides, the contrasting productivity of rice genotypes may be due to the differential in the dynamic assimilation partitioning within plants during the growth and development [21]. Therefore, the aim of this study was to evaluate photosynthetic and morphometric responses of two contrasting irrigated rice genotypes subjected to an above-optimal temperature at initial stages of development.

2. Materials and Methods

2.1 Plant Materials and Growth Conditions

The experiment was carried out in the summer season (Dec. 15 to Jan. 16) with two irrigated rice genotypes contrasting to elevated temperature (BRS Querência—sensitive and Nagina 22 (N22)—tolerant) [22]. The genotypes were previously selected based on studies of the authors' group (data not published).

Plants were grown in rhizotrons (120 cm \times 35 cm) from seeds, as shown in Fig. 1, containing soil (planosol hydromorphic eutrophic solodic) as substrate. After germination, only one plant was kept per rhizotron. To allow root growth within the rhizotron, it inclined 45° using pieces of wood as support. Both genotypes were exposed to two temperature gradients: *Out*—plants were grown in rhizotron under natural temperature conditions;

In—plants were grown in rhizotron inside a structure made of plastic (similar to a greenhouse) as shown in Fig. 1, which increased the temperature 3-5 °C during the day and 1-2 °C during the night, compared to plants grown under normal temperature conditions (external temperatures).

Soil moisture was measured daily after the

irrigation of the plants. Only one plant was kept in each rhizotron. Temperature conditions (*In* and *Out*) were monitored through sensors and were shown in Fig. 2.

2.2 Gas Exchange Analysis

Gas exchange and modulated fluorescence were



Fig. 1 Cultivation of irrigated rice genotypes in rhizotrons: In (left) and Out (right).



Fig. 2 Average temperatures of the environment (*Out*) and inside of the plastic structure (*In*) during the time course of the experiment.

measured in plants with 42 d after emergence by using a portable infrared CO₂ analyser (model LI-6400XT, LI-COR, Inc., Lincoln, NE, USA). The measurements were taken between 09:00 am and 11:00 am with an in-chamber CO₂ concentration of 400 µmol/mol and a photon flow density of 900 µmol photons/m²/s, using the light source LI-COR attached to the measuring chamber. Net assimilation rate (*A*), stomatal conductance (g_s) and transpiration rate (*E*) were measured.

2.3 Modulated Fluorescence Analysis

Modulated chlorophyll а fluorescence of dark-adapted leaf of plants was measured using a portable fluorometer (model PAM-2500 from Heinz Walz GmbH, Effeltrich, Germany). Leaves were kept in dark for at least 40 min and the fluorescence was induced by one saturating flash pulse with 7,000 µmol photons/m²/s. Maximum effective photochemical quantum yield of PSII (Fv/Fm), relative electron transport rate (ETR), the coefficient of photochemical fluorescence quenching (qP)and effective photochemical quantum yield of PSII (Y(II)) were measured.

2.4 Morphometric Analysis

Root morphometric analysis was taken by photographic camera and image analyser software (WinRHIZO Pro 2013), to measure root length (*RL*) and root volume (*RV*) with 7, 14, 21, 28, 35 and 42 d after plant emergence. In addition, after 42 d of plant emergence, LA was estimated with leaf area meter (model LI-3000, LI-COR), and root dry weight (*RDW*) and shoot dry weight (*SDW*) were quantified after drying the fresh tissues in an oven at 60 ° C.

2.5 Statistical Analysis

Each treatment consisted of three replicates and each replicate consisted of one rhizotron containing one plant in a fully randomized design. The data were previously analysed for homoscedasticity (Hartley's test) and normality (Shapiro-Wilk's test) and transformed when necessary. Afterwards, the data were analysed by analysis of variance (ANOVA). When *F* was significant, the treatment means for each genotype were compared by the Student-Newman-Keuls test or analysis of regression $(p \le 0.05)$.

3. Results and Discussion

3.1 Photosynthetic Responses of Rice to Above-Optimal Temperature

The above-optimal temperature effects on photosynthetic parameters of two irrigated rice genotypes were shown in Figs. 3 and 4. Regarding gas exchange analysis (Fig. 3) in plants cultivated in rhizotrons, A increased in plants of N22 genotype about twofold higher when cultivated inside a plastic structure (In-elevated temperature) in comparison to N22 plants under normal temperature conditions (*Out*—environmental temperature), while no differences in CO₂ assimilation were observed in BRS Querência (Fig. 3a).

Photosynthesis has been reported as highly sensitive to heat stress. The optimal temperature for CO₂ assimilation ranges from 20 °C to 35 °C [13], with increases from the minimum to the maximum temperature threshold. Although plants present a considerable amplitude in optimal photosynthesis temperature, inhibition of photosynthesis normally occurs when the temperature increases above 35 °C [23, 24], due to inhibition of activity of RuBisCO activase and concomitant reduction of RuBisCO activity [25], or to limiting supply of NADPH and ribulose bisphosphate [26] reflecting the loss of thylakoid pH gradient [27]. As the temperature threshold for rice in the experiment did not reach the threshold, there was an increase in photosynthesis of N22, which was also reported in tolerant rice genotypes by Scarfaro et al. [9], in a similar experiment carried out in this study under modified environment (In).



Fig. 3 Photosynthetic responses to above-optimal temperature in two irrigated rice genotypes (BRS Querência and N22). *A*—net assimilation rate (a), g_s —stomatal conductance (b), *E*—transpiration rate (c) and maximum effective photochemical quantum yield of PSII—Fv/Fm (d).

"In"—plants growing in rhizotrons under plastic protection; "Out"—plants growing in rhizotrons under environmental temperature conditions.

An asterisk (*) indicates significant difference by Student's test ($p \le 0.05$) between treatments (*In* and *Out*) for each genotype. Values represent the mean \pm SE (n = 3).

In an opposite way, there was a significant reduction (approximately 30%) in both g_s (Fig. 3b) and E (Fig. 3c) in plants of BRS Querência kept in the treatment *In* compared to plants in *Out*. Differently, plants of N22 tolerant to elevated temperature did not show alterations in g_s and E in response to

above-optimal temperature. Leakey et al. [28] and Poons and Welschen [29], reported that the reduction in these parameters was temperature-dependent and can be modulated by genetic traits.

Studies showed that sensitive rice cultivars decreased the g_s about 20%-50% upon elevated temperature

(40 °C), and it varies according to the phenological development stage of plants, being the reproductive one the most affected [30]. Maintaining g_s functioning is highly important to reduce leaf temperature some degrees below the air temperature under heat conditions through transpiration [31]. As environments with temperature above the optimal one induces stomatal closure and consequently reduction in *E*, the capacity of maintaining transpiration rates as in plants of N22 may be related to thermotolerance mechanisms, which can keep the photosynthetic process working or even increase it, differently from plants of BRS Querência that showed decreases in g_s and *E*.

Optimal temperature for net photosynthesis at current ambient CO₂ concentrations is around 30 °C or slightly above, whereas the optimum temperature for photosynthetic electron transport is typically 5-15 °C higher [32]. As shown in Fig. 3d, the maximum effective photochemical quantum yield of PSII (Fv/Fm) reduced in plants of N22 upon elevated temperature (In) in about 6%, while plants of BRS Querência did not decrease Fv/Fm in In compared to plants kept in Out.

Similarly to Fv/Fm, the *ETR* also reduced (29%) in plants of N22 under high temperature (*In*) compared to plants in *Out*, while plants of BRS Querência did not show difference between the treatments (Fig. 4a).

As shown in the study, the temperature *In* increased *A* (Fig. 3a). On the other hand, the rate of electron transport determined from modulated fluorescence decreased (Fig. 4a). Although impaired electron transport has been already demonstrated under moderate heat stress conditions, slightly exceeding the optimum temperatures [27], photosynthesis rates generally rapidly recover from mild heat stress [13].

The rate of PSII electron transport in leaves is strongly linked to the rate of CO₂ fixation, however, part of the electrons from PSII is partitioned to photorespiration and other processes [33]. Thus, the finding that leaves showed the maximum rates of PSII electron in BRS Querência and N22 in *Out* conditions



Fig. 4 Modulated chlorophyll *a* fluorescence to above-optimal temperature in two irrigated rice genotypes (BRS Querência and N22).

Electron transport rate—*ETR* (a), coefficient of photochemical fluorescence quenching—qP (b), effective photochemical quantum yield of PSII—Y(II) (c).

"In"—plants growing in rhizotrons under plastic protection; *"Out"*—plants growing in rhizotrons under environmental temperature conditions.

Values represent the mean \pm SE (n = 3).



Fig. 5 Length and volume of two rice roots in response to above-optimal temperature (BRS Querência (a and c) and N22 (b and d)).

"In"—plants growing in rhizotrons under plastic protection; "Out"—plants growing in rhizotrons under environmental temperature conditions (a and c).

Values represent the mean \pm SE (n = 3).

might be related to driving the energy flux of the photosystems through photorespiration as a mechanism to dissipate part of the energy produced by the photochemical process under normal environmental conditions [34], when temperature increases in *In* conditions, the energy flux is driven to photosynthesis and may decrease photorespiration.

In general, the response to the capacity of electron transport to elevated temperature changes among the

species [32]. Besides, plants under heat stress can adjust the metabolism, presenting strategies to maintain the structures of the photosystems, which in turn lead to a reduction in the *ETR* under stress [35]. Photosystems are also very sensitive to temperature variations due to its position within the membrane of the thylakoids [36], and a few degrees above in the temperature can increase the membrane fluidity, leading to disorganization of the photosystems apparatus



Fig. 6 *RDW* (a), *SDW* (b) and *LA* (c) of two irrigated rice genotypes in response to above-optimal temperature (BRS Querência and N22).

"In"—plants growing in rhizotrons under plastic protection; *"Out"*—plants growing in rhizotrons under environmental temperature conditions.

An asterisk (*) indicates significant difference by Student's test ($p \le 0.05$) between treatments (*In* and *Out*) for each genotype. Values represent the mean \pm SE (n = 3).

[37]. In this sense, Leakey et al. [28] showed that leaf temperature above 34 °C can slower the electron transport capacity, however, driving more efficiently the energy (ATP and NADPH) to photosynthetic processes by increasing CO_2 assimilation and may reduce photorespiration.

3.2 Morphometric Responses of Rice to Above-Optimal Temperature

The root length and volume were shown in Fig. 5. In both genotypes, the root length was not affected by increasing temperature during with the time course of the experiment (Figs. 5a and 5b). In relation to root volume, there was an increase in both genotypes in the condition In, with greater increase in N22, which ranged about 70% over the plants in *Out* (Figs. 5c and 5d).

RDW increased consistently about twice upon elevated temperature (In) compared to control (Out) in N22, while no changes occur in the genotype sensitive BRS Querência (Fig. 6a). In relation to SDW (Fig. 6b) and LA (Fig. 6c), both genotypes, BRS Querência and N22 showed a greater increase (about twice) upon elevated temperature (In) compared to the control (Out).

According to Arai-Sanoh et al. [38], environments with elevated air temperature lead to an increase in the soil temperature that can affect the root growth of plants. The rise in soil temperature has been reported to affect negatively when above 30 °C, the temperature limit for sensitive rice crops to develop the root system. As showed by the sensitive genotype, BRS Querência, there was no significant difference in *RDW* though slight decrease occurred, characterizing that the soil temperature reached the maximum to keep the growth of roots without several damages. Different from plants of BRS Querência, in N22, there was an increase in root growth in plants under In conditions compared with plants in Out (Fig. 6a). These differences may be related to the increased photosynthetic rate and carbohydrates partitioning

between root and shoot in N22 [39], while there was an increase in the respiration rate in BRS Querência [40].

LA of plants is strongly affected by temperature, radiation, shading, photoperiod, air moisture, water availability and mineral nutrients [41, 42]. As found in the experiment, Hay and Wilson [43] and McMaster et al. [44], showed that increases in the temperature close to the root zone affect the growth and development of leaves, besides several physiological processes in rice plants. In general, the greater response of N22 to above-optimal temperature may be related to a thermotolerance of this genotype over BRS Querência that showed to be more sensitive to the effects of elevated temperature.

4. Conclusions

Above-optimal temperature affects more negatively the photosynthetic and morphometric responses of BRS Querência genotype in comparison to N22. In general, N22 genotype showed greater response to above-optimal temperature due to its intrinsic thermotolerance traits over BRS Querência. Thus, N22 appears as a potential donor of heat tolerance genes aiming to obtain new cultivar to face current global warming.

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