Tolerance of lowland rice (*Oryza sativa*) genotypes to heat stress at anthesis

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Abstract – Global warming is occurring all over the world and climate changes are likely to affect agriculture by raising the frequency of weather events with very high and very low temperatures, which will increase the risks for food production. This study aimed to evaluate the effect of heat stress at anthesis on the agronomic performance of modern Brazilian lowland rice genotypes. The varieties SCS124 Sardo, SCS122 Miura, SCS121 CL, SCS116 Satoru, SCSBRS Tio Taka, Epagri 109 and the inbreeds SC 491 ME, SC 676, SC 792, SC 806, SC 817, SC 849 were tested. At anthesis, plants which received heat stress treatment were transferred to a growth chamber for four days at temperatures of 38°C (day) and 30°C (night). After that, they were returned to a greenhouse, remaining there until harvest, under temperatures of about 25°C. Spikelet sterility ranged from 4.0 to 84.1%. Yield varied from 10.2 to 101.2g pl^{-1}. Heat stress increased spikelet sterility and decreased grain production. The inbreeds SC 817 and SC 806 showed the lowest percentage of spikelet sterility and the highest yield under thermic stress and are promising genotypes to generate tolerant cultivars to high temperatures at anthesis.

Index terms: *Oryza sativa*; Anthesis; Heat stress; Sterility; Yield.

Tolerância de genótipos de arroz irrigado (*Oryza sativa*) ao estresse por calor na antese

Resumo – O objetivo deste trabalho foi avaliar o efeito do estresse térmico (calor) na antese sobre o desempenho agronômico de genótipos brasileiros modernos de arroz irrigado. As variedades SCS124 Sardo, SCS122 Miura, SCS121 CL, SCS116 Satoru, SCSBRS Tio Taka, Epagri 109 e as linhagens SC 491 ME, SC 676, SC 792, SC 806, SC 817, SC 849 foram avaliadas. Na antese, as plantas correspondentes ao tratamento de estresse por calor foram transferidas para uma câmara de crescimento por quatro dias sob temperaturas de 38°C (dia) e 30°C (noite). Em seguida, voltaram à casa de vegetação, onde permaneceram até a colheita sob 25°C aproximadamente. A esterilidade de espiguetas variou de 4,0 a 84,1%. A produtividade variou de 10,2 a 101,2g pl^{-1}. O estresse térmico aumentou a esterilidade das espiguetas e diminuiu a produção de grãos. As linhagens SC 817 e 806 apresentaram menor porcentagem de esterilidade de espiguetas e maior produção sob estresse de calor, sendo, portanto, genótipos promissores para gerar cultivares tolerantes a altas temperaturas na antese.

Termos para indexação: *Oryza sativa*; Antese; Estresse por calor; Esterilidade; Produtividade.

Introduction

Global warming is occurring all over the world and the Intergovernmental Panel on Climate Change (IPCC) observed a 0.3°C rise in temperatures every 10 years. Some studies indicate that if temperatures increase by 1°C, rice yields would decrease by 10% (BUU et al., 2021), whereas others estimate that the increasing temperature could reduce rice production by 41% at the end of the 21st century (KHAN et al., 2019). Heat stress has become increasingly important as a yield-limiting factor and the increased frequency of short-term but extremely high temperatures is particularly damaging (BUU et al., 2021). One of these high temperature events was reported in Santa Catarina at the 2009/2010 growing season. During eight consecutive days, in February 2010, maximum temperatures varied from 35°C to 40°C, which resulted in yield and quality losses in lowland rice in Santa Catarina (EBERHARDT, 2010).

High temperature negatively impacts all stages of rice growth but anthesis is the most susceptible stage. Temperatures above 35°C during anthesis cause irreversible damage to crops, harming the fertilization of spikelets (PRASAD et al., 2017, SOSBAI, 2018, BUU et al., 2021). High temperatures also inhibit photosynthesis and protein synthesis, increase respiration, and decrease enzymatic activity. These physiological changes hamper grain production and reduce crop yields (CUADRA et al., 2015, PRASAD et al., 2017). A review on heat stress tolerance in rice was recently written (BUU et al., 2021)

The damages related to high temperatures are similar to the injuries observed by the incidence of low temperatures. Both thermal stresses increase spikelet sterility and reduce pollen grain viability, directly affecting kernel development and decreasing the number of grains per panicle (SARSU et al., 2018, KHAN et al., 2019; BUU et al., 2021). Other effects of high temperature are lower assimilate partitioning in kernels and decreased grain filling stages, which can harm rice grain quality by reducing their amylose content and lead to white-back kernels (BUU et al., 2021).

Heat stress response in rice is a complicated process which is regulated

Received on 25/11/2021. Acepted for publication in 09/05/2022. https://doi.org/10.52945/rac.v35i2.1354

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by numerous proteins in different metabolic pathways. Moreover, the genetic basis of heat tolerance in rice is generally unknown. Heat stress usually induces the synthesis of heat shock proteins, which are universally observed in rice leaves. A cold shock protein was also induced in response to high temperatures in rice anthers. Some advances have been made in validating some heat tolerant genes (XIONG, 2013; KHAN et al., 2019)

Different strategies could be used to enhance rice tolerance to extreme temperatures, one of which is selecting genetically resistant genotypes by breeding (KHAN et al., 2019). However, temperature is an unpredictable and difficult factor to use in breeding programs to select for tolerant varieties. Nevertheless, some progress has been made, for example, in a similar way, in developing cold tolerant rice varieties in Hokkaido (SHINADA et al., 2013). The same efforts can be made for heat tolerance and therefore, it is important to design methodologies which can evaluate the tolerance of rice genotypes to heat stresses in the field and under controlled conditions. Conventional breeding is probably the best approach to dealing with heat tolerance, as transgenic efforts for this trait have failed to release any commercial cultivars in the last 20 years (BUU et al., 2021).

This study aims to evaluate the effect of controlled heat stresses during the anthesis of lowland rice genotypes to identify those which tolerate high temperatures. Heat stress is commonly defined as an increase in temperature above a threshold for a certain length of time which causes irreversible damage to the growth and development of plants, whereas the heat tolerance of a plant is its capacity to produce economical yield and show normal growth under high temperatures by adjusting their structural or metabolic properties (KHAN et al., 2019).

Material and methods

The experiment was conducted at the Itajaí Experiment Station (Epagri - Santa Catarina State Agricultural Research and Rural Extension Agency) during the 2018/19 growing season. The trial was set in buckets (experimental units) capable of conditioning 8kg of soil. The experimental design was entirely randomized. Treatments were arranged in a three-factorial grid (12x2x2) with three replications. The first factor corresponded to the genotypes; the second factor, to the application or not of thermal stress and the third factor, to the repetition of the experiment at different times.

In total, 12 genotypes were evaluated: six cultivars (Epagri 109, SCSBRS Tio Taka, SCS116 Satoru, SCS121 CL, SCS122 Miura, and SCS124 Sardo) and six inbreed lines (SC 491 ME, SC 676, SC 792, SC 806, SC 817, and SC 849). All genotypes belong to the *indica* subspecies, have late cycles, and were developed by Epagri or Epagri/Embrapa. The initial approach involved looking for genotypes which could face high temperature stresses. This initial group of genotypes was assembled considering their tolerance or susceptibility to another extreme abiotic stress, i.e., cold, in previous studies or observations. The inbreed lines had already been chosen by its good cold tolerance in trials conducted by the Epagri rice breeding program from about 2010 up to now (SOUSA et al., 2017; STÜRMER et al., 2019; MARSCHALEK et. al., 2019).

Sowing was performed in wooden boxes filled with a substrate composed of sand and clay. Five grams of seeds of each genotype were placed in lines in the boxes. After that, seeds were covered with substrate and watered. Sowing was done on 06/11/2018 and 08/14/2018 for the first and second experiment, respectively. After 10 days of seeding, eight seedlings of each genotype were transplanted to each bucket but only one plant/bucket was left in the V6 stage (COUNCE et al., 2000).

The six buckets for each genotype (in each experiment) were grown in a greenhouse at an average temperature of 25°C and average relative humidity of 70% from transplant to anthesis. At the beginning of anthesis, three buckets (out of six) from each genotype were subjected to a temperature of 38°C during the day and 30°C at night for four days, with a photoperiod of 12 hours of light (day)/12 hours of dark (night), and a relative air humidity of 55% in a growth chamber (made by Instalafrio – Pinhais – PR – Brazil). Each genotype had its three control buckets maintained during the whole crop cycle in the greenhouse. A similar methodology was developed in a study by Sarsu et al. (2018).

In this study, heat stress occurred between 10/01/2018 and 10/15/2018, and 11/12/2018 and 12/05/2018 for the first and second experiments, respectively. Stress began to be imposed in the growth chamber as panicles started emerging from the flag leaf, a characteristic observed between the end of stage R2 and the beginning of stage R3 (COUNCE et al., 2000). After heat stress was imposed, plants were returned to a greenhouse, in which they remained until maturity. Harvests were performed on 11/16/2018 and 01/20/2019 for the first and second experiments, respectively.

At the end of the crop cycle, tillers were harvested, and the panicles were manually threshed. Full spikelets were separated from empty ones using a forced air blower and subsequently counted (Contador – by Pfeuffer, Germany) and weighed. The following variables were determined: spikelet sterility, by counting full and empty spikelets and determining the percentage of empty spikelets; grain yield, by weighing full spikelets masses; 1,000-grain masses; and genotype tolerance to high temperatures at anthesis, by comparing the results of heat stress treatments with the respective three control buckets of each genotype which remained at the greenhouse.

Data were statistically evaluated by variance analysis using the Assistat Software Version 7.7 (SILVA & AZEVEDO, 2016). F values for treatment effects were considered at a 5% significance level ($P<0.05$). When significant, averages were compared by the Scott-Knott test at 5% significance level.

Results and discussion

The analysis of variance for spikelet sterility and grain production per plant indicated a significant triple interaction among genotype x replication x heat stress. That means that the genotypes responded differently according to heat stress application and experiment repetition. Thus, there was a need to unfold the interaction to evaluate the influence of these factors for each genotype. Table 1 shows the results.

Analysis of variance showed significant double interactions between genotype x repetition, genotype x temperature (heat stress/control), and repetition x temperature (heat stress/control) for 1,000-grain masses. Experiment repetition also impacted this variable differently with or without heat stress, regardless of genotype.

Regarding the range of spikelet sterility - from 4.0 and 84.1% (Table 1a) - inbreeds SC 817 and SC 806 showed the lowest sterility values under heat stress. Their percentage of empty spikelets at harvest was smaller than 26%, varying from 7.3 to 11.5% for the SC 806. The good performance of the two inbreed lines under heat stress resembles the spikelet sterility from Stürmer et al. (2019) found when they were exposed to low temperatures at crop microsporogenesis. Besides, in field trials at high altitudes (500-600m), the six experiments conducted (from crop season 2013/2014 to 2018/2019), published at CBAI by Marschalek et al. (2015, 2017 and 2019) by Epagri indicate that these two lines usually show high yields, validating their adaptability for colder areas, i.e., under potential temperature stress. This may indicate the existence of a similar or overlapping tolerance mechanism to extreme temperatures in the reproductive period of the crop, regardless of whether it is high or low, as Jagadish et al. (2010), Xiong (2013), and Baliuag et al. (2015) reported. Therefore, the results from SC 806 are especially promising since its low spikelet sterility is even lower than the classical N22 line, reported to be 29%, which the literature recognizes as one of the genotypes which best tolerates high temperatures (KHAN et al., 2019). Other Epagri cultivars (SCS) (Table 1a) showed high levels of sterility under high stress temperatures, indicating the risk for rice production if these events occur.

For grain yield per plant (Table 1b), inbreeds SC 806 and SC 817 showed the highest grain yields (weight/plant-bucket) at heat stress treatments. These genotypes also had the lowest spikelet sterility (Table 1a), contributing to their

Table 1. (a) Lowland rice genotype spikelet sterility and (b) grain production per plant (bucket) subjected to heat stress for four days at anthesis in relation to control. Itajaí-SC, 2018/2019

Tabela 1. (a) Esterilidade de genótipos de arroz irrigado e (b) produção de grãos por planta (balde) (b) submetidos à estresse por calor na antese, durante 4 dias, em relação à testemunha (controle). Itajaí-SC, 2018/2019

a) SPIKELET STERILITY (%)				
Genotypes	**Stress 1**[1/]	**Control 1**[1/]	**Stress 2**[2/]	**Control 2**[2/]
SCSBRS Tio Taka	84.1 aA*	19.0 dC	54.6 bA	31.2 cA
Epagri 109	82.7 aA	41.3 bA	34.5 bB	27.0 bA
SCS122 Miura	78.2 aA	12.9 cC	25.4 bC	10.2 cB
SC 676	71.1 aB	15.0 bC	20.2 bC	23.0 bA
SC 792	61.1 aB	10.3 cC	33.4 bB	18.0 cB
SC 491 ME	59.4 aB	19.1 bC	20.0 bC	15.8 bB
SCS121 CL	51.0 aC	9.6 cC	36.7 bB	17.9 cB
SC 849	46.5 aC	11.4 bC	25.9 bC	18.6 bB
SCS116 Satoru	41.0 aC	30.0 bB	46.0 aA	34.3 bA
SCS124 Sardo	36.3 aC	42.9 aA	30.7 bB	24.6 bA
SC 817	25.1 aD	18.3 aC	11.6 bD	9.4 bB
SC 806	7.3 bE	26.9 aB	11.6 bD	4.0 bB
CV% = 23.91				

b) GRAIN YIELD ($g\ pl^{-1}$)				
Genotypes	**Stress 1**[1/]	**Control**[1/]	**Stress 2**[2/]	**Control**[2/]
SC 806	101.2 aA*	63.0 bA	76.3 bA	90.0 aA
SC 817	64.3 aB	61.4 aA	75.8 aA	74.7 aA
SCS116 Satoru	56.4 bB	47.3 bB	49.3 bB	77.2 aA
SCS124 Sardo	47.6 aC	30.8 aB	41.7 aB	34.4 aB
SC 491 ME	45.8 bC	67.9 aA	82.2 aA	67.0 aA
SCS121 CL	45.3 bC	70.6 aA	59.2 bB	76.5 aA
SC 849	37.7 aC	62.2 aA	57.4 aB	63.4 aA
SC 792	30.6 bC	68.7 aA	54.7 aB	63.2 aA
SC 676	30.5 bC	72.8 aA	82.7 aA	63.5 aA
SCS122 Miura	20.9 bD	61.7 aA	62.7 aB	85.0 aA
Epagri 109	13.8 cD	37.6 bB	55.9 aB	64.3 aA
SCSBRS Tio Taka	10.2 cD	69.0 aA	35.8 bB	48.8 aB
CV% = 24.85				

[1/] First experiment repetition – sown on 06/11/2018. Heat treatment with 12 hours of light at 38°C (day)/12 hours of darkness (night) at 30°C in a growth chamber. Control at 25°C day/night in a greenhouse.

[2/] Second experiment repetition – sown on 08/14/2018. The same settings for light/darkness and temperature as the first experiment.

* Average followed by the same letter, lowercase in the line and uppercase in the column, fail to differ by the Scott-Knott test at the 5% significance level.

higher grain production. Thus, since spikelet sterility alone is an unreliable criterion to access heat tolerance - according to Khan et al. (2019) - SC806 especially shows its undoubted tolerance by having the best values for both traits.

Inbreeds SC817 and SC849 and the cultivar SCS124 Sardo showed no differences between the performed treatments (Table 1b). The other genotypes showed variation between at least one treatment (stress application or experiment repetition).

Cultivars SCS121 CL, SCSBRS Tio Taka, SCS116 Satoru, and SCS122 Miura showed susceptibility to high temperatures during anthesis (Table 1), with generally lower grain production under heat stress than their controls (Table 1b).

Regarding 1,000-grain mass variance analysis, the genotypes significantly differ, which is expected, as well as the two experiments (repetitions), the interaction between genotype and experiment repetition, and the interaction between genotype and temperature (Tables 2 and 3), in which one only genotype has a different 1,000-grain mass (higher mass under temperature stress). So, the genotypes failed to significantly differ for this variable between stressed plants and the control, showing that heat stress during anthesis was unable to reduce 1,000-grain masses, regardless of genotype. The thermic stress group failed to significantly differ from control, showing that temperatures are unable to affect 1,000-grain masses, whereas they differed in two previous experiments (1 and 2) which, nonetheless, involved a different set of genotypes and five different temperatures (SOUZA, 2020). Souza (2020) confirms that maximum temperatures of 38°C at anthesis for four days failed to significatively modify 1,000-grain masses, which will occur at 40°C and 42°C.

The mass of 1,000 grains is established between the stages R4 (anthesis) and R8 stages (grain physiological maturity), according to the scale of Counce et al. (2000). Climatic conditions especially affect it during this period (SOSBAI, 2018). The plants which underwent heat stress remained for four days under high temperatures

Table 2. Mass of 1,000 grains of lowland rice genotypes subjected to heat stress for four days at anthesis in relation to control. Itajaí-SC, 2018/19

Tabela 2. Massa de 1000 grãos de genótipos de arroz irrigado submetidos à estresse por calor durante quatro dias na antese, comparada com a testemunha. Itajaí-SC, 2018/2019

MASS OF 1,000 GRAINS (g)		
Genotypes	**Heat treatment1/**	**Control2/**
SC 676	27.0 aA*	26.6 aA
SC 491	27.0 aA	25.4 aB
SCS121 CL	26.9 aA	27.1 aA
SCS116 Satoru	26.8 aA	26.0 aB
Epagri 109	26.7 aA	25.3 aB
SC 806	26.3 aA	25.5 aB
SC 849	26.0 aA	27.3 aA
SC 817	25.9 aA	25.2 aB
SC 792	24.6 aB	25.2 aB
SCS124 Sardo	24.1 aB	22.1 bC
SCSBRS Tio Taka	23.9 aB	25.4 aB
SCS122 Miura	23.7 aB	24.9 aB
CV% = 5.62		

1/ Heat treatment with 12 hours of light (day) at 38º/12 hours of darkness (night) at 30°C in the growth chamber.
2/ Control at 25°C day/night in a greenhouse.
* Average followed by the same letter, lowercase on the line and uppercase on column, fail to differ by the Scott-Knott test at the 5% significance level.

Table 3. Average 1,000-grain mass of 12 irrigated rice genotypes subjected to heat stress for four days at anthesis in relation to control. Itajaí-SC, 2018/2019

Tabela 3. Massa média de 1000 grãos de 12 genótipos de arroz irrigado submetidos à estresse por calor na antese, em relação à testemunha. Itajaí-SC, 2018/2019

MASS OF 1,000 GRAINS (g)		
	Experiment 1 2/	**Experiment 2 2/**
Heat treatment 1/	25.3 bA*	26.2 aA
Control 1/	24.5 bB	26.6 aA
CV% = 5.62		

1/ Heat treatment with 12 hours of light at 38°C (day)/12 hours of darkness at 30º (night) in the growth chamber. Control at 25°C day/night in the greenhouse.
2/ Experiment 1 – sown on 06/11/2018. Experiment 2 – sown on 08/14/2018.
* Average followed by the same letter, lowercase in the line and uppercase in the column, fail to differ by the Scott-Knott test at the 5% significance level.

at the beginning of anthesis. After that, they returned to the greenhouse joining the controls plants. Therefore, both treatments had the same climatic conditions during grain filling, which possibly contributed to the absence of significant differences in 1,000-grain masses between heat stressed plants and the controls.

Regardless of genotype, the 1,000-grain masses of the second experiment (sown 08/14/2018) failed to significantly differ despite heat stress treatment (Table 3). On the other hand, in the first experiment (sown 06/11/2018), the control plants presented lower 1,000-grain masses (24.5g) than those subjected to heat stress (25.3g). The greater sterility which heat stress produced in the first replication may have contributed to this result, leading to heavier seeds. As the panicles of the heat-treated plants had fewer fertile spikelets, there was greater availability of photoassimilates to fill the remaining grains.

In general, higher sterility percentages were observed after stressing the plants in the first experiment than in the second one (Table 1a). Conversely, grain production per plant showed an inverse response, having lower values in the first experiment (Table 1b). This behavior was unexpected because the two experiments were conducted using the same methodology in the same way. However, due to the limited space in the growth chamber, sowing dates of the first and the second experiments differed by two months. Therefore, differences in sowing dates might have influenced plant growth and development, interfering in the impact of heat stress on spikelet sterility and grain yield.

The main aim of this study was to evaluate the effect of heat stress at anthesis in different lowland rice genotypes, seeking to identify high temperature tolerant genotypes. This objective was achieved, because important differences among genotypes were observed in spikelet sterility and grain production per plant when under heat stress. The inbreeds SC806 and SC817 demonstrated high productive potential and stability in their spikelet sterility percentages, both with the application of stress and in their controls. Therefore, they can generate cultivars which tolerate high temperature at anthesis. This will be probably the case for the SC806 since field experiments in high altitudes and other studies on cold tolerance and normal field trials have successfully tested this line. Therefore, and because of other suitable agronomical, qualitative, and industrial traits, SC 806 will be released soon (for growing season 2023/2024 probably) as a new rice variety tolerant to high and low temperatures stresses at the reproductive stages.

Conclusions

The inbreed lines SC806 and SC817 showed the lowest spikelet sterility and highest grain yield per plant under four-day heat (38°C) stress at anthesis. A temperature of 38ºC fails to reduce the 1,000-grain mass of the tested lowland rice genotypes.

Acknowledgements

To Epagri Technician Samuel Batista dos Santos.

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