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WATER STRESS IN MODERN UPLAND RICE CULTIVARS: A MULTIVARIATE STUDY BETWEEN PHYSIOLOGICAL TRAITS AND YIELD

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1 ABSTRACT

Water stress negatively affects upland rice production. The objective of this study was to identify physiological traits that could depict yield responses under water stress conditions. Three modern upland rice cultivars (C): BRS A501 CL (C1), BRS Esmeralda (C2) and BRS Serra Dourada (C3) were subjected to three water availability levels (W): Control (100% of the field capacity throughout the growing cycle) and 70 and 40% of the water applied to the control during flowering. Yield, spikelet sterility, and 1000-grain weight were influenced by the water availability level ($p < 0.05$), whereas for the cultivar, only 1000-grain weight was significant. The W × C interaction was not significant for the analyzed yield components. Multivariate analysis revealed that well-irrigated plants were positively associated with grain yield and gas exchange traits, whereas the 40% water availability level was highly related to spikelet sterility and the crop water stress index. The best-fitted model for grain yield was obtained using photosynthesis, stomatal conductance, and transpiration ($R^2 = 0.76$). Thus, physiological parameters can be used to explain the variations in upland rice yield under water stress.

Keywords: *Oryza sativa*, drought, multiple linear regression.

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ESTRESSE HÍDRICO EM CULTIVARES MODERNOS DE ARROZ DE TERRAS ALTAS: UM ESTUDO MULTIVARIADO ENTRE VARIÁVEIS FISIOLÓGICAS E DE RENDIMENTO

2 RESUMO

O estresse hídrico afeta negativamente a produção do arroz de terras altas. O objetivo deste estudo foi identificar variáveis fisiológicas que representem as respostas de rendimento em condições de estresse hídrico. Três cultivares modernos de arroz de terras altas (C): BRS A501 CL (C1), BRS Esmeralda (C2) e BRS Serra Dourada (C3) foram submetidos a três níveis de

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disponibilidade de água (W): Controle (100% da capacidade do campo durante todo o ciclo de cultivo) e 70 e 40% da água aplicada ao controle durante a floração. O rendimento, a esterilidade das espiguetas e o peso de 1000 grãos foram influenciados pelo nível de disponibilidade de água ($p < 0,05$), enquanto que para a cultivar, apenas o peso de 1000 grãos foi significativo. A interação W × C não foi significativa para os componentes de rendimento analisados. A análise multivariada revelou que as plantas bem irrigadas estiveram positivamente associadas ao rendimento dos grãos e às trocas gasosas, enquanto que o nível de 40% de disponibilidade de água esteve altamente relacionado com a esterilidade das espiguetas e o índice de estresse hídrico da cultura. O modelo mais adequado para o rendimento de grãos foi obtido utilizando fotossíntese, condutância estomática e transpiração ($R^2 = 0,76$). Assim, os parâmetros fisiológicos podem ser utilizados para explicar as variações no rendimento do arroz em terras altas sob estresse hídrico.

Palavras-chave: *Oryza sativa*, seca, regressão linear múltipla.

3 INTRODUCTIONS

Brazil is the largest producer of upland rice in Latin America (Pinheiro; Castro; Guimarães, 2006). The rice produced under upland conditions plays a vital role in both food security and economic income in central Brazil. However, the cropped area has been reduced by up to 70% since 1970. The main factor associated with this reduction was climatic risk (water stress), because upland rice commonly grows under rainfed conditions (Heinemann *et al.*, 2011). In response, EMBRAPA’s Brazilian breeding program in recent years have released drought-tolerant cultivars (Heinemann *et al.*, 2019).

According to Chauhan (1989), spikelets per panicle, spikelet sterility, and 1000-grain weight are the main yield components in rice affected under water stress. Multiple physiological alterations may underlie yield responses to this abiotic stress. For example, under water stress, stomata close rapidly, and photosynthesis is reduced (Vijayaraghavareddy et al., 2020). However, in upland rice, physiological responses are less studied compared to lowland rice. Reductions in photosynthesis during flowering lead to poor anther dehiscence, reducing spikelet fertility and, hence, yield (Quiloango-Chimarro *et al.*, 2022).

The photosynthetic performance of crops under stress conditions can be indirectly estimated through gas exchange measurements (Mathobo; Marais; Steyn, 2017). The photosynthetic rate, stomatal conductance, and transpiration are robust indicators of plant health and functional performance (Flexas; Medrano, 2002). For example, upland rice plants under water stress show significant decreases in gas exchange traits (Lanna et al., 2020; Quiloango-Chimarro *et al.*, 2022). In addition, low water availability is accompanied by high canopy temperature (Almeida *et al.*, 2022). Canopy temperature through indices such as the Crop Water Stress Index (CWSI) has been used as an indicator of plant water status and even to evaluate drought-tolerant cultivars (Biju *et al.*, 2018).

Although great efforts have been made to cope with water stress in upland rice, little attention has been given to new upland rice cultivars (drought tolerant) (Heinemann *et al.*, 2019). These cultivars could even be included in crop rotations with soybean (Nascente; Stone, 2018). Comprehensive research integrating both physiological and yield responses may be useful for upland rice genotype evaluation.

Thus, the objective of this study was to identify physiological traits that could depict yield responses under water stress conditions.

4 MATERIALS AND METHODS

4.1 Study site, field preparation, and treatment description

The experiment was conducted under rain shelter conditions in Piracicaba, São Paulo State, Brazil (22°46'39" S, 47°17'45" W, altitude of 570 m) from September to December 2020. Air temperature, relative humidity, and global solar radiation were recorded inside the shelter area and the reference evapotranspiration (ET_o) was calculated using the Penman-Monteith method. Three modern upland rice cultivars with a medium cycle (BRS A501 CL, BRS Esmeralda and BRS Serra Dourada) commonly used in central Brazil were obtained from the National Research Center for Rice and Beans germplasm bank, EMBRAPA, Brazil (Table 1).

The experiment was based on a randomized block design with split plots and four replications per treatment. The main plot was the water availability level (W), and the subplots were the upland rice cultivars (C). The three upland rice cultivars were subjected to three water availability levels: irrigation at field capacity (Fc) (Control) and 70% and 40% of the irrigation depth applied to the control at the flowering stage.

Table 1. Characteristics of the upland rice cultivars used in this study.

Cultivar	**Drought tolerance**	**Yield potential (Mg ha^{-1})**	**Description**
BRS A501 CL (C1)	S	8.1	This is the first upland rice cultivar that is resistant to the herbicide Kifix®. This cultivar has high stability in whole grain yield and good tolerance to diseases.
BRS Esmeralda (C2)	I	9.2	This cultivar is highly stable, which stands out for its rusticity and grain quality. It is moderately resistant to brusone in the panicles and grain spots.
BRS Serra Dourada (C3)	I	6.0	This cultivar is suitable for use in low-technology agricultural systems. Additionally, it is moderately resistant to brusone in the panicles and grain spots, and has an intermediate resistance to lodging.

S, susceptible; I, intermediate. **Source:** Embrapa (2022).

Upland rice seeds were manually sown on September 1, 2020, in a single row per plot. Ten days after sowing, the plants were thinned, leaving 60 plants per meter row length (60 plants plot^{-1}). Each plot consisted of a large waterproofed container with dimensions of 1.04 × 0.41 × 0.76 m (length, width, and depth), filled with soil characterized as Oxisol Typic Ustox with a sandy-loam texture.

4.2 Irrigation management

Irrigation water was provided using a drip-irrigation system. A small drip line (1 m length) with six emitters and a flow rate of 3.6 L h^{-1} was installed in each plot. In each replication of the control of each cultivar, a set of three tensiometers was installed to provide soil matric potential records for the soil layers 0.0-0.2, 0.2-0.4, and 0.4-0.6 m, respectively. Tensiometers were read every day and irrigation was triggered when the soil water potential reached -20 kPa in the first soil layer (0.0-0.2). Irrigation for control plots was computed by applying water to bring the soil water to the Fc in the first two layers (0.0-0.4), while the third layer was used for drainage control. The volumetric soil water content for each layer before irrigation was estimated from matric potential readings using the Van Genuchten (1980) approach. Plots corresponding to 70 and 40% received a fraction of the water applied to the control at the flowering stage.

4.3 Physiological traits

Physiological traits were measured at the end of the flowering stage (101 days after sowing). Net photosynthesis (A), stomatal conductance (gs), and transpiration (E) were measured in a leaf flag of each replication with a portable infrared gas analyzer (IRGA) (LiCOR-Inc, Lincoln, Nebraska, USA). The leaf gas exchange measurements were performed between 9:00 am and 12:00 pm using a concentration of 400 µmol CO_2 mol^{-1} in the leaf chamber and a photon flux density photosynthetic active of 1000 µmol m^{-2} s^{-1}.

Predawn leaf water potential was measured using a pressure chamber model 3005 (Soil Moisture, Santa Barbara, California, USA). One flag leaf from each plot was sampled between 3:00 and 5:00 AM and processed in the laboratory (Quiloango-Chimarro et al., 2022). The chlorophyll index was determined by averaging five flag leaf readings per plot using a chlorophyll meter, CFL1030 (Falker, Porto Alegre, Brazil). The canopy temperature of the rice plants was measured using an infrared sensor, TIV 6500 (Vonder, Curitiba, Brazil). Using the thermal data, CWSI was computed using the Equation 1 proposed by Idso (1980).

$$\mathrm{CWSI} = \frac{(T_c - T_{air}) - T_{wet}}{T_{dry} - T_{wet}} \quad (1)$$

Where Tair is air temperature (°C), Tc is canopy temperature (°C), Twet is the non-water stressed baseline (temperature of fully transpiring leaves with open stomata) and Tdry is the water stressed baseline (temperature of non-transpiring leaves with closed stomata). Baselines were determined using the calculation method outlined in the study by Bian et al. (2019), where Twet and Tdry were defined as the minimum and maximum temperature differences between Tc and Tair, respectively.

4.4 Yield data

At physiological maturity, plants from the central part of the row were harvested and dried in a forced ventilation oven at 60°C for 72 h. Spikelet sterility, 1000-grain weight, and grain yield were measured. Grain yield was adjusted to 130 g kg^{-1} moisture.

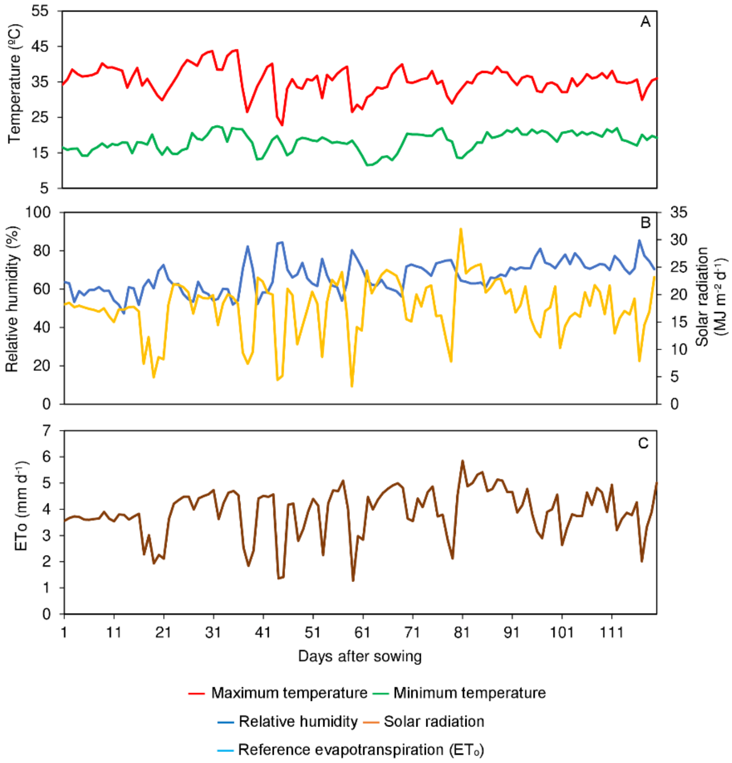
4.5 Statistical analysis

All the statistical analyses were performed with R Studio (R Core Team, 2021). Two-way analysis of variance (ANOVA) was performed after testing the homogeneity of variances and normality of the residuals using Levene and Shapiro-Wilk tests, respectively. Means were compared using Tukey's test at the 5% probability level. Principal component analysis (PCA) was conducted to examine the relationship between grain yield and physiological traits after Bartlett's test of sphericity, which was used to check the appropriateness of the dataset. Simple and multiple linear regressions were fitted to model yield, spikelet sterility and 1000-grain weight as functions of physiological traits. A backward stepwise variable selection procedure was run to identify significant variables (at the 0.05 probability level) (Borboudakis; Tsamardinos, 2019). Model selection was based on Bayesian information criterion (BIC), residue analysis, and determination coefficient (R^2).

5 RESULTS AND DISCUSSION

The mean maximum and minimum air temperatures recorded during the entire growing cycle were 35.5 and 18.7 °C, respectively (Figure 1). The average maximum air temperature slightly exceeded the optimal range for rice growth, particularly during the booting and flowering stages (Shah et al., 2011). Additionally, the average reference evapotranspiration was 3.9 mm day^{-1} between sowing and maturity.

Figure 1. Meteorological variables.



The cumulative irrigation in the control plots varied between 792 and 876 mm, which is consistent with the results of Kato, Kamoshita and Yamagishi (2006) and Suleiman *et al.* (2022) for other upland rice cultivars. It is remarkable that water consumption differed by 83 mm between the largest and smallest water-consuming cultivars, since all cultivars had the same growing cycle duration (Table 2).

Table 2. Irrigation water amount for three upland rice cultivars.

	Irrigation water applied (mm)								
	Control			70%			40%		
Growing stage	**C1**	**C2**	**C3**	**C1**	**C2**	**C3**	**C1**	**C2**	**C3**
Sowing to anthesis	487	531	473	487	531	473	487	531	473
Anthesis to end of flowering	213	206	179	149	144	125	85	83	72
End of flowering to end of grain filling	136	138	140	136	138	140	136	138	140
Total	836	876	792	772	814	738	708	752	685

C1, BRS A501 CL; C2, BRS Esmeralda; C3, BRS Serra Dourada. **Source:** The authors.

Yield, spikelet sterility, and 1000-grain weight were influenced by the water availability level (W), but only 1000-grain weight was significant for cultivar (C) (Table 3). No significant differences were observed between the cultivars. According to Fukai and Mitchell (2022), rice cultivars with the same growth cycle exhibit similar yield. In this study, all cultivars reached physiological maturity at 121 days, and the yields among cultivars for each irrigation management were similar. The W × C interaction was also insignificant for these three variables. For further analysis, cultivar data were pooled.

Table 3. ANOVA for yield components.

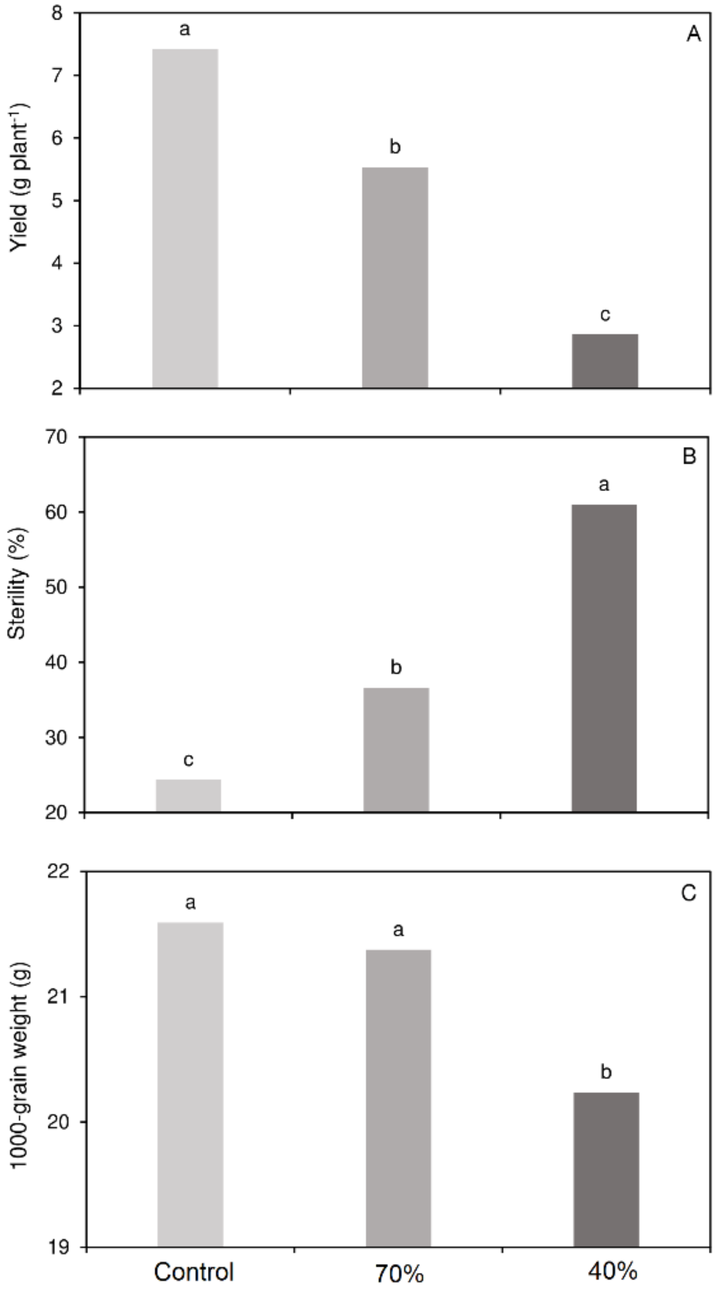
Source	Yield	Spikelet sterility (%)	1000-grain weight (g)
Water availability (W)	**	**	*
Cultivar (C)	ns	ns	**
W X C	ns	ns	ns

Source: The authors.

Grain yield, spikelet sterility, and 1000-grain weight were influenced by water stress. Moderate water stress (70% Fc) significantly reduced grain yield and increased spikelet sterility by 27 and 14%, respectively (Figure 2). According to Melandri et al. (2021), moderate stress during flowering can result in strongly reduced grain yield in rice. For example, Kitilu, Nyomora and Charles (2019) reported a 32% reduction in grain yield under moderate stress during flowering, which is similar to the results of our study.

Severe stress (40% Fc) affected all grain yield components evaluated. Grain yield and 1000-grain weight were reduced by 60 and 6%, respectively, whereas spikelet sterility was increased by 64%. These results suggest that severe water stress is a robust indicator of reduced grain yield, spikelet, and 1000 grain weight in upland rice, as suggested by Lafitte et al. (2007) Additionally, spikelet sterility is the main factor associated with grain yield reduction when stress occurs during flowering (Boonjung; Fukai, 1996).

Figure 2. Effect of water availability level over grain yield components.



Physiological parameters were significantly affected by water stress, particularly under severe water stress conditions (40% Fc) (Table 4). Moderate water stress resulted in variations in photosynthesis, stomatal conductance, transpiration, and CWSI compared with the control treatment (100%). Under severe water stress, all physiological parameters examined showed significant differences from the control treatment, with the exception of the chlorophyll index.

Water stress reduces photosynthesis, stomatal conductance, and transpiration (Akram *et al.*, 2013). When plants are under water stress, they may close their stomata to conserve water, thereby reducing their photosynthetic rate (Quiloango-Chimarro et al., 2022). No changes were expected in the chlorophyll index under water stress because the effect of water stress on chlorophyll content in rice can vary depending on the rice variety and severity of the stress (Khan *et al.*, 2017). Reductions in the leaf water potential indicate that water stress can cause a reduction in the water content of rice plants, which can ultimately lead to a decrease in photosynthetic activity (Khorsand *et al.*, 2021). CWSI decreased even under moderate stress; therefore, this canopy temperature-derived index can provide insights into how rice plants respond to water stress (Biju *et al.*, 2018). For example, Heravizadeh *et al.* (2022) reported that in rice, with each degree of increase in canopy temperature, the grain yield decreased by 1942 kg ha^{-1}. Overall, by assessing physiological parameters, researchers may better understand the physiological responses of rice plants to water stress and their effects on grain yield reductions.

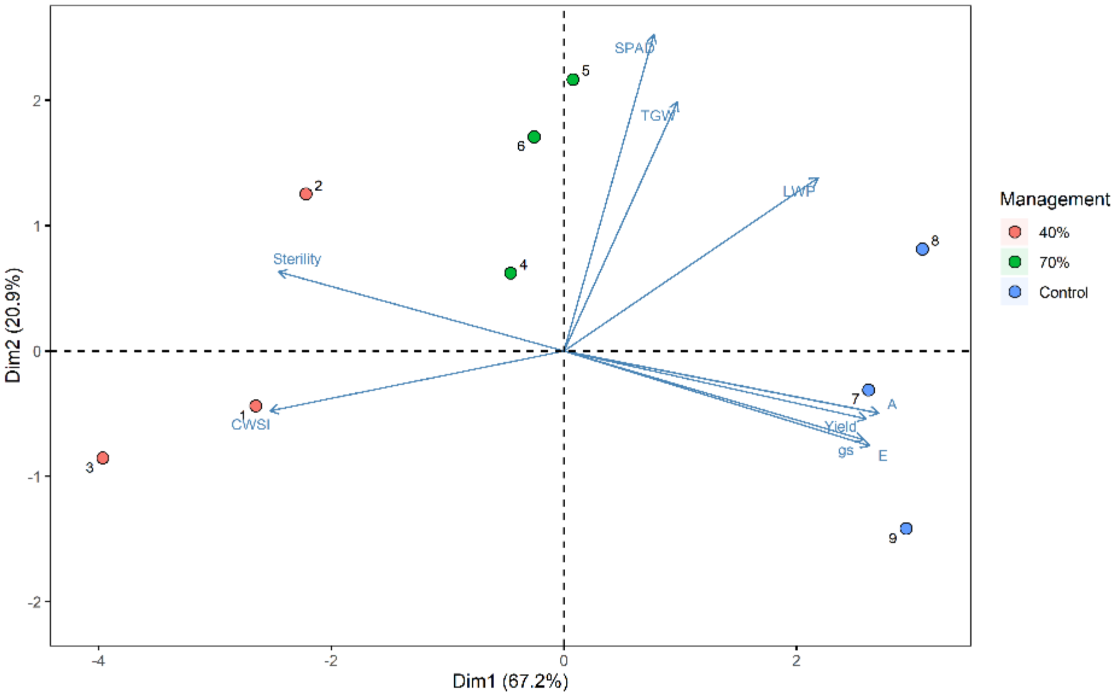
Table 4. Effect of water availability level over physiological traits.

Variable	Control	70%	40%
Photosynthesis	20.22 ± 1.10 a	11.35 ± 1.11 b	2.39 ± 0.65 c
Stomatal conductance	0.26 ± 0.02 a	0.09 ± 0.01 b	0.03 ± 0.01 b
Transpiration	7.18 ± 0.34 a	3.27 ± 0.35 b	1.23 ± 0.15 c
Chlorophyll index	47.13 ± 1.07 a	47.56 ± 0.79 a	45.92 ± 0.73 a
Leaf water potential	-0.65 ± 0.05 a	-0.77 ± 0.09 a	-1.21 ± 0.09 b
CWSI	0.32 ± 0.04 c	0.48 ± 0.05 b	0.65 ± 0.05 a

Source: The authors.

The first two principal components (PCs) explained 88.1% of the total variance, with PC1 and PC2 accounting for 67.2 and 20.9%, respectively (Figure 3). The control was concentrated on the positive side of PC1 and was highly related to the leaf water potential, photosynthetic rate, stomatal conductance, and transpiration. A water availability level of 40% was on the negative side of PC1 and was correlated with CWSI and spikelet sterility. A water availability level of 70% was concentrated on the positive side of PC2 and correlated with the chlorophyll index and 1000-grain weight.

Figure 3. Principal component analysis of the evaluated traits in three upland rice cultivars. TGW, 1000-grain weight; A, photosynthetic rate; gs, stomatal conductance; E, transpiration; LWP, leaf water potential; SPAD, chlorophyll index. Each point within each management represents one cultivar.



To establish potential associations between yield components and physiological traits, fitted regression models including photosynthetic rate, stomatal conductance, transpiration, leaf water potential and chlorophyll index were performed (Table 5). The best fitted regression for yield was a multiple regression (BIC = -39.6) that included photosynthesis, stomatal conductance and transpiration, explaining 76% of its total variability. The strong association observed between these variables and crop yield suggests that yield is dependent on photosynthetic assimilates in the later stages of the growth cycle, particularly when the crop experiences significant source limitations (Ergo *et al.*, 2018).

The regression equation for spikelet sterility showed a significant linear contribution of stomatal conductance and transpiration (BIC = -29.4), explaining 61% of spikelet sterility across treatments. As reported by Shah et al. (2011), elevated temperatures have been observed to cause spikelet sterility. The decrease of stomatal conductance contributes to higher canopy temperatures, resulting in elevated spikelet sterility. Furthermore, alterations in stomatal conductance can substantially influence transpiration, ultimately affecting spikelet sterility (Li *et al.*, 2017).

Linear regression analysis showed that the chlorophyll index was the best predictor of 1000-grain weight (BIC = -4.39), explaining 28% of the total variability of this yield component. The fitted model indicated that the response of 1000-grain weight to the chlorophyll index was linear and positive, with a slope of 0.33 units. The 1000-grain weight is an important factor that determines rice yield (Xu; Chen; Xu, 2015). However, the low R-squared value suggests that the linear model was inadequate. Thus, future research should explore other models to explain the 1000-grain weight better.

Table 5. Regression equations for soybean yield (g plant^{-1}), spikelet sterility (%) and 1000-grain weight (g) on physiological variables during flowering across the three water availability levels (Control, 70% and 40%).

Dependent variable	Explanatory variable	Regression coefficient	Standard error	p-value	Adjusted R^2
Grain yield	Bo	1.91	0.39	0.0002	0.76
	A	0.12	0.06	0.0566	
	gs	-20.82	8.53	0.0203	
	E	1.19	0.38	0.0037	
Spikelet sterility	Bo	68.61	4.59	0.0003	0.61
	gs	205.74	99.72	0.0471	
	E	-13.91	3.97	0.0013	
1000-grain weight	Bo	5.65	4.32	0.2004	0.28
	CI	0.33	0.09	0.0011	

Bo, Constant; A, Photosynthesis; gs, Stomatal conductance; E, Transpiration; CI, Chlorophyl index. **Source:** The authors.

6 CONCLUSIONS

Water stress in upland rice influenced the physiological and yield traits to a large extent under severe water stress. Remarkably, the grain yield did not differ among the modern upland rice cultivars used in this study.

The main component that reduced grain yield was spikelet sterility. In contrast, high photosynthetic rates were linked to high grain yields.

A reasonable model to predict grain yield was found using gas exchange traits: photosynthesis, stomatal conductance, and transpiration (R^2 = 0.78).

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