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Gas exchange and chlorophyll fluorescence of four sorghum genotypes under drought stress and rehydratation

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Abstract: Water deficit (drought) is an important environmental factor affecting physiological processes in plants. The present work focuses on the study of changes in physiological responses of juvenile plants (plants in the vegetative phase of growth BBCH 14–16) of selected sorghum genotypes Dokok, 30485, Barnard Red and Ruzrok to water deficit and after rehydration. Water deficit affected the observed physiological parameters – gas exchange and chlorophyll fluorescence. Genotypic differences were also confirmed, with Dokok appearing to be the more sensitive genotype and Ruzrok and Barnard Red appearing to be tolerant. Following rehydration, these parameters increased but did not reach the levels of the control plants. A significant decrease in photosynthetic rate (P_n), transpiration (E) and fluorescence compared to the control was found in the water-deficient variant twice for 10 days and 6 days between rehydration periods. Only in the variant where water deficit (14 days) was followed by irrigation (10 days) transpiration increased in genotype 30485. Chlorophyll fluorescence (F_v/F_m) also decreased significantly in this cultivar. The results suggest that a rehydration period of 14 days is insufficient to restore the photosynthetic functions of stressed sorghum plants.

Keywords: photosynthesis; transpiration; genotype; *Sorghum bicolor* (L.) Moench; water deficit

Globally, water deficit (drought) is a primary factor in reducing crop yields, more than the combined effect of all other factors affecting crop production (Manivannan et al. 2008). According to Yang et al. (2021), drought can inhibit plant respiration, photosynthesis and stomatal movement, thereby affecting plant growth and metabolism. Visual symptoms of water deficit during the growing season include reduction in plant height, as documented by Anjum et al. (2017) for maize and Patmi et al. (2020) for rice, leaf wilting, and changes in leaf number and area (Hosseini et al. 2017, Mishra et al. 2018, Patmi et al. 2020).

Leaves of plants growing under drought conditions have lower leaf area, greater thickness and higher tissue density (Xiong et al. 2016, Dong et al. 2020). According to Prasad et al. (2019) and Djanaguiraman et al. (2020), this is due to a reduction in turgor, photosynthetic rate and assimilate availability (Zhang et al. 2022). Net photosynthetic rate is a direct reflection of material productivity per leaf area. Photosynthesis and transpiration rates decrease with decreasing relative soil water content. Water deficit directly reduces photosynthesis by decreasing CO_2 availability, reducing stomatal and mesophyll diffusion (de la Riva et al. 2016, John et al. 2017, Nardini 2022). In wheat, for example, results from Ashraf et al. (2017) show that drought reduces stomatal conductance and increases stomatal resistance, reducing photosynthesis and transpiration rates. Similar findings have also been confirmed in cotton (Deeba et al. 2012) and sorghum (Fracasso et al.

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2016, Lopez et al. 2017, Zhang et al. 2019b), causing an overproduction of reactive oxygen species (ROS), leading to oxidative stress (Kar 2011). In addition, changes in photochemical and biochemical processes, such as a decrease in electron transfer rate (Wang et al. 2018, Aliyeva et al. 2020, Todorova et al. 2022) and photophosphorylation (Yang et al. 2021) are also observed.

Reduction in photosynthetic rate in stressed plants also occurs due to reduction in photosynthetic pigments (Sapeta et al. 2013). According to Munné-Bosch et al. (2001), Fadoul et al. (2018), and Amoah and Antwi-Berko (2020), sorghum is affected by drought stress due to reduction in chlorophyll content, chlorophyll *a* and *b* ratio and carotenoids. The reason for the decrease in leaf chlorophyll content may be due to chlorophyll degradation directly caused by drought, a conclusion confirmed by Mafakheri et al. (2010) in chickpeas. Changes in plant pigments lead to a change in the plant's colour to yellow-brown when it suffers from drought. Regarding drought tolerance, plants with high chlorophyll content generally have higher drought tolerance (Yang et al. 2021).

Sorghum [*Sorghum bicolor* (L.) Moench], a C4 plant, is the fifth most important cereal in the world in terms of global production and one of the most drought-tolerant cereals (Rooney 2004). Although sorghum is considered a drought-tolerant crop, water deficit can affect its ability to take nutrients from the soil and mobilise and transport nutrients (Sarshad et al. 2021).

According to Husen et al. (2014) and Zhang et al. (2019a), plant responses to stress include changes in water use efficiency, transpiration rate, and remobilisation of photosynthetic assimilates, as well as biochemical changes involving proline and other metabolites. The ratio of variable to maximum F_v/F_m fluorescence, which refers to the maximum quantum yield of photosystem II, is an important tool for measuring the impact of drought stress on photosynthesis (Husen 2010). It is used as an indicator of the level of photosynthetic efficiency, which is significantly lower in sorghum grown under drought-stress conditions (Johnson et al. 2014). Sukumaran et al. (2016) state that tolerant sorghum genotypes have significantly higher F_v/F_m values and photosynthetic rates under drought stress conditions. In addition, drought-tolerant genotypes showed significantly higher water use efficiency (WUE) than drought-sensitive genotypes (Fracasso et al. 2016). Given the above, the aim of this study was to investigate changes in the physiological response of juvenile plants (plants in the vegetative phase of growth BBCH 14–16) of selected sorghum genotypes; its main objective was to determine the suitability of physiological parameters used to detect resistance/sensitivity of sorghum plants to water deficit.

MATERIAL AND METHODS

Plant material and experimental conditions. The effect of long-term water deficit was studied in selected sorghum (*Sorghum bicolor* (L.) Moench subsp. *bicolor*) genotypes. These were genotype Dokok (S1), originating from Argentina; genotype 30485 (S2), originating from the Russian Federation; genotype Barnard Red (S3), also originating from Argentina; genotype Ruzrok (S4), a Czech cultivar.

Gas exchange rate and chlorophyll fluorescence were monitored in experimental sorghum plants at the juvenile stage of development; this is the vegetative phase, stage 4–6 leaves (BBCH 14–16).

Seeds were obtained from the RICP Genetic Bank, v.v.i. Prague-Ruzyně, Czech Republic. Sorghum plants were grown in 1 650 cm^3 containers. The greenhouse was located on the premises of the Czech University of Life Sciences, Prague, and the air temperature during the experiment was maintained at 25 °C during the day and 19 °C at night, with a natural light regime of 14 h of light and 10 h of darkness, and a relative humidity of 66%. Sorghum plants were irrigated to 70% substrate moisture by volume (150 mL of water per container). The experimental plants were grown in the horticultural substrate (AGRO CS: pH 5–6.5, nutrient content: 160–240 mg N/kg, 44–88 mg P/kg, 166–248 mg K/kg; 80% white peat, 20% black peat, 20 kg soil/m^3, texture 0–10 mm). It also contained 55% of the combustible matter in the dried sample and a maximum of 5% of particles larger than 25 mm. The experimental design included four variants (Table 1).

Gas exchange parameters. Gas exchange was measured using a non-destructive method, an integrated fluorometer, and a gas exchange system called iFL (ADC Bioscientific Ltd., Hoddesdon, UK). Net photosynthetic rate (P_n) and transpiration rate (E) were measured on a photosynthetically mature leaf in the central part of the leaf blade. Gas exchange rate and stomatal conductance (g_s) were derived from P_n (Kuklová et al. 2016). The gas exchange rate was measured in the morning (8–13 h UTC) at an irradiance density of 650 μmol/m^2/s and temperature

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Table 1. Experimental design

Variant	Day of experiment					
	0–5th	6th–10th	10th–14th	14th–19th	19th–24th	24th–28th
Control (CC)	irrigation					
Stress 1 (CS)	irrigation		drought			
Stress 2 (SC)	drought		irrigation	drought		irrigation
Stress 3 (SS)	drought		irrigation			

of 25 °C according to the methodology of Kuklová et al. (2016). The CO_2 levels were natural, with no artificial increase. To obtain a balanced CO_2 level in the measuring chamber, the instrument was connected to a CO_2 supply from a height of about 2.5 m, where the CO_2 concentration was 370–380 mmol/mol and was relatively stable.

Fluorescence parameters. Fluorescence was measured on the same leaves as the photosynthetic rate. These were the maximum quantum yield of photosystem II (F_v/F_m), the ratio of maximum fluorescence to initial fluorescence (F_m/F_0) and the ratio of variable fluorescence to initial fluorescence (F_v/F_0). An integrated fluorometer and gas exchange system – iFL (ADC Bioscientific Ltd., Hoddesdon, UK) was used to measure fluorescence parameters. Plant leaves were adapted to darkness for 30 min. They were then exposed to a light saturating pulse of 7 000 mmols for 0.30 s. After that, the saturating light pulse was lowered by 20% (5 600 mmol). The ramping rate is less than 0.01 mol photons/m^2/s. The final phase is at 7 000 mmols to check for saturation pulse.

Statistical analysis. Five independent biological replicates were used within the respective variant in the experiments. There were always 5 repetitions per measurement. Physiological characteristics were measured non-destructively on one average plant per pot. Three additional containers were always available as technical replicates. Variability in differences in parameters of interest for all treatments was tested using two-way ANOVA ($P < 0.05$) followed by Tukey's post hoc test for significant differences between treatments. Data were analysed using Statistica 13.5 software (StatSoft, Tulsa, USA).

RESULTS AND DISCUSSION

Bicoloured sorghum is considered a drought-tolerant crop and, therefore, has the potential to be grown in more arid conditions. The focus of this research was to investigate the tolerance of juvenile sorghum plants to alternating periods of water deficit and subsequent rehydration.

The photosynthetic rate was significantly affected by the experimental variant and genotype at the alpha = 0.05 significance level, as documented in Figure 1. From these graphs, it can be seen that genotype S3 exhibited the lowest P_n during the experiment, with an average photosynthetic rate of 13.19 mmol CO_2/m^2/s. On the other hand, genotype S2 had the highest average photosynthetic rate (15.07 mmol CO_2/m^2/s).

From the results obtained, it is clear that genotypic differences in response to water deficit and irrigation have been confirmed, as genotype S1 appears to be more sensitive to water deficit, while S4 and S3 appear to be tolerant. Genotypic differences in sorghum are confirmed by Fracasso et al. (2016), Verna et al. (2018), and Gano et al. (2021). Similar results for slagwood are confirmed by Zhang et al. (2023) and Hamouzová et al. (2024). Physiological changes have been demonstrated for sorghum genotypes sensitive to water deficit, mainly involving changes in gas exchange rates (Zhang et al. 2019b).

The highest P_n was measured in control plants (CC) for all genotypes studied, increasing during ontogenetic development. The range of measured P_n values of control plants was 13.13 mmol CO_2/m^2/s (S3, day 0) to 16.01 mmol CO_2/m^2/s (S2, 28 days). The photosynthetic rate decreased in all genotypes due to water deficit. After rehydration, photosynthesis increased relative to the water deficit but did not reach the values of control plants. The highest decrease in photosynthesis due to water deficit (SS) was found in genotype S1, where the photosynthetic rate decreased from 13.13 mmol CO_2/m^2/s (day 0) to 12.77 mmol CO_2/m^2/s (day 10); during rehydration, photosynthesis decreased inconclusively, and the decrease was observed until the end of the experiment (12.21 mmol CO_2/m^2/s). On the other hand, in the case of cultivar S3, the decrease in photosynthetic rate was conclusively the lowest. In the case of the

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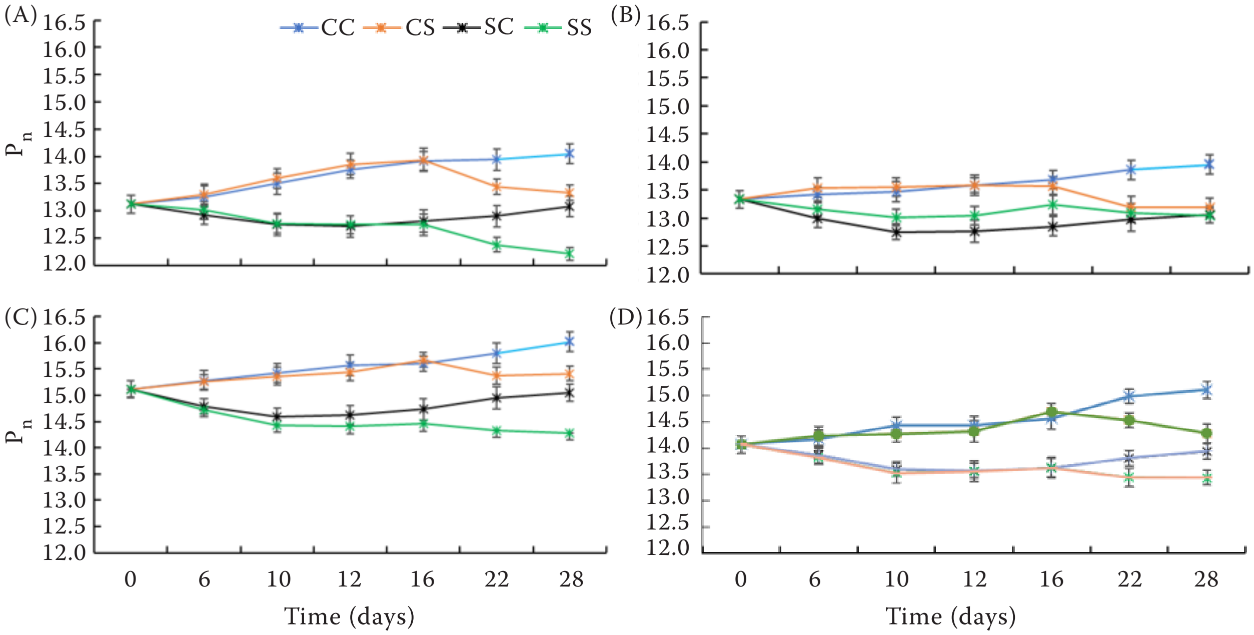

Figure 1. Changes in photosynthetic rate (P_n) (mmol $CO_2/m^2/s$) in juvenile sorghum plants as a function of duration of water deficit and rehydration. (A) Dokok (S1); (B) 30485 (S2); (C) Barnard Red (S3), and (D) Ruzrok (S4)

SS variant, the photosynthetic rate of this cultivar decreased by 0.33 mmol $CO_2/m^2/s$ (2.4%) before rehydration and by 0.19 mmol $CO_2/m^2/s$ (1.44%) after subsequent rehydration.

Under the influence of water deficit, sorghum plants showed a gradual decrease in the rate of gas exchange (A, E), which was probably caused by a reduction in stomatal conductance, the content of photosynthetically active pigments, and a change in electron transport within photosystem II, as well as a decrease in the activity of photosynthesis-related enzymes such as Rubisco (Simova-Stoilova et al. 2020, Amaral et al. 2024) and PEPCase (Bao et al. 2017). Thus, photosynthesis is one of the metabolic processes affected by water deficit (Gano et al. 2021, Zhang et al. 2022). According to Hnilicka et al. (2023), the sink-source relationship and the distribution of ATP and NADPH are disrupted in wheat plants due to water deficit. The above effect can also be expected in sorghum plants.

However, the rehydration duration was insufficient to restore full photosynthesis to the control plants. According to Martínez-Goñi et al. (2023), a rehydration period of 7 days is short. The results suggest that the rehydration duration should be longer than 14 days.

Figure 2 shows the changes in the transpiration rate of the sorghum genotypes studied as a function of the effect of water deficit and rehydration. From the results obtained, it is clear that the transpiration rate, like the photosynthesis rate, was influenced by the genotype. The lowest transpiration rate was observed for genotype S1 (0.96 mmol $H_2O/m^2/s$), while the highest transpiration rate was observed for genotype S4 (1.72 mmol $H_2O/m^2/s$).

The control plants had the highest transpiration throughout the study period, with values increasing in all genotypes depending on the ontogenetic development of the plants. The highest increase in transpiration was observed in genotype S2 (76.26%; 1.82 mmol $H_2O/m^2/s$) and the lowest in S3 (13.96%; 1.81 mmol $H_2O/m^2/s$). However, this is not a significant difference. On the other hand, genotype S4 showed the most significant reduction in transpiration of 0.51 mmol $H_2O/m^2/s$, with transpiration of 1.12 mmol $H_2O/m^2/s$ at the end of the experiment. This was a significant reduction.

There was a gradual reduction in transpiration in all genotypes due to water deficit; since a reduction in transpiration due to water deficit was demonstrated, it can be assumed that stomatal inhibition of gas exchange is involved. In the case of the variant where water deficit followed irrigation, it can be noted that only in genotype S2 the transpiration rate first increased and then decreased, but the transpiration value at the end of the water deficit was 0.11 mmol $H_2O/m^2/s$ higher than at the end of the irrigation (1.12 mmol $H_2O/m^2/s$).

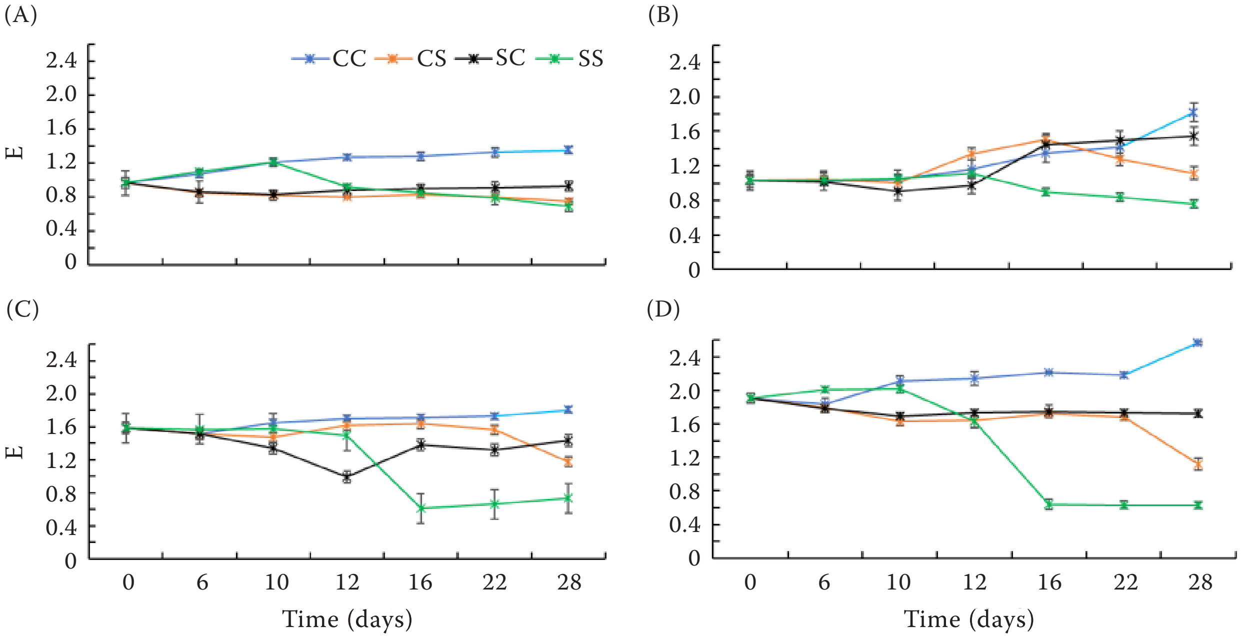

Figure 2. Changes in transpiration rate (E) (mmol $H_2O/m^2/s$) in juvenile sorghum plants as a function of duration of water deficit and rehydration treatment. (A) Dokok (S1); (B) 30485 (S2); (C) Barnard Red (S3), and (D) Ruzrok (S4)

The reduction in transpiration due to drought was confirmed by the work of Wasaya et al. (2021), and Hnilicka et al. (2023) for wheat plants, but the results obtained were also consistent with the work of Van Ooster et al. (2021) and Raymundo et al. (2024) for sorghum. The resistant sorghum genotypes S4 and S2 had a lower transpiration rate than the other genotypes. Thus, it can be assumed that lower transpiration rates are associated with resistance to water deficit, as also reported by Lopez et al. (2017). This is also pointed out by Martínez-Goñi et al. (2023).

In the case of rehydration, there is a gradual increase in transpiration in all the genotypes studied, but at the end of rehydration, the transpiration rate was lower than at the beginning of the experiment, except for genotype S2. In this genotype (Figure 2B), transpiration increased significantly compared to the beginning of the experiment. A similar trend was also observed in the SS variant, where water deficit was induced twice for 10 days, and the rehydration period was 6 days. During the subsequent rehydration period, an increase was recorded for all the parameters and sorghum genotypes studied, which, except for the transpiration of genotype S2, was lower than that of the control plants. This trend is probably related to the subsequent recovery of plant growth. The increase in gas exchange rate due to rehydration is probably related to turgor recovery, long-lived cell growth and new tissue formation. Deligoz and Gur (2015) state that water deficit affects cell division in pinyon pine leaves.

An important parameter in determining the degree of damage to the photosynthetic apparatus of plants is the ratio of variable to maximum chlorophyll fluorescence. According to Lichtenthaler et al. (2005), fluorescence values of 0.750–0.840 are considered to be those of unstressed plants. The above statement is confirmed by control plants of all genotypes. Furthermore, Figure 3 shows no clear F_v/F_m ratio differences are found during ontogenetic development. Furthermore, genotypic differences within control plants were not confirmed. For all stressed variants and genotypes, the F_v/F_m ratio decreased, but the differences were inconclusive. The changes in fluorescence values are consistent with the work of Bashir et al. (2021) and Peršić et al. (2022). Therefore, it can be concluded that these results are consistent with the work of Chen et al. (2016) and Aliyeva et al. (2020), which suggest a high adaptability to water deficit.

In the CS variant, fluorescence clearly decreased during the period of water deficit, whereas the decrease was linear in genotypes S1 and S3. In these genotypes, fluorescence decreased from a value of 0.811 (day 10) to values of 0.769 and 0.767, respectively. Physiological changes have been demonstrated in sorghum genotypes sensitive to water deficit, mainly including changes in the maximum quantum yield

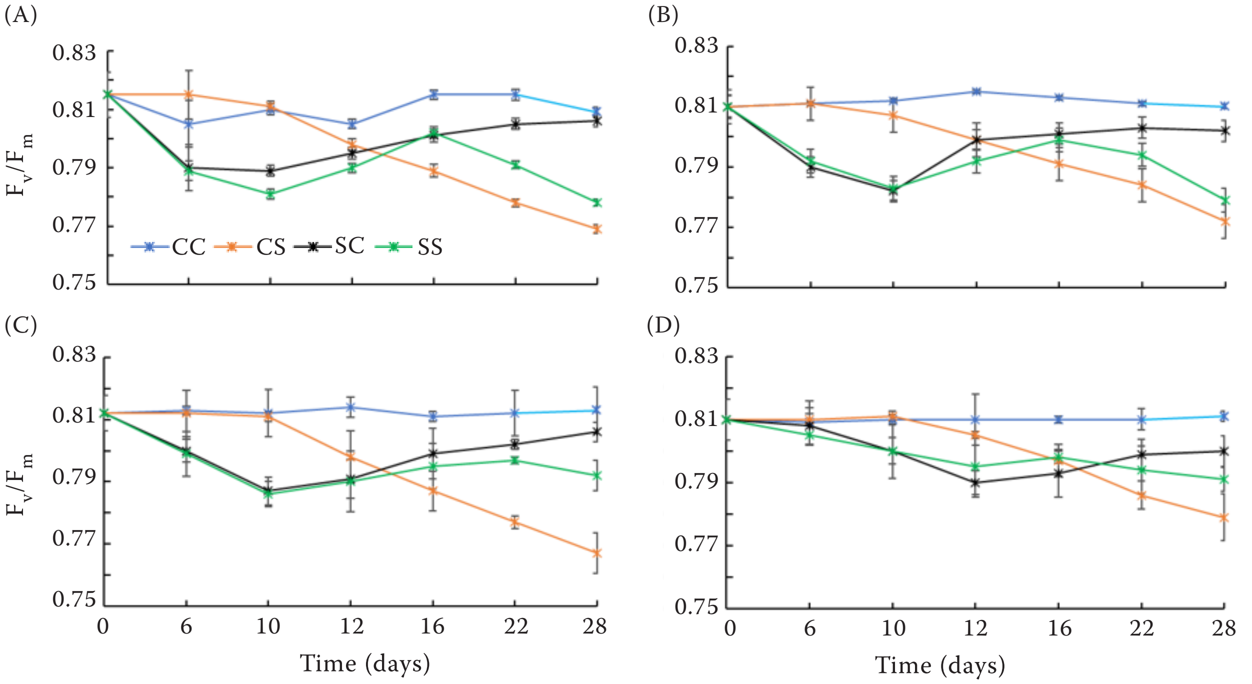

Figure 3. Changes in chlorophyll fluorescence (F_v/F_m) values in juvenile sorghum plants as a function of the duration of water deficit and rehydration. (A) Dokok (S1); (B) 30485 (S2); (C) Barnard Red (S3), and (D) Ruzrok (S4)

of photosystem II (F_v/F_m) (Husen et al. 2014, Ali et al. 2019, Sherin et al. 2022).

Genotype S4 showed the lowest reduction in fluorescence, with an F_v/F_m ratio of 0.811 at the end of irrigation and 0.779 at the end of the experiment.

Genotype S4 showed the lowest reduction in fluorescence, with an F_v/F_m ratio of 0.811 at the end of irrigation and 0.779 at the end of the experiment. Figures 3A and 3C show that the effect of rehydration after the water deficit period (SC) resulted in a clear increase in the F_v/F_m ratio for genotypes S1 and S3. In contrast, an inconclusive increase was observed for genotypes S2 and S4 (Figures 3B, D). The Fv/Fm ratio decreased in all genotypes studied for the SS variant due to both water deficit periods. During the first drought period, there was an inconclusive decrease in fluorescence in genotypes S1 and S3. For these genotypes, the Fv/Fm values range from 0.815 and 0.812 (day 0) to 0.781 and 0.786 (day 10), respectively. In contrast, genotype S4 seemed to be tolerant to water deficit. In this genotype, the fluorescence decreased from 0.010 to 0.791 (day 10). From the results, it is clear that tolerant sorghum genotypes have significantly higher F_v/F_m values, which is also confirmed by the work of Fracasso et al. (2016), Sukumaran et al. (2016). Changes in F_v/F_m in stressed plants may be induced by plant defence mechanisms related to energy dissipation, heat dissipation, reduced photosynthesis and photoinhibition. The effect of photoinhibition on fluorescence parameters has been reported by Stefanov et al. (2023).

On subsequent rehydration, fluorescence increased but did not reach the levels of control plants. In the second water deficit period, fluorescence decreased again. An effect identical to that of the first water deficit period was confirmed. In sorghum plants, F_v/F_m values increased after subsequent rehydration, whereas no clear differences were found between control and stressed plants. This is probably related to the rapid regeneration of photosystem II and subsequent photosynthesis. Sorghum plants appear to use water resources to restore normal photosynthetic activity after drought, restoring photosynthesis by repairing the photosynthetic apparatus, as reported by Martínez-Goñi et al. (2023).

In greenhouse experiments, the effect of water deficit and subsequent rehydration on sorghum plants of genotypes Dokok, 30485, Barnard Red and Ruzrok in the vegetative stage of development was studied. Selected physiological traits were used as criteria for evaluating resistance or sensitivity to water deficit: gas exchange rate and fluorescence. These parameters were reduced by water deficit in all genotypes studied, with the Dokok genotype being more sensitive and the Ruzrok and Barnard

Red genotypes tolerant. The results further showed that a rehydration period of 14 days is insufficient to restore the photosynthetic functions of stressed sorghum plants.

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