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Effects of progressive soil drying on sorghum leaf physiology

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Abstract
Sorghum [*Sorghum bicolor* (L.) Moench] is an important dryland cereal grown in arid and semi-arid regions to achieve food and nutritional security. The major problem associated with arid and semi-arid regions of the world is drought stress, limiting the sorghum yield. Therefore, one of the approaches to increase sorghum productivity in dryland agriculture is understanding the mechanism of drought tolerance. Therefore, the present study was conducted to (i) quantify the diurnal variation in transpiration rate of sorghum genotype differing in root angle and (ii) quantify the effect of progressive soil drying on leaf physiological traits. Two sorghum lines, IS13540 and IS23143, were grown under fully irrigated conditions up to the six-leaf stage; after that, the plants are subjected to progressive soil drying conditions for four days to understand the mechanism of drought tolerance. Between the lines, the line IS13540 had a lower transpiration rate than IS23143 from the start of drying to progressive soil drying. The results indicated that a higher fraction of transpirable soil moisture (FTSW) threshold value (0.622) was observed for the line IS13540 than for IS23143 (0.531). In contrast, a lower stomatal conductance and higher photosynthetic rate were observed in line IS13540 than IS23143. Overall, it is evident that the line IS13540 is more tolerant to drought than IS23143, as evidenced by a lower transpiration rate and higher photosynthetic rate.

Keywords: Drought, sorghum, progressive soil drying, FTSW, lower transpiration, break point

Introduction
Sorghum is the fifth most grown cereal and staple food crop for millions of people in arid and semi-arid regions. Sorghum has high yield potential, but due to several abiotic stress at critical growth stages, the grain yield of sorghum is highly reduced. Among the abiotic stress, drought is the most important stress that leads to reduced grain yield in sorghum. It was predicted that the intensity of drought would increase (IPCC 2021) [1], and every 0.5 °C increase in air temperature will increase the extremes of drought stress (IPCC 2021) [1]. Therefore, to improve the drought tolerance of sorghum, it is crucial to understand the drought tolerance mechanisms.

Sorghum drought tolerance mechanisms are (i) water savers and (ii) water spenders. The plant exhibits strong stomatal control in the water saver mechanism, thereby conserving soil moisture through reduced stomatal conductance (Beebe *et al*., 2013) [2]. In the water spender mechanism, the plant increases the rooting depth (Beebe *et al*., 2013) [2], which could increase the water acquisition from deeper soil layers. Osmotic adjustment is another mechanism associated with water spender to maintain tissue water status by accumulating compatible and osmotically active solutes (Acevedo *et al*., 1979) [3]. Reduction in soil moisture also leads to the accumulation of leaf level abscisic acid (ABA), which can cause stomatal closure. ABA can also reduce the leaf level hydraulic conductance, eventually results in a reduced transpiration rate (Pantin *et al*.2012) [4].

The detailed mechanism of drought tolerance in sorghum was explained. However, the response of genotype differing in root angle for progressive soil drying was not quantified earlier. Therefore, the present study was conducted to (i) quantify the diurnal variation in transpiration rate of sorghum genotype differing in root angle and (ii) quantify the effect of progressive soil drying on leaf physiological traits.

Materials and Methods
Plant materials and crop husbandry
An outdoor dry-down experiment in a randomized block design with five replications was

conducted at the Department of Crop Physiology, Tamil Nadu Agricultural University, Coimbatore (11°N; 77°E; 426.7 m MSL), India, to understand the response of sorghum line differing in root angle to progressive drying soil. The 2mm sieve was used to sieve the clay loam soil, and the fraction that passed through was again sieved with a 1mm sieve. The final fraction was collected and mixed with vermicompost in the ratio of 20:1. This mixture is collectively called soil thereafter. 22 kg of soil was filled in a pot (30 cm diameter and 25 kg capacity) having three holes at the bottom for drainage and to each pot, 3 g of urea, 2 g of diammonium phosphate, and 2 g of muriate of potash was added on top of the soil and mixed well. The pots were irrigated up to 100% field capacity (FC), and then three seeds of each sorghum line (IS13540 and IS23143) were sown at 3 cm depth in each pot. The genotype IS13540 had a narrow root angle, and IS23143 had a wider root angle. After seedling emergence, the seedling in the pot was thinned to one and maintained till the completion of the experiment. Plants were grown under the natural sunlit condition at photosynthetic active radiation (PAR) value of 1500 - 1600 μmol m^{-2} s^{-1} from sowing to the six-leaf stage (50 DAE). The plants were irrigated from emergence to 50 d of emergence on an alternate day until water leaks from the bottom. On the 50th day evening (04.00 – 05.00 PM), the plants were irrigated to FC, and the top of the pot with the plant was completely covered with a PVC sheet by making a small slit, and there was no space between the plant and the sheet/slit. The slit was covered with white packing adhesive tape around plant collars to minimize evaporation from the soil surface (Fracasso *et al*., 2016) [5].

Then, the pot weight was recorded in the morning to get the weight at FC on the following day. The pots were weighed daily at an hourly interval from 8.00 AM to 4.00 PM. The environmental condition during the drought stress period was presented in Fig. S1. During the dry-down period, the daytime maximum temperature ranged between 39 and 41 °C, and the nighttime minimum temperature ranged from 22 to 24 °C. Similarly, the daytime relative humidity ranged between 30 to 40% and nighttime humidity from 80 to 95%. The pots were dry over approximately four days, and during this period, water was not added to the pot. The total transpirable soil water content was determined as the difference between the soil water content at FC and wilting point (WP). As described above, the FC and WP were determined by a pressure plate experiment, and using those values, the FTSW was calculated as FTSW = (actual water content – water content at the wilting point) / (water content at field capacity - water content at the wilting point) (Sinclair and Ludlow, 1986) [6].

Physiological measurements

During the stress period, plant transpiration rate was estimated from the decrease in the pot weight between two consecutive weight measurements (Luquet *et al*., 2008; Xin *et al*., 2008) [7, 8] On all the days of stress, the weight of the pot was recorded from 8.00 AM to 4.00 PM at an hourly interval. Similarly, the pigments, leaf area, canopy temperature, chlorophyll *a* fluorescence kinetics, gas exchange were recorded from day 1 to day 4 of drying soil. The chlorophyll index, canopy temperature, minimum fluorescence yield (F_o), and F_v/F_m ratio were recorded on the attached tagged fully expanded top leaf from each replication between 10:00 and 14:00 hours. Chlorophyll content was measured using a chlorophyll meter [Soil Plant Analysis Development (SPAD); Model 502, Spectrum Technologies, Plainfield, IL, USA] and expressed as SPAD units. Canopy temperature was measured using an infrared camera (FLIR Systems, Inc., Wilsonville, OR, USA) and expressed as °C. The minimal fluorescence yield (Fo), maximum fluorescence yield (Fm), and maximum quantum yield of photosystem II (F_v/F_m ratio) were recorded at dawn and dusk, and the data were averaged.

Photosynthetic rate, stomatal conductance, transpiration rate, and Ci/Ca ratio

The leaf-level gas exchange measurements (photosynthesis, stomatal conductance, transpiration rate, and Ci/Ca ratio) were measured on the tagged leaf of each replication using an LI-COR 6400XT portable photosynthesis system (LI-COR, Lincoln, NE, USA). The gas exchange measurements were taken at daytime growth temperature (measured using LI-COR 6400XT) and ambient CO_2 conditions (410 ppm). The internal light-emitting diode light source in the LI-COR 6400XT was set at 1600 µmol m^{-2} s^{-1} to ensure a constant, uniform light across all measurements. (Djanaguiraman *et al*., 2014) [9].

Statistical Analysis

The progressive soil drying experiment was conducted in a randomized block design with five replications. The rate of transpiration of each line was regressed against FTSW. The data were first submitted to a two-segment linear regression analysis intersecting at a common point. This method relied on the iterative procedure starting with the initial value provided by the user. All the treatments were checked with 200 iterations, and convergence happened below 100 iterations for each treatment. Physiological data were analyzed using the PROC GLM procedure of the SAS program (SAS Institute, 2003) [10]. Standard error was shown as an estimate of variability, and means of various variables were separated for significance by the least significant difference test at a probability level of 0.05.

Results

Transpiration rate and soil moisture content

There were significant differences (P<0.01) between the day of observation, time of day, and line for transpiration rates (Fig. 1a-d), and to quantify the main differences between lines for daily transpiration rate under drying soil, the individual day data was analysed separately and presented. Across the days of observation, there were significant differences (P<0.01) between the lines for the transpiration rates on an hourly basis. The highest transpiration rate was recorded on days 1 and 2, followed by days 3 and 4. On all the days, from 8 AM to 4 PM, the transpiration rate was higher in IS23143 compared to IS13540 (Fig. 1a-d).

The fraction of transpirable soil moisture (FTSW) was significantly (P<0.001) decreased from the start of the experiment and reached <0.3 FTSW on the 4th day (Fig. 2a-b). The estimated FTSW threshold upon soil drying for the line IS13540 was 0.622 (Fig. 2b; Table 1). In contrast, the estimated FTSW threshold for the line IS23143 was 0.531 (Fig. 2a; Table 1). The correlation coefficients for the FTSW threshold value determination ranged above 0.65 (Table 1).

Chlorophyll index (SPAD units), canopy temperature (°C), minimum fluorescence yield (F_o; relative units) and maximum quantum yield of photosystem II (F_v/F_m ratio; relative units)

Significant (P<0.01) differences in chlorophyll index (SPAD units), canopy temperature (°C), minimum fluorescence yield (F_o; relative units), and F_v/F_m ratio for days of soil drying, lines and the interactions of line and days of soil drying was observed (Fig. 3a-d). The chlorophyll index was decreased significantly (P<0.01) from day 1 to day 4 of soil drying in IS13540; however, there was no variation in chlorophyll index in line IS23143 during progressive soil drying (Fig.3a). In both the lines, the canopy temperature was significantly (P<0.01) increased from day 1 to 2 of soil drying, and then it remained around 40- 42 ^{o}Cat days 3 and 4 of soil drying (Fig. 3b), and the line IS13540 had a subtle higher canopy temperature (0.7 ^{o}C) than IS23143.

The F_o value increased from day 2 to 4 of soil drying, and the line IS23143 had the highest F_o value than IS13540 on days 3 and 4 of soil drying (Fig. 3c). However, the F_v/F_m ratio was significantly (P<0.01) decreased from day 2 to day 4 of soil drying, and the line IS23143 had a more significant (P<0.01) decrease than IS13540 (Fig. 3d).

Photosynthetic rate (μmol m^{-2} s^{-1}), stomatal conductance (mol m^{-2} s^{-1}), transpiration rate (mmol m^{-2} s^{-1}), and Ci/Ca ratio

Significant differences (P<0.01) in photosynthetic rate (μmol m^{-2} s^{-1}), stomatal conductance (mol m^{-2} s^{-1}), transpiration rate (mmol m^{-2} s^{-1}), and Ci/Ca ratio between lines, days of soil drying, and the interactions of lines and days of soil drying were observed (Fig. 4a-d). Overall, photosynthetic rate, stomatal conductance, transpiration rate, and Ci/Ca ratio decreased with increasing soil drying duration. Between the lines, IS13540 had a higher photosynthetic rate than IS23143 (Fig 4a); however, the stomatal conductance, transpiration rate, and Ci/Ca ratio were higher in IS23143 in most of the day of soil drying than IS13540 (Fig.4b-d).

Discussion

Drought is an important abiotic stress, limiting sorghum yield in arid and semi-arid regions (Zandalinas *et al*., 2021) [11], and targeting on stomatal conductance can be an approach to improve drought tolerance. (Beebe *et al*., 2013) [2]. Concerning drought, stomatal conductance may be one of the traits for drought tolerance mechanism because the transpiration rate is regulated by stomatal conductance under drying soil, thereby maintaining a favourable tissue water status. (Beebe *et al*., 2013) [2].

Previous studies have reported tight coordination between above-ground and below-ground morphological changes under drought stress (Yoshida *et al*., 1982; Ekanayake *et al*., 1985; Xu *et al*., 2015) [12, 13, 14]. In general, drought avoidance in plants is achieved by maintenance of turgor either through increased water absorption from deeper soils through increased rooting depth or reduction in water loss through decreased leaf area and stomatal conductance under drought stress (Dobra *et al*., 2010; Sofi *et al*., 2018; Saradadevi *et al*., 2017; Munns and Sharp, 1993) [15, 16, 17, 18]. In this study, it is observed that the line IS13540 had decreased transpiration rate under limiting soil moisture (Fig. 2a) under progressive soil drying (Fig. 1a-d) than IS23143. Furthermore, the decrease in transpiration rate in IS13540 was associated with decreased stomatal conductance (Fig. 4b,c).

In general, the transpiration rates in various species are unaffected by drying soil until the FTSW threshold decreases around 0.25 and 0.35 (Ritchie, 1973; Sinclair and Ludlow, 1986; Ray and Sinclair, 1997; Gholipoor *et al*., 2013) [19, 6, 20, 21]. The relationship between FTSW and transpiration rate is similar, as reported by Sinclair and Ludlow (1986), Ray and Sinclair (1997), and Gholipoor *et al*. (2013) [6, 19, 20]. In this study, the line IS13540 had an FTSW threshold value of 0.622; whereas, line IS23143 had an FTSW threshold of 0.531. The low FTSW threshold suggests that the cultivar can sustain the gas exchange process for a more extended period under drying soil, and it would be advantageous under short-period drought stress compared to genotypes with a high FTSW threshold (Ray and Sinclair, 1997) [19]. In contrast, the line with a high FTSW threshold like IS13540 can perform better under prolonged drought because it conserves soil moisture under soil drying by closing the stomata very early (Ray and Sinclair, 1997) [19]. The restricted transpiration rate is likely due to strong stomatal control which is the result of leaf level hydraulic conductance. Sadok and Sinclair (2010) [22] indicated that break point in soyabean may be due to hydraulic limitation. Hence, it can be concluded that the line IS23143 can tolerate short episodes of drought stress, and IS13540 can tolerate long episodes of drought stress comparatively.

Chlorophyll pigment is involved in capturing light energy, and a decrease in chlorophyll content under drought could be associated with damage to the chloroplast structure (Bolat *et al*., 2014; Zhang *et al*., 2020) [23, 24]. Canopy temperature is lower in IS23143 than IS13540, lower canopy temperature may be due to higher transpiration rate as it aids in canopy cooling. Between the line, IS13540 had a lesser decrease in stomatal conductance, transpiration rate, ci/ca ratio than IS23143. The stomatal conductance and transpiration rate were higher in IS23143 than IS13540 over the days of soil drying whereas, the photosynthetic rate was lower in IS23143 than IS13540, which indicates that the reduction in photosynthetic rate in IS23143 is due due to non- stomatal limitations evident from decreased F_v/F_m and higher F_o (Farquhar and Sharkey, 1982) [25].

Upon soil drying, in both the genotypes, the F_o value was increased, but the line IS23143 had a higher increase than IS13540 (Fig. 3c). The increase indicates that photoinhibition is happening and damage of PS II (Xu *et al*., 2020) [26]. Furthermore, the occurrence of photoinhibition was validated as an increased C_i value in IS23143 than IS13540 (Zhang *et al*., 2020) [23]. The decrease in F_v/F_m ratio may be associated with the inactivation of reaction centers due to drought stress (Wang *et al*., 2012) [27]. We hypothesize that greater inactivation of the reaction center may be the reason for the higher dissipation of absorbed light.

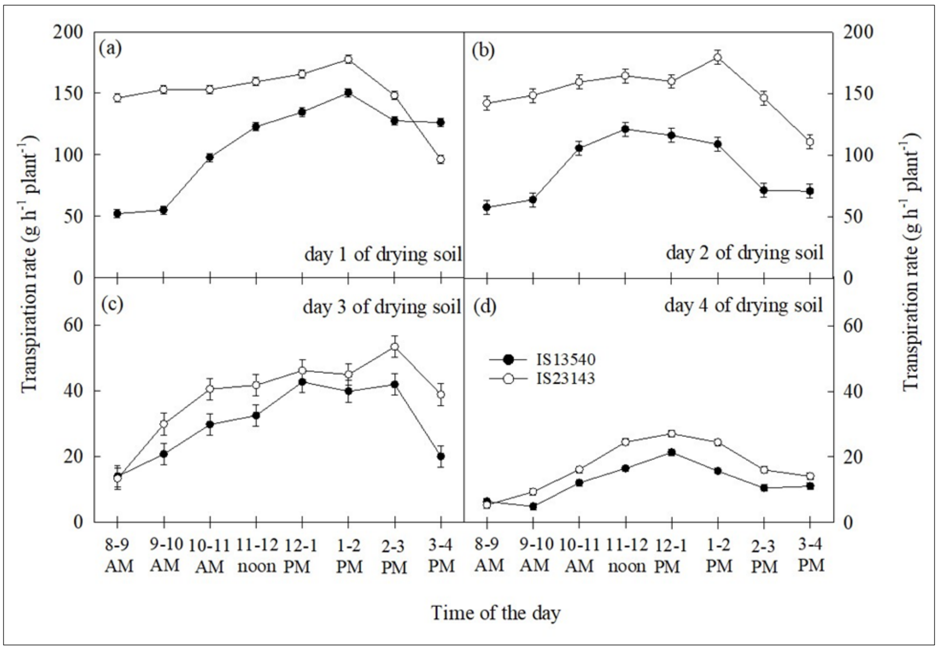

Fig 1: Genotypic variation in hourly transpiration rate in sorghum genotype differing in root angle

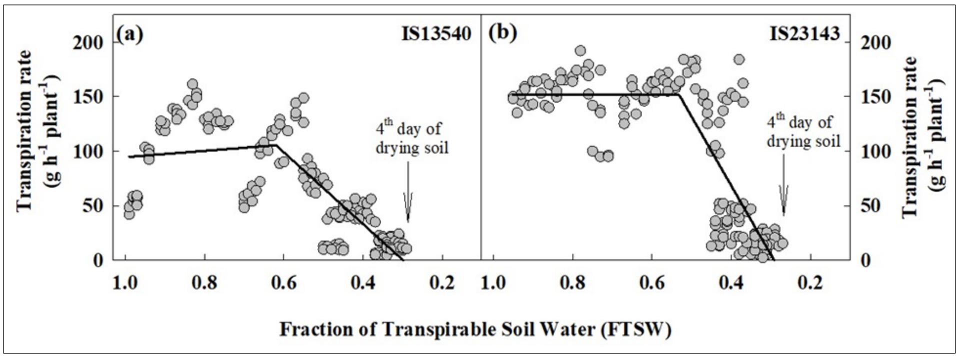

Fig 2: The relationship between fraction of transpirable soil water (FTSW) and transpiration rate in sorghum lines differing in root angle

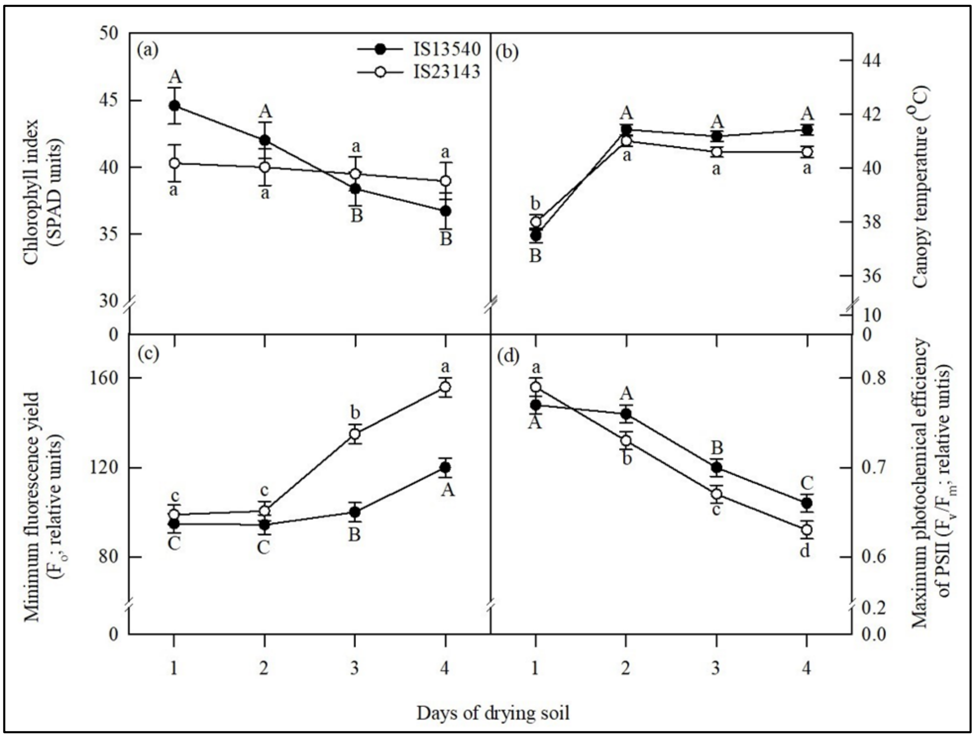

Fig 3: Effect of progressive soil drying on (a) chlorophyll index (SPAD units), (b) canopy temperature (°C), (c) minimum fluorescence yield (Fo; relative units); and (d) maximum quantum yield of photosystem II (F_v/F_m ratio; relative units) in sorghum lines differing in root angle. Each datum is the mean ± SEM of three plants (n = 3). Means with different letters are significantly different at $P \leq 0.05$

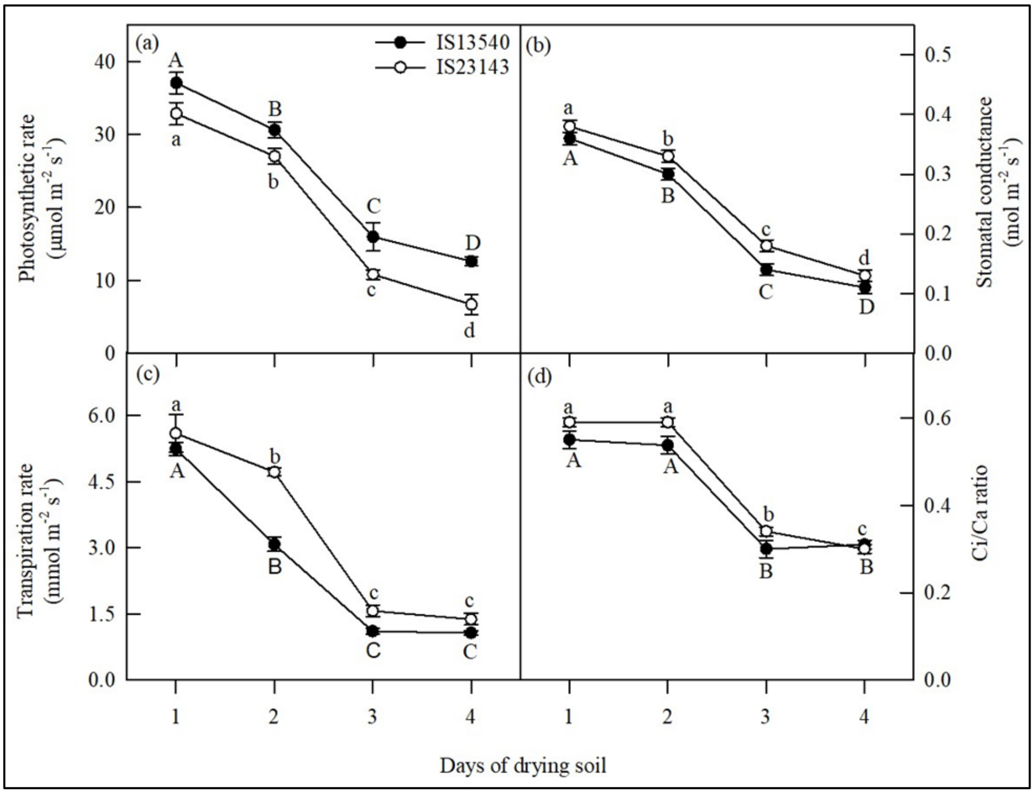

Fig 4: Effect of progressive soil drying on (a) photosynthetic rate (μmol m^{-2} s^{-1}), (b) stomatal conductance (mol m^{-2} s^{-1}), (c) transpiration rate (mmol m^{-2} s^{-1}), and (d) Ci/Ca ratio in sorghum lines differing in root angle. Each datum is the mean ± SEM of three plants (n = 3). Means with different letters are significantly different at $P \leq 0.05$

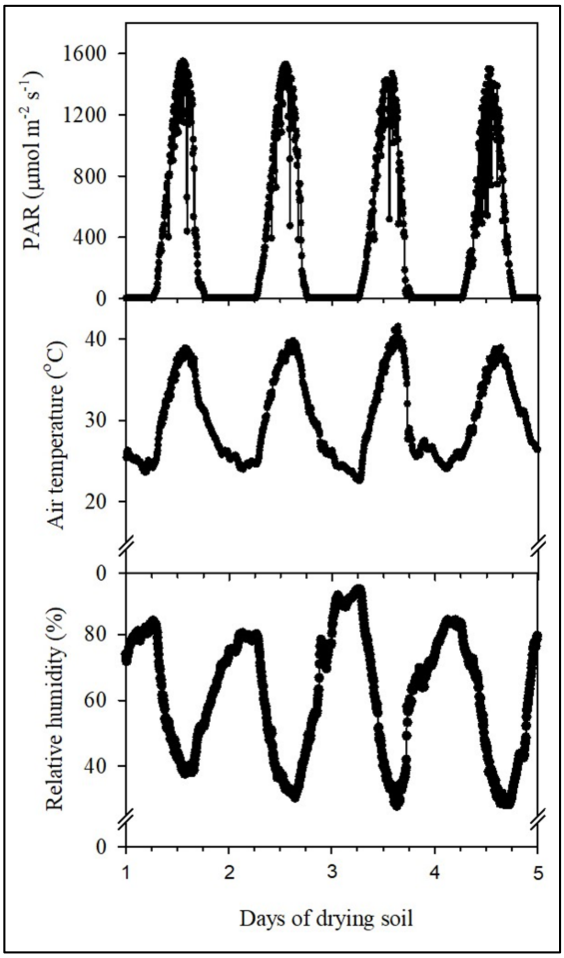

Fig S1: Weather condition during the experimental period

Table 1: Result of the dry-down experiment of two sorghum genotypes: leaf area (cm^2 $plant^{-1}$) transpiration rate ($g\ h^{-1}$ $plant^{-1}$), and regression [FTSW threshold and slopes of two linear regression segments ($g\ h^{-1}$ $plant^{-1}$) and R^2]

Genotypes	Description of the genotype	Leaf area (cm^2 $plant^{-1}$)	Transpiration rate ($g\ h^{-1}$ $plant^{-1}$)	FTSW threshold	Slope 1 ($g\ h^{-1}$ $plant^{-1}$)	Slope 2 ($g\ h^{-1}$ $plant^{-1}$)	R^2
IS13540	Wide root angle	1054.40 ± 278^a	94.0 ± 0.88^a	0.622^a	151.5 ± 8.84	-13.82 ± 7.1	0.72
IS23143	Narrow root angle	954.80 ± 278^a	61.8 ± 0.88^b	0.531^b	105.4 ± 6.56	-3.01 ± 4.80	0.66

Conclusion
Overall, it is evident that IS13540 is a drought-tolerant line, and the tolerance is associated with higher FTSW threshold value. This line possesses better stomatal control than IS23143, as evidenced by a lower transpiration rate throughout the daytime. In spite of higher stomatal conductance, the decrease in photosynthetic rate in IS23143, indicates the involvement of non-stomatal factors. Photo inhibition is a primary factor involved in non-stomatal limitations.

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