Sorghum landraces perform better than a commonly used cultivar under terminal drought, especially on sandy soil

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ABSTRACT

Landraces of sorghum [*Sorghum bicolor* (L.) Moench] have a high potential for drought adaptations to increasingly extreme climates. We investigated the performance of five sorghum genotypes (four landraces and one commonly grown elite line) under water-limited conditions. Plants were grown until maturity in field-like columns on soils of four textures (silty clay, sandy loam, loamy sand, sand), which were dried during flowering stage down to 30 % usable field capacity. Plant transpiration, physiological characteristics, and yield were measured. For most of the measured parameters, the interaction between genotypes and soils was statistically significant. Alongside the gradient in available water between soils, plants had the highest total transpiration, transpiration efficiency (TE), harvest index (HI), and nutrient uptake in silty clay, steadily reduced towards soils with higher sand content. Especially in sandy soil, all measured plant performance parameters were significantly reduced compared to the other soils. There was a significant negative relationship between later flowering time and HI. While the elite cultivar M35–1 showed the highest TE, it suffered from late flowering and yield loss on all soils, especially when growing on sandy soil. The landraces IS 29914 and IS 8348 had a stable HI irrespective of their lowest TE. The shorter the plant, the better it coped with water and nutrient limitation and high transpiration efficiency was not connected to water conservation. The study overall emphasizes the high potential of sorghum landraces to overcome more extreme droughts as imposed by climate change. It also underlines the importance and strong interaction effect of soil texture on plant performance and transpiration efficiency, which is crucial to be considered in crop production. This outlines that specifically regions with sandy soils, characterized by low water-holding capacities, need genotypes that efficiently utilize the limited available water and nutrient resources – a genetic potential hidden in many landraces.

Introduction

Drought tolerance in agriculture refers to a plant's ability to maintain yield production during gradual and moderate water deficits (Tardieu et al., 2018), and is becoming increasingly important when facing the combined challenges of reduced water availability for crop cultivation due to climate change (Gupta et al., 2020) and simultaneous increase of the world population (UN, 2022). Depending on the drought scenario (Tardieu, 2012) and plant type, three main strategies exist to overcome it: (a) escape, like having a shortened plant reproduction cycle, early maturity, adapted leaf area (van Oosterom et al., 2011), and fast flowering (Abraha et al., 2015), as drought stress during reproduction time can lower yield or lead to grain abortion (Tardieu et al., 2018); (b) avoidance, i.e. plants such as succulents maintain high water content and protect their leaves, trying to survive through drought periods (Basu et al., 2016); (c) tolerance, which means plants maintain

functions through dry periods (Tardieu, 2012). Having good coping mechanisms is crucial, especially as drought is often accompanied by other risks for the plants such as a higher vulnerability to biotic stresses like pathogens, heat or salinity which can impose further damage, grain abortion or premature plant death (Ahluwalia et al., 2021).

To keep up plant functions during drought, strategies have evolved to use water more efficiently, prevent water loss, and facilitate water uptake. Transpiration efficiency (TE) refers to the amount of biomass produced per unit of water transpired and can be an important trait under drought conditions, although the exact characteristics that make a plant highly transpiration efficient are still unknown (Vadez et al., 2024) and TE is not the only factor determining a plants success. In a terminal drought scenario, it is necessary to manage the available water resources by saving water and enhancing uptake. In the short-term, plants may save water by closing stomata, e.g. through hormones like ABA (abscisic acid) (Bharath et al., 2021), which changes hydraulic conductance and regulation of water potential and uptake within the plant (Maseda and Fernández, 2006), or reduction of sun-exposed leaf area through leaf rolling as a response to drying soil (Echarte et al., 2023). Water uptake can be facilitated by altering rhizosphere properties and enhancing water flow towards the root, for example by root exudation, secretion (Ahmed et al., 2014), root hair formation (Carminati et al., 2017), or mycorrhizal networks (Pauwels et al., 2023). To access further water sources, plants develop deeper or wider spread root systems (Vadez et al., 2011), or cooperate with symbionts like mycorrhiza to transport water to the plant (Püschel et al., 2020).

However, water uptake also depends on soil characteristics, mainly soil texture, which determines soil hydraulic properties and overall water availability. As water potential around the roots can drop quickly and consequently limit water uptake (Abdalla et al., 2022) under drought, this soil-specific drop in turn affects the plant response to various soil textures, such as an earlier limitation of transpiration in drying sandy soil (Cai, et al., 2022a). While this can be a sensible reaction to prevent excessive water loss, transpiration restriction comes at the cost of reduced photosynthetic activity, which means lower productivity (Ahluwalia et al., 2021). Further, low soil water potential can make plants vulnerable to atmospheric drought already at lower levels of VPD (Vapor pressure deficit) (Koehler et al., 2022). Overall, it is essential for crop productivity to utilize water as efficiently as possible while at the same time maintaining enough water available for all growth stages which means depending on the scenario, different water management strategies can be beneficial (Tardieu, 2012).

The texture of soil however can also be greatly related to the availability of nutrients. As smaller soil particles like clay or silt offer a much bigger surface area and cation exchange capacity, nutrients can be sustained much better than in sandy soil with coarse texture and less surface area, where leaching can occur more easily (Huang and Hartemink, 2020). Next to the essential nutrients nitrogen (N) and phosphorus (P), silicon (Si) and potassium (K) can play key roles in the regulation of root water uptake and transpiration, also in drought scenarios (Mostofa et al., 2022; Wang et al., 2021; Zörb et al., 2014). However, as nutrients are taken up together with water, a reduced water uptake due to drought can also impose nutrient deficiencies, leading to a reduction in growth and possibly also yield (Ahluwalia et al., 2021; Akman et al., 2020). An adequate nutrient supply and the plants ability to take up these nutrients are therefore essential and tightly linked to the water availability.

Due to its adaptation to dry conditions, sorghum (*Sorghum bicolor* (L.) Moench) is widely grown in water-limited environments like the semi-arid tropics. Sorghum is considered the staple food of large populations in semi-arid regions of sub-Saharan Africa and Asia and mostly food-insecure people (Taylor, 2012). Biomass of sorghum serves as fodder for livestock (Patil, 2017) and a source for biofuel (Vinutha et al., 2014). In India, sorghum is among the most popular cereals, most prominently in rural regions of low income (Rao et al., 2010). Sorghum is commonly cultivated in the post-rainy season (rabi season) in India, where plants need to manage the water stored from the rainy season

(Kholová et al., 2013). In this season, the variety M35–1 has been popular in India for decades, as it produces stable grain and stover yields despite varying sowing dates. It therefore often serves as a control variety during germplasm studies or as breeding material for new cultivars and hybrids (Reddy et al., 2009).

In general, breeding efforts need to develop varieties adapted to more unforeseeable climates like more frequent droughts. A much-neglected source for genetic variability in breeding has been landraces, i.e. locally adapted varieties that have not undergone a planned breeding process and are adapted to local circumstances. Recently, it has been advocated to utilize landraces more for breeding crops better adapted to future challenges such as drought (Adhikari et al., 2022; Marone et al., 2021). Various studies show a promising variety of sorghum landraces for this purpose, especially in Sub-Saharan Africa, where sorghum originates (Chivenge et al., 2015; Devnarain et al., 2016; Kumar et al., 2011; Mace et al., 2013).

This study aimed to observe the response of different sorghum genotypes (four sorghum landraces from Pakistan, Sudan, Cameroon, and Zimbabwe, along with the common Indian variety M35–1) to a range of water-limited conditions on soils of four textures during an entire crop cycle and evaluate which plant characteristic may be important to maintain yield under terminal drought conditions. We hypothesize that (1) under terminal drought, landraces can achieve a higher transpiration efficiency and hence are more likely to produce yield than the elite genotype; (2) this effect will be especially pronounced under sandy soils with low water holding capacity as landraces may be better adapted to these harsh soil conditions.

Materials and methods

The experiment was conducted in the Lysi-Field facility of ICRISAT (International Crops Research Institute for the Semi-Arid Tropics) located in Patancheru, India. The different steps of the study are summarized in Fig. 1. 200 cylindric PVC-columns of 2 m depth and 25 cm diameter were used, 50 each filled with soils of one of four different textures: silty clay, sandy loam, loamy sand, and sand. Two of the used soils were the local soil types alfisol and vertisol which have a sandy loam and silty clay texture, respectively. To achieve soils with two additional soil textures, alfisol was mixed with sand at a 2:1 ratio resulting in a loamy sand, and a mixture of alfisol with sand at a 1:3 ratio resulted in a soil with sandy texture. The soils have been described and characterized in several previous studies (Bhattacharyya et al., 2016; Vadez et al., 2011, 2021). The columns hold a soil volume equivalent to the volume that crops can use in a real field setting (Vadez et al., 2008). The columns are organized in four trenches with one soil texture per trench and in ten rows of five columns next to each other. In each of these rows, five sorghum genotypes were distributed randomly (full setup in suppl. Fig. S1). During nights and in the event of rain, a mobile rainout shelter was used to prevent unwanted rainfall.

Environmental data

Weather data were logged every 30 min at canopy height next to the experiment site. Temperatures during the growing season ranged between 19 and 35 °C in the daytime, with a higher VPD of around 2 kPa at the beginning of the growing season until December, and lower VPD around 1.5 kPa during flowering and ripening stages (daytime weather data and VPD in suppl. Fig. S2). To characterize the soil hydraulic properties of all four soils, the retention curve and hydraulic conductivity were determined using the evaporation method of the HYPROP2 (METER ENVIRONMENT, Munich, Germany). For fitting the retention curve, the bimodal porosity model of van Genuchten was used (Durner, 1994) as it could best capture the various pore-size distributions of the mixed soils (RMSE soil moisture 0.0435, hydraulic conductivity 0.6224; both are averages for all soils). The soils were further analyzed for particle size distribution with PARIO (METER ENVIRONMENT, Munich,
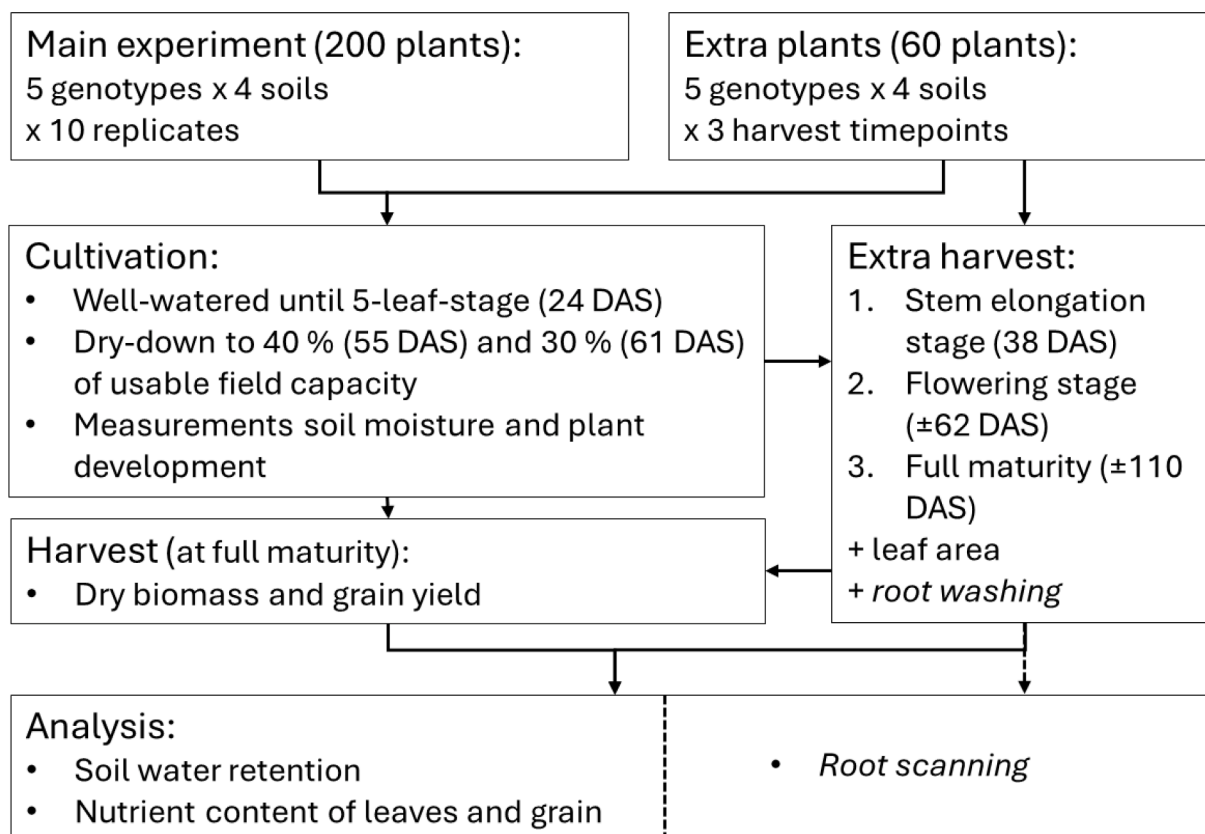
Fig. 1. Flowchart summarizing how the study was conducted.

Germany) and the soil texture was classified with the german system KA5 (Suppl. Table S1 with reference to USDA classification). To monitor soil moisture throughout the drying period, 1 m long plastic tubes were installed before sowing in a few columns of each soil. Once per week, soil moisture was measured in seven different depths with TDR (time-domain reflectometry).

Sorghum cultivation

Five varieties of sorghum were sown on 19.10.2018 at the beginning of the post-rainy season with six seeds per column to ensure at least one healthy plant in each column: four landraces (IS 8348 from Pakistan, IS 12447 from Sudan, IS 15945 from Cameroon, and IS 29914 from Zimbabwe) as well as the Indian control (M35–1). Ten replicates of each variety were sown per soil treatment, randomly distributed within each of 10 rows. Each column was fertilized with 2 g di-ammonium phosphate (DAP) on the day of sowing and additionally 2 g urea on 21 days after sowing (DAS). Another sorghum variety was sown in pots surrounding the columns to minimize border effects. The seedlings were watered regularly and gradually thinned down to one plant per column. At the growth stage of five developed leaves, 24 DAS, the columns were saturated to field capacity (i.e. watered until water drained from the bottom), and the soil surface was covered with a polyethylene sheet and a layer of 2 cm polyethylene beads on top, which could prevent approximately 90% of evaporation from the soil. The columns were weighed the next day individually to calculate the volume of water at 80% available field capacity in each column (Vadez et al., 2008).

Weighing was repeated weekly, and the columns were dried to 40% (55 DAS) and 30% (61 DAS, both during flowering stage) usable field capacity by calculating the amount of water remaining in the columns. Those drying too fast were watered to compensate for further water losses below the threshold value and to prevent plants from dying due to drought stress. The measurements of soil moisture with TDR showed the

gradual reduction of soil moisture, and that the water content could be held at a constant low level throughout the rest of the season (Suppl. Fig. S3). Towards the end of the season the loamy sand and sandy soil treatment dried also below 30% usable field capacity.

Plant development was monitored biweekly, recording the height until the upmost developed leaf and numbers of developed, still developing, and senesced leaves as well as the number of tillers and their development status.. The flowering date was recorded as the point of more than 50% coverage with anthers and the panicles were immediately packed in light nylon bags to prevent damage by birds. From November 2018, carbofuran (2,2-Dimethyl-2,3-dihydro-1-benzofuran-7-yl methylcarbamate) was regularly sprayed against fall armyworm (*Spodoptera frugiperda*) which successfully prevented biomass loss.

Sorghum was harvested during late January and early February 2019, always per soil treatment and variety, once all panicles of a treatment were physiologically mature. The stem diameter was measured immediately after harvesting. The plants were separated into stems, leaves, and panicles, oven-dried for three days at 60 °C, and then weighed. Tillers were packed separately. The grain was separated from the panicles, weighed, and the grain number per plant was counted. Finally, all plant parts were milled individually, and subsamples were analyzed for their nutrient content in shoot and grain. Nutrients were extracted by nitric acid pressure digestion (Heinrichs et al., 1986) and were measured on an inductively coupled plasma-optical emission spectrometer (ICP-OES, Thermo Scientific iCap 6000 Series).

Additional columns for root assessment

To monitor root development and different growth stages without interrupting the main experiment, 60 additional, smaller columns (depth 1.20 m, diameter 0.16 m) were cultivated and monitored similarly. There were 15 columns for each soil with three replicates per genotype. One replicate per genotype and soil treatment was harvested

at each of three physiological stages: stem elongation stage (38 DAS), flowering stage (62 DAS), and maturity/ripening (110 DAS). At harvest, plant height was measured, leaves were scanned and then the plants were separated, dried, weighed, and milled as in the main experiment. Additionally, the root system was washed, separated in a water basin, scanned without overlaying roots in a flatbed scanner, then dried and weighed. The scanned images were analyzed with the software WinRHIZO 2013e (Regent Instruments Inc, Québec, Canada) for root length, root surface area, and specific root density, which was calculated by dividing root length [cm] by root mass [g].

Data analysis

The statistical analysis and visualization were done in R (version 4.1.1). Transpiration was calculated as the weekly weight difference of each column. Falsely noted weights were corrected by changing the weight using the average transpiration of the treatment in the respective week.

Various parameters were calculated as follows: Transpiration Efficiency (TE) is defined as the unit of total aboveground dried biomass [g] per unit of water transpired [kg] (Vadez et al., 2014):

$$TE = \frac{Total\ Dry\ Biomass\ Plant\ [g]}{Total\ Transpiration\ [kg]} \tag{1}$$

The Harvest Index (HI) is calculated as the percentage proportion of the total grain [g] in reference to the total aboveground dried biomass [g] (Donald and Hamblin, 1976):

$$HI = \frac{Dry\ Biomass\ Seeds\ [g]}{Total\ Dry\ Biomass\ Plant\ [g]} * 100 \tag{2}$$

Significant differences between treatments were confirmed statistically using ANOVA (Analysis of Variance). Based on the randomized block design (RBD) of the experiment, a split-plot analysis was conducted, with soil texture as the main factor and genotypes being the factor of the subplot. Post-hoc LSD (least significant difference) tests were conducted as follows: If the interaction of soil texture and genotype was significant ($p < 0.05$), LSD tests were individually done within each soil texture treatment, comparing the five genotypes. Otherwise, in the case of non-significant interaction, LSD tests were done within genotypes and/or soil textures depending on the significant factor (e.g. comparing the data of all genotypes per soil texture if soil texture was significant).

To get a better insight into the interaction and connection of variables, principal component analysis (PCA) was conducted. Here, 15 variables were analyzed (total and vegetative dry weight (DW), DW of stem, leaves, seeds, and panicle, stem diameter, flowering date, HI, total transpiration, transpiration before and after flowering, TE, total leaf area, plant height). The data points were colored in the different treatments (soil texture, genotypes) to determine whether clustering happened depending on the treatment.

Further, correlations between several parameters (panicle DW, HI, total transpiration, TE, and flowering date) were calculated with data pooled across all soils as well as separately per soil texture. We used panicle DW instead of seed DW to be able to include at least all plants which flowered and therefore increase replicates for all treatments.

As the panicle DW was strongly correlated to the flowering date and HI, residuals of these relationships were calculated to compare the genotypes without the effect of these relationships. This enables a more robust evaluation of the results, where the observed trends could be confirmed (residuals around zero), would have been even stronger (positive residuals), or less pronounced (negative residuals) without the effect of flowering date or HI, respectively. We also calculated the residuals of TE without the effect of flowering date.

The scanned roots were analyzed with the software WinRHIZO 2013e (Regent Instruments Inc., Québec, Canada). Root length

(Rlength) [cm] and root surface area (SA) [cm^2] were used as further root parameters. The aim was to estimate the linkage of soil texture and root parameters on the plants' water use and biomass production (shoot and panicle) under drought. Therefore, the data of the flowering and maturity stages were used together to perform correlation analysis over all genotypes ($n = 10$) per soil type.

Results and discussion

We observed a reduction of biomass, transpiration, nutrient uptake, and yield on soils with a higher proportion of sand, although the magnitude was genotype-dependent, showing a Genotype by Environment (GxE) interaction. Varieties with earlier flowering time points could maintain higher yields, even when grown in sandy soils compared to varieties that flowered later, although HI was not related to the total water use.

Soil texture affects water and nutrient availability

The water retention and hydraulic conductivity curves of all four soils are shown in Fig. 2 (fitting parameters in suppl. Table S2). The soils with the different textures had a strongly different total volumetric water content at various matric potentials. The saturated water content was mostly similar for all soils except the silty clay texture soil (40–47% vol. water content compared to 59% in silty clay soil), however, the differences became more apparent during soil drying. Sandy soil lost water content quickly due to the great volume of bigger pores, which was visible in the early onset of the steep drop in water content at relatively low absolute soil water potentials compared to the other soils. Similarly, soil with loamy sand texture was drained at lower absolute soil water potentials than sandy loam, while the two textures otherwise dried quite similarly, only showing differences again in the very dry range. Silty clay had the highest plant available water, followed by sandy loam, loamy sand, and, lastly, sand. In wet conditions, silty clay soil was less conductive than the other soils with an increase in conductivity towards higher sand content. During drying all soils showed a seemingly similar reductance in hydraulic conductivity with sandy soil being the least conductive. However, considering the double logarithmic scale, the difference between the most and least conductive soil at a certain soil matric potential was up to one order of magnitude, which is very considerable for plant water uptake.

Interaction of soil texture and genotypes was significant for total transpiration, TE, and transpiration before and after flowering (Suppl. Table S3). Matching the gradient in available water between soils of different textures, the same gradient is visible for total transpiration, being highest for plants grown in silty clay soil and lowest in sandy soil. However, there are significant differences between genotypes within the soil texture treatments (Fig. 3, Table 1). The landrace IS 8348 and the control M35–1 tend to transpire more in total, the landraces IS 29914 and IS 15945 less, with the differences being higher in silty clay than sandy soil. A similar pattern was observed for transpiration before flowering (Table 1), except that in sandy soil, no significant differences between genotypes were found. Post-flowering, differences between genotypes were most pronounced in silty clay soil. The landrace IS 12447 transpired most and IS 8348 least in soils with silty clay, sandy loam, and loamy sand textures, which is the opposite trend as seen for pre-flowering transpiration (Table 1).

Generally, trends in TE seem not to be related to total transpiration across the texture treatments. TE was slightly higher for sorghum grown on silty clay than on sandy soil. In silty clay soil, plants of IS 29914 had the highest transpiration efficiency, while they had a significantly lower TE than other varieties when growing on other soils. While M35–1 was always among the most transpiration-efficient varieties, IS 8348 tended to have lower TE values than average (Table 1, Fig. 3).

For all analyzed nutrient contents in the shoot (Na, K, Ca, Mn, Mg, S, P, Si, Zn, and Cu; suppl. Table S3), the interaction of soil texture and
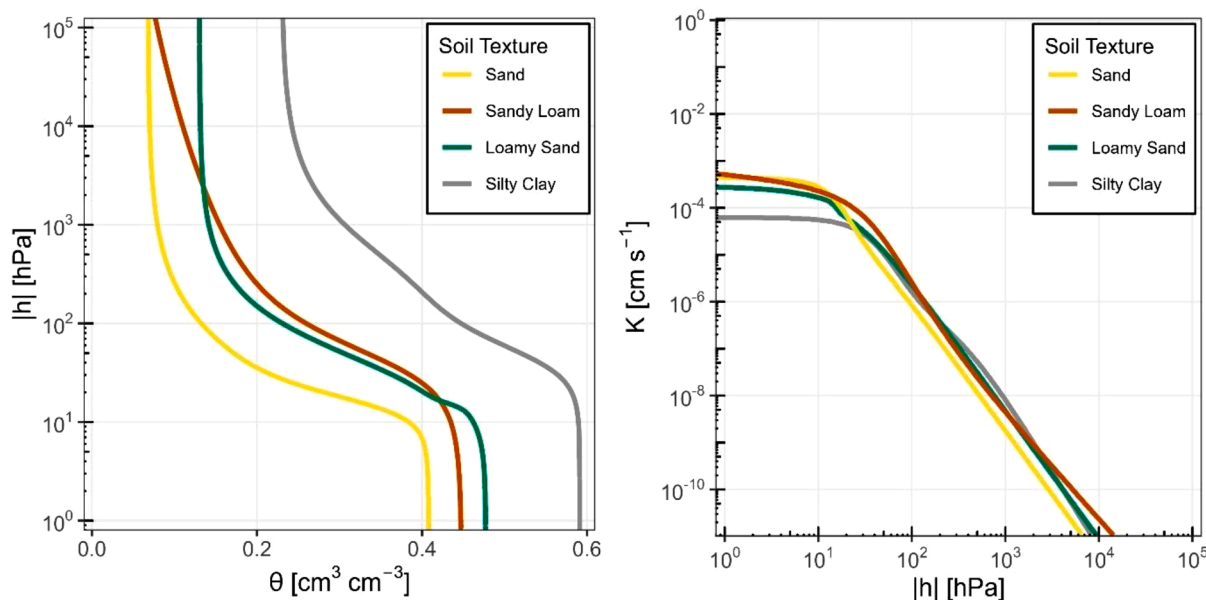
Fig. 2. Water retention and hydraulic conductivity curves of the four soils with contrasting texture measured with the HYPROP system and fitted with the bimodal porosity model of van Genuchten.
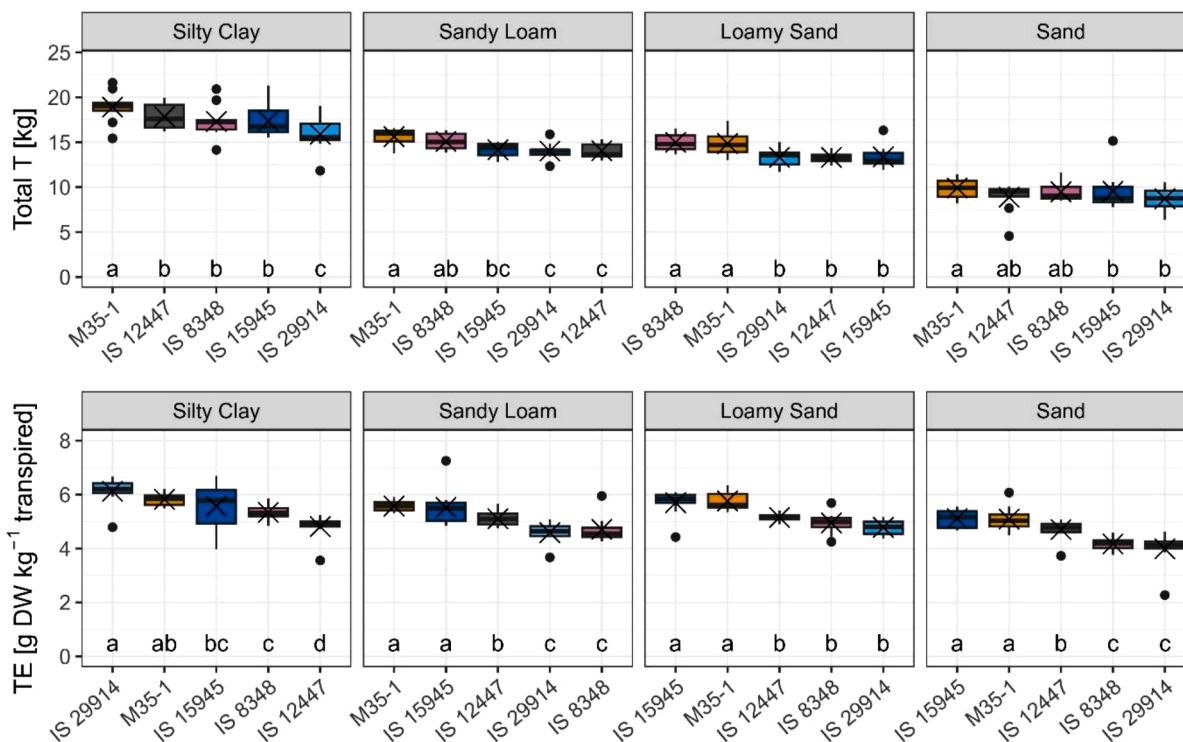

Fig. 3. Total transpiration (upper panel) and TE (lower panel) per genotype and soil texture and sorted by average, showing less total transpiration with higher sand content and differences between genotypes. The letters indicate significant differences ($p \leq 0.05$, LSD-tests performed individually for the four soils). Horizontal lines inside the boxes show the median, averages are marked with crosses and outliers with points.

genotype was significant. While most nutrients showed the trend to have higher nutrient content in soils with higher water availability and total transpiration (Fig. 4), no such relationship was observed for Ca. For Na and Mg this trend was reversed with higher content in more sandy soils. Si and Cu content was almost zero in plants grown in loamy sand and sandy soil. For most nutrients, the control M35–1 tends to have significantly higher nutrient contents in the shoot than the other genotypes in soils with a silty clay, sandy loam, and loamy sand texture, while this

trend was not observed in sandy soil (shown for K and Si in suppl. Fig. S4). The landrace IS 8348 tends to have lower nutrient contents in most cases. The other genotypes show no clear trend.

In the grain, interaction of soil texture and genotype was significant for K, Mn, P, and Si; the difference between soil texture treatments and genotypes were significant independently for Ca, Mn, S, Zn, and Cu; only the different soil textures was significant for Na (suppl. Table S3). For all nutrients in grain there is a clear trend to accumulate more nutrients

Table 1

Results from split-plot-ANOVA-test with soil as main factor and genotypes as subfactors for transpiration and TE.

Variable	Genotype	Silty Clay		Sandy Loam		Loamy Sand		Sand	
Total transpiration [kg]	IS 12447	17.849	b	14.051	c	13.313	b	8.877	b
	IS 15945	17.365	b	14.157	bc	13.362	b	9.544	ab
	IS 29914	15.883	c	14.015	c	13.318	b	8.710	b
	IS 8348	17.312	b	15.089	ab	14.987	a	9.482	ab
	M35–1	18.907	a	15.617	a	14.853	a	9.907	a
Transpiration efficiency [kg⁻¹]	IS 12447	4.812	d	5.104	b	5.153	b	4.704	b
	IS 15945	5.569	bc	5.524	a	5.701	a	5.111	a
	IS 29914	6.122	a	4.586	c	4.784	b	3.988	c
	IS 8348	5.339	c	4.710	c	4.950	b	4.170	c
	M35–1	5.824	ab	5.575	a	5.763	a	5.091	a
Transpiration preflowering [kg]	IS 12447	8.298	d	8.611	c	8.907	b	6.450	a
	IS 15945	9.250	cd	9.921	b	9.659	b	6.223	a
	IS 29914	9.820	bc	10.268	b	9.610	b	6.304	a
	IS 8348	11.738	a	12.262	a	12.001	a	7.045	a
	M35–1	10.898	ab	11.972	a	11.184	a	6.581	a
Transpiration postflowering [kg]	IS 12447	9.551	a	5.440	a	4.406	a	2.427	b
	IS 15945	8.115	b	4.236	b	3.703	ab	3.321	a
	IS 29914	6.063	b	3.747	b	3.708	ab	2.406	b
	IS 8348	5.574	c	2.827	c	2.986	b	2.437	b
	M35–1	8.009	b	3.645	bc	3.669	ab	3.326	a

Due to significant interaction of main and subfactor LSD-Posthoc-tests were performed separately per each soil texture; significant differences are indicated by letters.
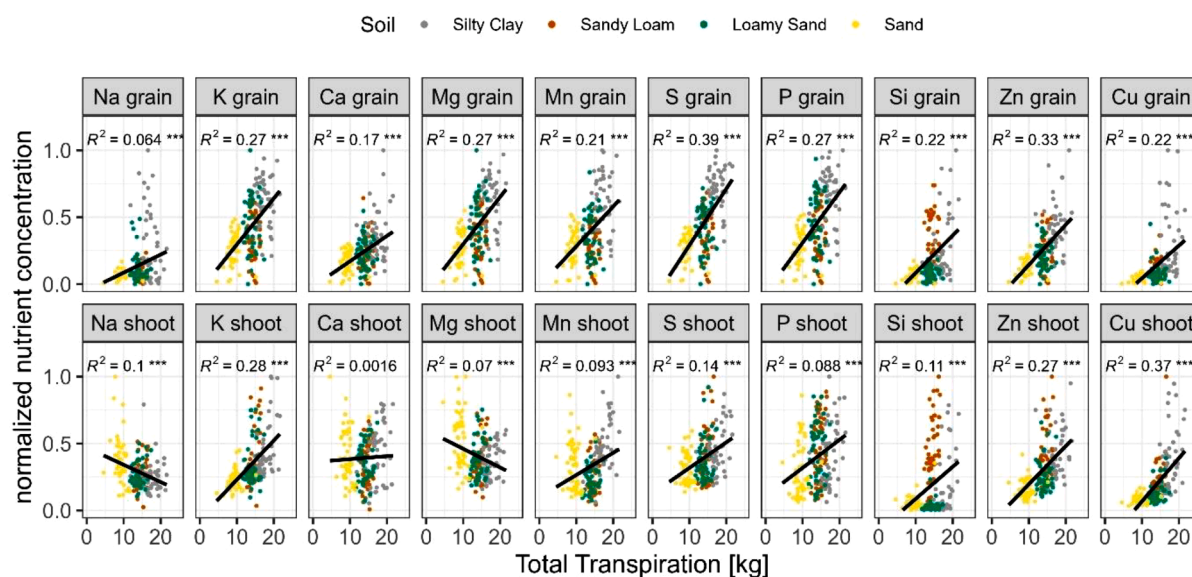

Fig. 4. Relationship of normalized nutrient contents (normalized to maximum observed values of each nutrient) of Na, K, Ca, Mg, Mn, S, P, Si, Zn, and Cu in dried grain (upper panel) and shoot (lower panel) with total transpiration, colored by soil textures. Black lines indicate linear models, R^2 calculated across all soil textures, stars indicate p-values ($< 0.001 = ***$; $<0.01 = **$; $< 0.05 = *$).

from soils with higher water availability, i.e. highest from silty clay soil (Fig. 4). In almost all cases, the landraces IS 29914 and IS 8348 have the highest nutrient contents among the genotypes, irrespective of the soil. Either M35–1 or IS 15945 always have the lowest grain nutrient content.

Comparing nutrient contents in grain and shoot, both show tendencies of plants being able to accumulate more nutrients when growing on soils with more water availability and lower sand content (Fig. 4). We could confirm a higher percentage of C and N with a lower sand content in the soils (Suppl. Table S1). However, considering the different genotypes, no clear connection between shoot and grain nutrient concentrations was revealed. The correlation of nutrient uptake with total transpiration could be attributed to the fact, that nutrients tend to leach from more sandy soils (Huang and Hartemink, 2020), while soils with a higher percentage of clay minerals can hold and release higher rates of nutrients (Simonsson et al., 2007). It is further possible that root growth was stimulated strongly close to the soil surface by the irrigation, so that nutrients that leached to deeper soil, especially in the sandy soils, could

not be accessed by many roots. Different experiments with sorghum and wheat showed a higher root density in topsoil layers when irrigated (Fang et al., 2017; Pabuayon et al., 2019).

Biomass partitioning and root morphology affect drought tolerance

For most plant parameters, the interaction of soil texture and genotype was significant (Suppl. Table S3). A clear relationship between available water and growth was observed, with plants grown on silty clay soil growing tallest and most vigorously, while smallest with the least biomass on sandy soil (Fig. 5, Table 2). While these differences are visible as a gradient, often plants grown on silty clay, sandy loam, and loamy sand textured soils are rather similar with small differences, compared with bigger differences to plants growing on sandy soil.

Biomass partitioning was very different between genotypes and soil textures. While the landrace IS 8348 produced average to low amounts of total biomass compared to the other varieties, and had significantly
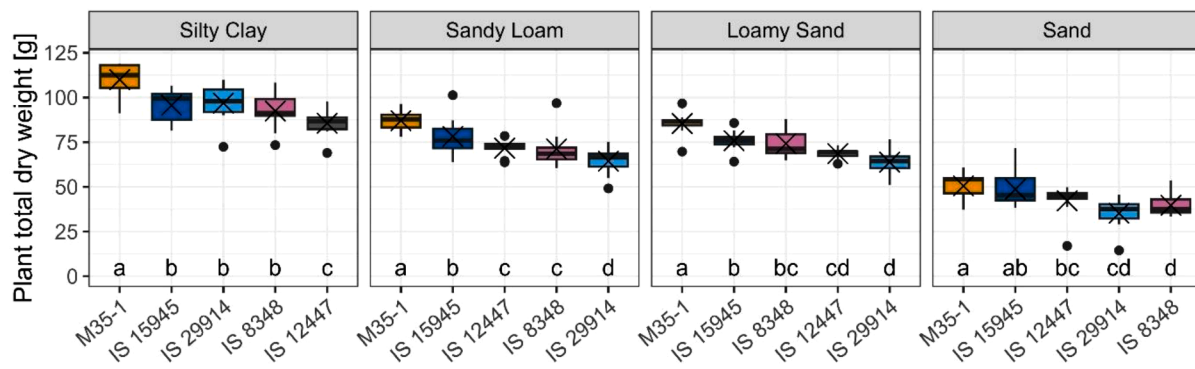
Fig. 5. Plant total DW per genotype and soil texture and sorted by average, showing lower weights with higher sand content and differences between genotypes. The letters indicate significant differences ($p \leq 0.05$, LSD-tests performed individually for the four soil textures). Horizontal line inside the boxes shows the median, averages are marked with crosses and outliers with points.

Table 2

Results from split-plot-ANOVA-test with soil texture as main factor and genotypes as subfactors for biomass, leaf area and yield parameters.

Variable	Genotype	Silty Clay		Sandy Loam		Loamy Sand		Sand	
Stem DW [g]	IS 12447	10.861	c	8.445	d	8.947	d	4.827	c
	IS 15945	27.921	b	28.685	b	26.187	b	10.857	b
	IS 29914	13.875	c	16.130	b	14.820	c	6.590	c
	IS 8348	29.369	ab	26.700	b	28.230	b	10.890	b
	M35–1	32.284	a	36.803	a	32.610	a	15.586	a
Leaves DW [g]	IS 12447	31.523	b	25.200	b	26.490	b	21.900	b
	IS 15945	30.260	b	28.175	b	25.813	b	21.810	b
	IS 29914	31.940	b	11.999	c	14.636	c	9.617	c
	IS 8348	11.771	c	11.328	c	10.501	d	7.575	c
	M35–1	39.498	a	40.141	a	37.140	a	31.238	a
Leaf area [cm²]	IS 12447	2915.97	b	1734.406	b	2222.811	c	1696.087	b
	IS 15945	2769.93	b	1602.985	b	2637.572	bc	1723.746	b
	IS 29914	3143.10	b	1306.475	bc	3117.592	b	2112.293	a
	IS 8348	2752.34	b	989.516	c	2400.301	c	1689.981	b
	M35–1	4323.84	a	2381.251	a	4084.289	a	2710.161	a
Grain yield [g]	IS 12447	33.345	c	27.482	a	24.381	a	9.578	b
	IS 15945	33.465	bc	11.667	d	17.468	bc	9.234	b
	IS 29914	39.539	ab	24.280	ab	26.820	a	15.490	a
	IS 8348	39.980	a	19.970	bc	23.130	ab	16.241	a
	M35–1	28.639	c	14.130	cd	11.285	c	3.757	b
Panicle DW [g]	IS 12447	37.390	a	37.390	a	32.960	a	15.410	b
	IS 15945	16.990	c	16.990	c	23.200	b	15.880	ab
	IS 29914	30.440	b	30.440	b	33.770	a	19.020	ab
	IS 8348	32.630	ab	16.990	b	34.030	a	21.210	a
	M35–1	12.610	c	12.610	c	15.650	c	7.100	c
HI [%]	IS 12447	38.678	ab	38.116	a	35.248	ab	21.623	b
	IS 15945	33.543	bc	14.897	c	23.118	c	19.618	b
	IS 29914	41.075	ab	37.665	a	41.828	a	44.044	a
	IS 8348	43.276	a	28.282	b	31.046	b	42.403	a
	M35–1	26.400	c	15.570	c	12.737	d	8.819	c
Flowering date [DAS]	IS 12447	59.400	b	53.600	b	53.400	c	58.700	b
	IS 15945	60.000	b	59.300	a	58.200	b	59.700	b
	IS 29914	55.400	c	54.700	b	55.000	c	55.500	c
	IS 8348	51.700	d	50.800	c	50.500	d	51.600	d
	M35–1	65.100	a	60.000	a	62.400	a	64.700	a

Due to significant interaction of main and subfactor LSD-Posthoc-tests were performed separately by soil textures; significant differences are indicated by letters.

lower leaf biomass, it had mostly the highest panicle weights (Table 2). The landrace IS 29914 showed a similar trend. The control M35–1 on the other hand, produced significantly more vegetative (stem and leaf) but also total biomass (Fig. 5) and had also significantly the highest total leaf area irrespective of the texture of the soil, it was growing on. However, the panicle weight of M35–1 was always the lowest (Table 2).

The lower water and nutrient availability may have also caused the lower biomass and yield production in the more sandy soils. Several studies similarly showed that sorghum reduces biomass production under drought stress in general (Gano et al., 2021; Kapanigowda et al., 2013). Changes in yield and transpiration could also be found depending on soil texture in a study on quinoa, where plants grown on the soil with

the highest clay content also had the highest transpiration and yield (Razzaghi et al., 2012).

These trends also reflected in the PCA analysis. The two first components of PCA explained a total of 62.74% of variance, with 41.12% and 21.62% for PC1 and PC2, respectively (Fig. 6). Plants grown on sandy soil were grouped in one visible cluster on the left side of the biplot, irrespectively of genotype. Plants grown on silty clay soil clustered on the other side of the plot are associated positively with seeds and panicle DW, stem diameter, total and post-flowering transpiration, total leaf area, and total plant DW. The sandy loam and loamy sand soil treatments are scattered between sandy and silty clay soils and like in the other analysis, do not show considerable differences. The most
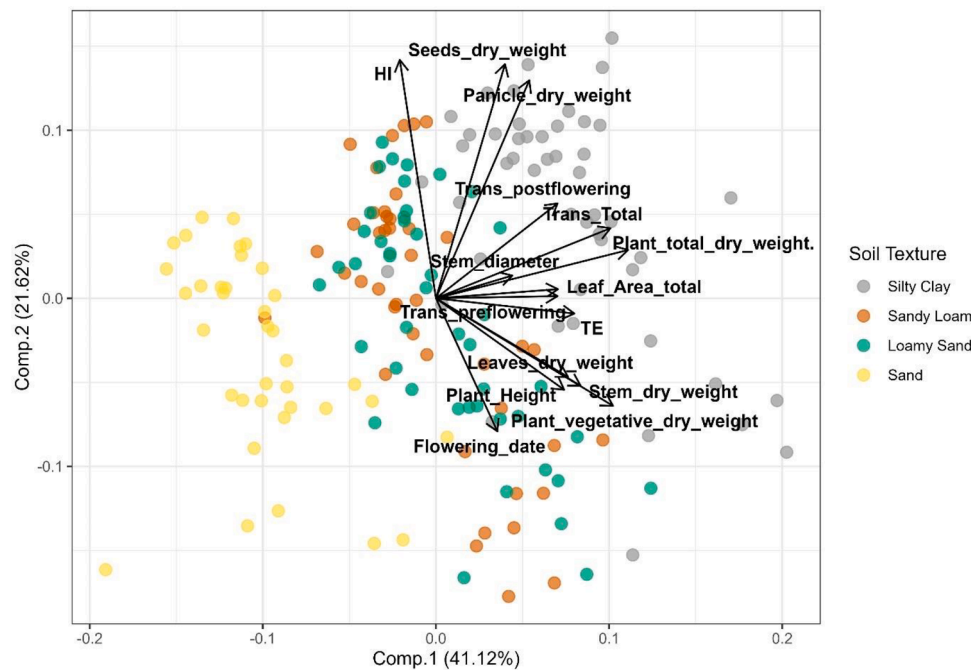
Fig. 6. Principal component analysis of 15 variables explaining 62.74 % of variance. The data points are colored by soils.

important variables were total and vegetative plant biomass, and total transpiration for PC1, and HI and seed and panicle DW for PC2. The same PCA colored by genotypes showed less clustering but rather tendencies, such as an association of M35–1 with various vegetative biomass variables in the bottom right of the biplot, the landrace IS 15945 clustering closest to the elite line M35–1, and the other three landraces being mixed up towards the top left of the biplot and associated with yield parameters (suppl. Fig. S5). HI is at a 90 ° angle with TE, LA, Plant total DW and total transpiration, showing no relationship with these parameters, while HI is also pointing the opposite direction of flowering date, indicating the negative relationship they share. Seeds and panicle DW are at a 90 ° angle with vegetative biomass parameters, showing no relationship between yield and the investing into vegetative growth.

Soil texture also seemed to have influenced root morphology and potentially the drought impact. In the correlation analysis of the extra plants, the results of all genotypes were pooled by the soil treatments (Fig. 7). For sorghum in silty clay soil, the root-shoot ratio was positively correlated with panicle DW and negatively correlated with the flowering date. So, early flowering sorghum invested more in root than shoot biomass, which is also shown by the negative correlation between the root-to-shoot ratio with the shoot DWA higher root-shoot ratio could have played a role in achieving higher yield and may have been a strategy of plants that flowered relatively early. Also, a negative correlation between panicle DW and shoot DW as well as TE showed preferential resource partitioning in the plants. Furthermore, panicle DW was positively correlated with transpiration rates, while shoot DW had a slightly negative interaction with transpiration rates (Fig. 7, Silty Clay). Root length showed a positive interaction with transpiration and root surface area (SA) in loamy sand soil. The investment in nodal/crown roots and other root parameters appeared to have contradicting effects on the panicle DW in treatments with sandy loam and loamy sand soil. While in both treatments the amount of nodal roots was correlated with increased transpiration rates, the number of nodal roots decreased panicle DW of plants in sandy loam soil, but root length increased panicle DW in the loamy sand soil treatment. In sandy loam and loamy sand soil plants had a negative correlation of TE with flowering date and with root parameters. In sandy loam soil, TE was negatively correlated with the number of crown roots and root length and in loamy sand soil

with root DW and root-shoot ratio. In all soils except sandy loam, TE was also positively correlated with shoot DW (Fig. 7, Sandy Loam & Loamy Sand). So plants with higher TE flowered later and were negatively correlated with different root parameters like root-shoot ratio, at the same time having a higher shoot DW. In the main experiment, TE was indeed also positively correlated to shoot DW for sorghum growing in sandy loam soil, and the association of TE with vegetative biomass could also be observed in the PCA (Fig. 6). On the opposite, this may imply that plants with a lower TE - which only accounts for aboveground biomass – and also had a higher root-shoot ratio, invested proportionally less into aboveground biomass and instead more into roots. This can be backed up by the fact, that panicle DW for plants growing in loamy sand was also positively correlated with root length (Fig. 7, Sand). However, panicle DW was negatively correlated with root and shoot DW for plants growing in sandy soil. Possibly in sandier soils, there was a tradeoff to utilize the available resources either above– or below ground, which may have resulted in lower TE values for those plants that invested proportionally more into roots, i.e. had a higher root-shoot ratio, as the investment into root biomass is not accounted for in the TE calculation here, as it is common practice at the single plant-level (Vadez et al., 2014). Also in the main experiment, these genotypes with lower TE are tendentially those with a higher HI (landraces IS 8348 and IS 29914). In sand also, transpiration was negatively correlated with panicle DW and root-shoot ratio, implying that plants that used less water – whether they saved it or were not able to extract more – had a higher root-shoot ratio and achieved a higher panicle DW. The positive correlation of transpiration with root and shoot DW in sand could also indicate that these plants which transpired less were also the ones with a reduced vegetative biomass overall, leaving more resources for producing yield. It seems that overall, the extremely limited resources in the sandy soil meant that any investment into above- or belowground biomass led to a shortage in water and/or nutrients for growth elsewhere. At the same time, in silty clay soil, the positive correlation of panicle DW with transpiration can indicate that plants with a higher water extraction rate can directly utilize these resources for producing more yield. In a meta-analysis, Poeplau and Kätterer (2017) showed, that soil texture has a significant effect on the root-shoot ratio. In their test with spring barley, soil texture affected root growth more than nutrient availability did, with the root-shoot ratio being largest in sandy soil and smallest in
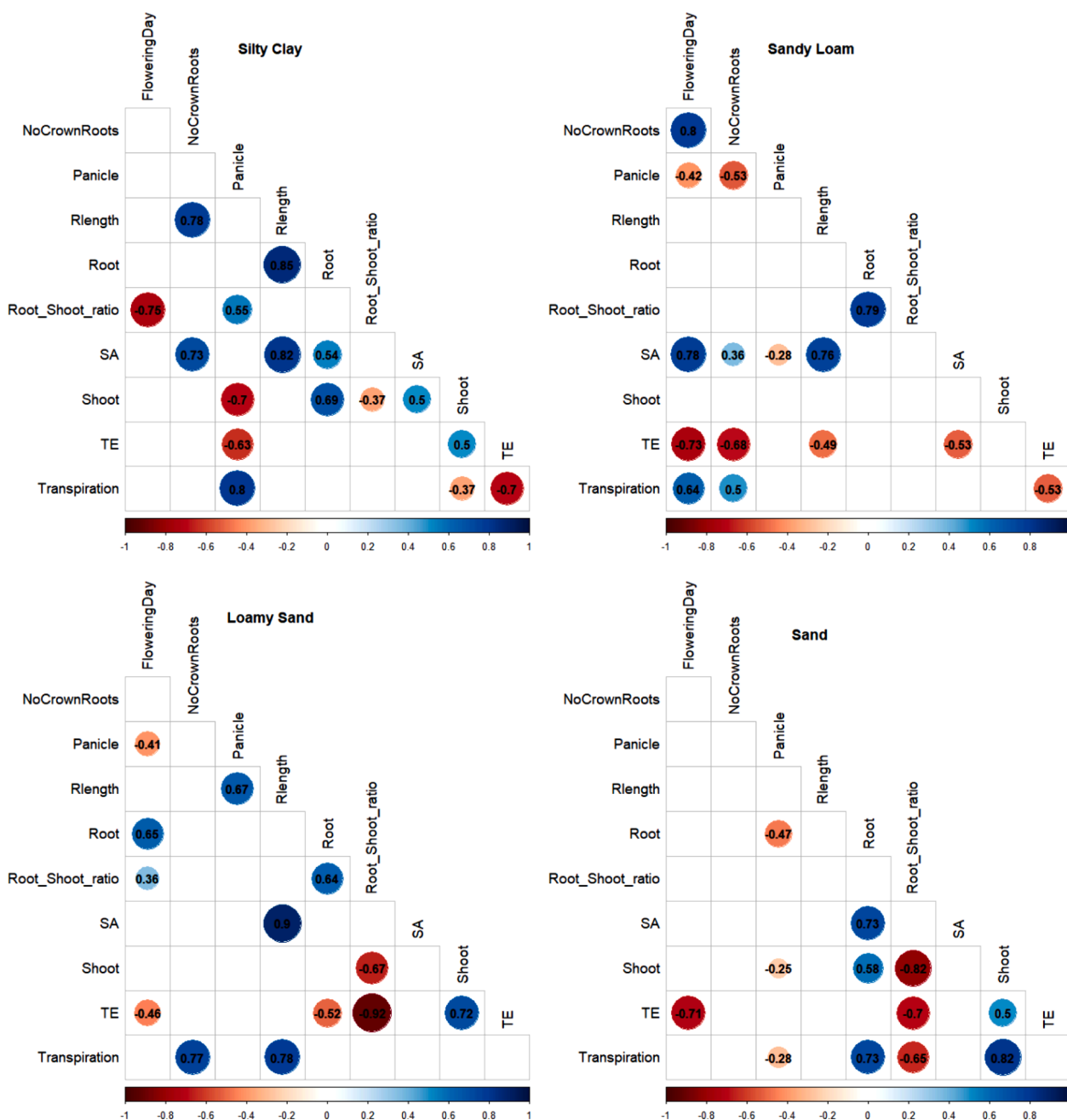
Fig. 7. Correlation plots of above and below-ground sorghum biomass and growth parameters and their water use plotted over the soil texture types ($n = 10$ soil type^{-1}). Included parameters: days till flowering (FloweringDay), number of crown/nodal roots (NoCrownRoots), panicle DW (Panicle), root length (Rlength), root DW (Root), root-shoot ratio (Root_Shoot_ratio), root surface area (SA), shoot DW (Shoot), transpiration efficiency (TE) and transpiration (Transpiration). Spearman's Rank correlation test was applied to calculate correlation coefficients and only significant ($p < 0.05$) results are displayed. Blue and red colors indicate a positive or a negative correlation, respectively. Color intensity and the size of the circles are proportional to the correlation coefficients.

clay loam soil, which they attributed to differences in water availability.

Transpiration efficiency is reduced in sandy soils

The effect of soil texture was also observed for the TE of our sorghum genotypes, with sand having the lowest (4.74 g kg^{-1}) and silty clay the highest (5.66 g kg^{-1}) TE (Fig. 3). In the correlation analysis, TE also increased with later flowering date across and within soils, except for silty clay soil. Total transpiration increased with flowering date across soils and on silty clay soil; HI was correlated with a higher total transpiration on silty clay soil (Table 3). The residual panicle DW, not explained by HI or flowering time, were both significantly positively

correlated to TE ($R^2 = 0.35$, $p < 0.001$ and $R^2 = 0.2$, $p < 0.001$). Residual TE not explained by flowering date was negative for sandy soil and positive for silty clay soil, among genotypes positive for M35–1 and IS 15945 and negative for IS 29914. Residual TE not explained by flowering date was significantly positively related to panicle DW ($R^2 = 0.21$, $p < 0.001$). This means our observed trend with lowest TE for sorghum grown in sandy soil would have been even more pronounced without the effect of the flowering date (Suppl. Fig. S6).

Our values are in line with a TE range of 3.21 to 6.09 g kg^{-1} in a study on 146 sorghum genotypes grown in sandy loam soil with a drought treatment (Vadez et al., 2011), and 16 sorghum genotypes in various treatments and similar soils as in this study, both in the same

Table 3

Correlations of Panicle DW, Total Transpiration, TE, HI, and Flowering Date analyzed with data of all soil treatments pooled ("All Soils") and separately.

Y variable	X variable	Soil Texture	R	R²	Significance
Panicle DW	Flowering date	All soils	−0.26	0.07	***
		Silty clay	−0.74	0.55	***
		Sandy loam	−0.56	0.32	***
		Loamy sand	−0.69	0.47	***
		Sand	−0.64	0.40	***
Panicle DW	HI	All soils	0.59	0.34	***
		Silty clay	0.66	0.43	***
		Sandy loam	0.79	0.62	***
		Loamy sand	0.84	0.71	***
		Sand	0.60	0.36	***
Panicle DW	Total transpiration	All soils	0.64	0.41	***
		Silty clay	0.02	0	
		Sandy loam	−0.02	0	
		Loamy sand	0.01	0	
		Sand	0.59	0.35	***
Panicle DW	TE	All soils	0.30	0.09	***
		Silty clay	0.25	0.06	
		Sandy loam	−0.23	0.06	
		Loamy sand	−0.42	0.17	***
		Sand	−0.02	0.01	
Total transpiration	Flowering date	All soils	0.19	0.03	*
		Silty clay	0.30	0.09	*
		Sandy loam	0.07	0.01	
		Loamy sand	−0.03	0	
		Sand	0.07	0.01	
TE	Flowering date	All soils	0.30	0.09	***
		Silty clay	0.01	0	
		Sandy loam	0.39	0.15	**
		Loamy sand	0.53	0.28	***
		Sand	0.38	0.15	*
HI	Total transpiration	All soils	0.05	0.01	
		Silty clay	−0.36	0.13	*
		Sandy loam	−0.26	0.07	
		Loamy sand	−0.25	0.06	
		Sand	−0.09	0.01	

Stars indicate p-values ($< 0.001 = $ ***; $<0.01 = $ **; $< 0.05 = $ *).

Lysi-field facility (Vadez et al., 2021). Comparing maize, sorghum and pearl millet grown on soils of contrasting textures, Vadez et al. (2021) proposed the differences in TE stem from the impact of grain size distribution on soil matric potential which in turn leads to differences in root hydraulic conductance. Regarding the soil matric potential, they state that higher soil matric potentials in sandy soil make water being taken up more quickly in scenarios of high demand by high VPD which would lead to a reduced TE in more sandy soil. Several studies on maize proved that stomatal regulation changed with soil hydraulic properties and found that the decrease of transpiration rates during soil drying occurred at higher matric potentials in sandy soil than in loamy soil (Cai et al., 2022a; Koehler et al., 2022). In a review including other cereals and tomatoes, the distinct difference of sandy and loamy soil has been confirmed (Cai et al., 2022b). Regarding the root hydraulic conductance, Cai et al. (2022b) suggested that root hydraulics are also affected by soil texture. While the maximum root conductance is plant-specific, it seems root water uptake of plants with a higher root conductance is already limited by the soil at less negative soil matric potential. The specific drying behaviour of soils is in turn again linked to soil texture, as soil matric potential drops more drastically in sandy soil due to the big pores and non-uniform pore-size distribution. Based on the measured hydraulic properties of our soils (Fig. 2) linking transpiration and even TE to differences in soil matric potential across soil textures is a likely explanation as soil matric potential differed greatly between the soils of different textures at one moisture level, while soil hydraulic conductance was rather similar. This difference is also reflected in the amount of theoretically plant-available water ($<$ pF 4.2) which was not taken up by the plants in the different soil textures. The least amount of water was left in sandy soil (1.2 L on average), while in loamy sand soil, it was about 1.6 times more water (1.9 L), in sandy loam soil 5.3 (6.3 L), and in silty clay soil 7 times more water (8.4 L). These observations can underline the strong effect of soil texture on the total amount of water availability but also extractability.

The effect of genotypic variation on TE

We detected no relationship between TE and total water use which was in line with previous studies (Mortlock and Hammer, 1999; Vadez et al., 2011), showing that a high water extraction from soil is not a good indicator for TE. This was well observed for the elite line M35–1, reaching both the highest total transpiration as well as TE values (5.69 g kg^{-1}) among the genotypes, while IS 8348 had the lowest TE (4.76 g kg^{-1}) but transpired similar total amounts of water as M35–1 (Fig. 3). In a mini-lysimeter experiment, M35–1 also had the highest TE values compared to other genotypes (9.15 g kg^{-1}); however, absolute numbers are not comparable as the plants were harvested already near anthesis (Mortlock and Hammer, 1999). While in the same study, no relationship between plant size and TE was reported, a trend of rising TE with higher biomass was found in our study, similar to previous studies (Vadez et al., 2011; Xin et al., 2009). The relationship is strongest for the landraces IS 29914 and IS 8348, but also visible for the other varieties (Fig. 8). Interestingly, these two genotypes were those with the lowest total biomass and leaf biomass, but at the same time the highest panicle weights, emphasizing on the importance of biomass partitioning. Both genotypes also showed rather low TE rates compared to the other genotypes.

Taller plants suffer more during terminal drought

Plant height was reduced strongly on sandy soil compared to others soil types, with the taller genotypes (IS 15945, M35–1, and IS 8348) showing a more drastic (32, 41, and 37% from silty clay to sandy soil) reduction in height than shorter genotypes (IS 29914 and IS 12447: 24 and 29%).We observed a negative correlation between plant height and HI, which was significant in sandy loam and loamy sand soil treatments when analyzed separately by soil texture (Suppl. Fig. S7). These findings are in line with other studies on sorghum (Murray et al., 2008; Ritter et al., 2008; Zhao et al., 2009) and wheat (Devesh et al., 2021). It should be pointed out that the low HI of the landrace IS 12447 grown on sandy loam soil is likely the result of stem breakage below the panicle as many of these very tall plants were damaged by wind or passing the weighing instrument every week. However, the plant size and their vulnerability to lodging might be an issue for harvest practices and reduce possible yields on farm level as well. Shorter genotypes, on the other hand, seemed to be more robust against wind and other influences, but may also have been protected by taller genotypes. Kholová et al. (2013) also argue that tall cultivars like M35–1 need to invest more N into structural stem tissue (van Oosterom et al., 2010), leading to an earlier depletion in soil N supply and may even be associated with earlier senescence, which may also take away nutrients for grain filling and a higher HI.

Differences between the elite line M35–1 and the landraces

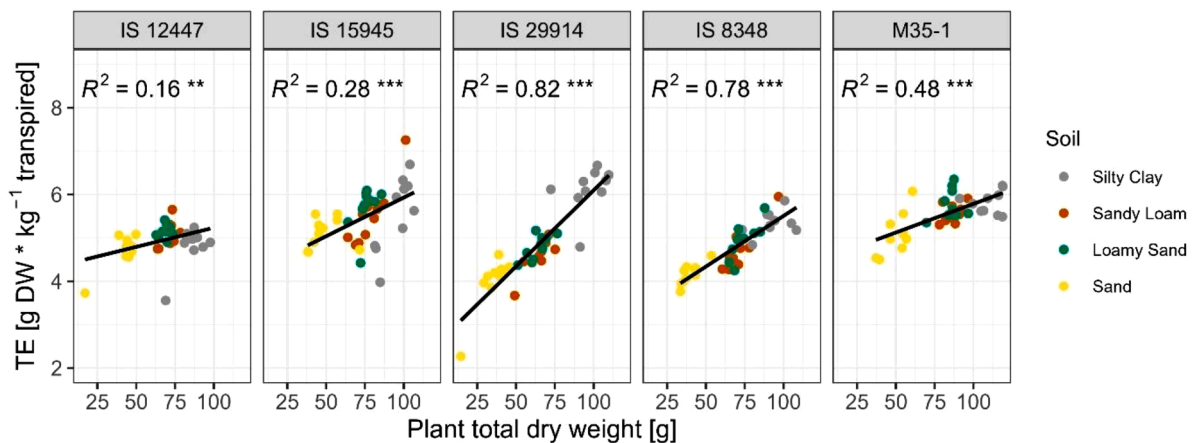Even though the genotypes were selected carefully with matching

Fig. 8. Transpiration Efficiency plotted over total dry biomass per genotypes and soil textures, indicating a positive relationship for all varieties. Colors indicate soil texture treatment, solid lines indicate linear regression, R^2 provided, stars indicate p-values ($< 0.001 = ***$; $<0.01 = **$; $< 0.05 = *$).

flowering time points as the flowering time is genotype-specific (Castro-Nava et al., 2012), significant differences could also be found (Table 2). The elite line M35–1 flowered significantly later than the landraces at about 63 DAS, which resulted in yield failure in almost all plants grown on the sandy soils and reduced yields on the other soils with finer textures. This flowering time point showed no negative effect in field experiments. A long-term field experiment in the post-rainy season at ICRISAT on a vertisol, i.e. a silty clay soil, revealed flowering DAS of 75 to 82 for M35–1, depending on the year, while achieving average yields (Reddy et al., 2009). Screening of 245 genotypes in Kansas, US on a silt loam soil showed drought-adapted lines to flower between 61 and 75 DAS (Kapanigowda et al., 2013). New sorghum hybrids resulting from crossing of post-rainy season adapted landraces in India and developed at ICRISAT also had a mean flowering time point of 74 DAS (range 71 to 81 DAS) (Kumar et al., 2011). It seems like the imposed drought stress of this experiment was more severe or started at an earlier stage than in average post-rainy seasons.

It is noted that the late flowering date of the control M35–1 corresponds to the high vegetative biomass, higher total number of leaves, and increased leaf area per plant for M35–1 than the landraces (Table 2). It appears that the M35–1 genotype has a relatively longer duration than the other tested landraces, emphasizing the impact of phenology on drought adaptation. Compared to the landraces, stress onset occurred relatively earlier in the life cycle of M35–1 around the time of flowering, leading to a more frequent abortion of panicles than for the landraces. Nevertheless, even the residual analysis of the panicle DW without the effect of flowering date could mostly support the trends of lower yield of M35–1 seen in this experiment. The negative residuals of M35–1 for all soils except the silty clay soil mean panicle DW without the flowering effect was even lower, while the positive residuals of the landraces IS 12447 and IS 29914 underline their strong performance in these harsh conditions (Suppl. Fig. S8).

However, the elite line M35–1 had also the highest transpiration and TE values as well as significantly higher nutrient concentrations in the shoot except when grown in sandy soil (in silty clay, sandy loam, and loamy sand (Na, K, Ca, Mg, Mn, and S), and silty clay and sandy loam (Cu and Si), respectively). K and Si are nutrients connected to transpiration, especially under drought and it can be speculated that the enhanced transpiration and TE could be connected to the higher accumulation of these nutrients in the shoot of M35–1 plants. Si is known to improve crop performance by accumulating in the leaves and regulating transpiration (Vandegeer et al., 2021), improving root-soil contact and thus water uptake by promoting the growth of roots and root hairs (Cheraghi et al., 2024), enhancing nutrient acquisition and regulating enzyme activity during drought stress (Wang et al., 2021). In sorghum, it was reported to improve the performance of a genotype sensitive to drought at

pre-flowering stage (Avila et al., 2020) and in general, improve plant-water relations and increase chlorophyll contents (Ahmed et al., 2011). While the mentioned studies looked at the effect of plants actively treated with Si, M35–1 had a higher Si content than the landraces when growing in silty clay and sandy loam, suggesting a genotype-specific ability to acquire more Si. The difference of K uptake was even greater between M35–1 and the landraces, being about double the concentration of K taken up by any of the landraces in all soils except sandy soil (Suppl. Fig. S4). K is involved in many plant functions, among which are also stomatal regulation, osmoregulation, and photosynthesis, which are crucial during drought events (Mostofa et al., 2022). In general, M35–1 seems to harbor certain root traits which enable it to acquire nutrients more efficiently than the landraces, except when growing in sandy soil. The root analysis showed that this genotype had a greater root length, root biomass and root surface area, and more crown roots than any of the landraces. As there are not enough replicates this is just a mentionable trend, although a possibly good explanation for the increased nutrient uptake. This is a good basis for a stable performance on soils with a lower sand content (Reddy et al., 2009). On the other hand, though, the longer physiology can have a negative effect on water use patterns in early-onset drought scenarios like in this study.

Early flowering date is advantageous

The landrace IS 8348 always flowered first around 51 DAS, while the elite line M35–1 was always significantly latest at about 60 to 65 DAS with a high variability in silty clay (Table 2). The landrace IS 29914 mostly flowered second, when grown in sandy loam and loamy sand soil it flowered together with IS 12447 (about 55 DAS). The latter generally flowered around the same time, just when grown in silty clay soil it happened later than in the other soils (59 DAS). IS 15945 flowered around 58 to 60 DAS, always later than the other landraces, and when grown on sandy loam soil it even grouped similarly as the control M35–1 in the LSD-test. In total, 23 plants did not reach the flowering stage, out of which 16 were M35–1. Panicle DW decreased significantly with flowering date and increased significantly with HI, both across and within the soils of different textures (Table 3). Panicle DW also increased significantly across all soil textures with total transpiration and TE, and within sandy and loamy sand soils, respectively.

Generally, the variability of data was very high for HI. The elite line M35–1 always had the lowest values, which was especially pronounced when grown on sandy soil ($< 10\%$). It should also be noted that M35–1 often did not produce grain at all and those plants could not even be included in the calculation of HI. Comparing the varieties in each soil, the landrace IS 29914 showed the highest HI on all soils (38% and higher) except for the silty clay soil. Here IS 8348 had the highest value

(44%) and also performed very well on sandy soil (42%), otherwise medium compared to other genotypes. IS 12447 had a high HI but also a high variability when growing on sandy loam soil (average 38%) and otherwise also performed well to medium (22 to 39%). IS 15945 reached medium HI values and performed significantly lower than the other landraces on sandy loam and loamy sand soil (15 and 23%). A lower HI was closely linked to a later flowering date, a relationship which could explain 9 to 46% of data depending on soil (Fig. 9). The genotypes which flowered earlier (IS 8348, IS 29914) usually have also a higher HI, with the trend being opposite for the late flowering IS 15945 and especially M35–1.

Harvest Index and days to flowering were negatively related (Fig. 9) as also shown in a screening experiment of 245 genotypes (Kapanigowda et al., 2013). In a terminal drought, early flowering dates are most advantageous, as water resources are not yet depleted, and the plants can still maintain photosynthetic activity for grain filling (Barnabás et al., 2008). Early flowering genotypes also tend to have a reduced canopy size through reducing the number of produced leaves (Hammer et al., 2010). Additionally, Ahmed et al. (2018) argued that the distribution of water usage throughout the season is crucial for achieving a high HI. In a terminal drought, not those crops succeed, which hold root traits enabling them to extract water the fastest, but those which preserve about 30% of available water for the grain filling period. Generally in sorghum, it has been observed that yield is vulnerable to drought occurring during the reproductive phase (Gupta et al., 2020; Kholová et al., 2013). In this early drought onset, the escape strategy by maturing as early as possible but also conserving water to be used for the grain filling period seems to have been most advantageous.

Diverse interactive effects of genotypes with soil textures

Based on the PCA (Fig. 6), overall effect of soil texture seemed to dominate the results, overlaying the influence of the genotypes at the first look. However, there are trends visible for certain genotypes or groups of genotypes. The tall genotypes (IS 15945, M35–1, and IS 8348) had a stronger reduction of biomass on sandy soils than the smaller genotypes (Table 2). This could indicate that while the tall genotypes are better at utilizing all available resources and grow very vigorously under good conditions, they suffer more in a shortage of water and nutrients as they utilize more resources for growth of a supportive stem (Kholová et al., 2013). On the other hand, the smaller genotypes (IS 29914 and IS 12447) may not be able to exploit all available resources under ideal conditions but maintain stable growth even in extreme situations like

very dry and sandy soils with sparse nutrient availability. Interestingly, the same trend was observed for the amount of theoretically extractable water ($<$pF 4.2) which was left in the columns. In all soils except the sandy soil, M35–1 always extracted more water than the landraces, closely followed by IS 8348, while IS 12447 always left the most water in the columns. The variability between genotypes regarding plant available water which was not taken up was greatest in silty clay (about 3 L) and sandy loam soil (about 2 L), while in the more sandy soils variability was very low.

The interaction of genotypes and soil textures regarding yield and HI was diverse. While the landrace IS 29914 always reached high (38 to 44%) and the control M35–1 constantly lower (9 to 26%) HI, the other genotypes were more variable between textures (Table 2). This range of results is in line with a genotype screening of 146 genotypes at ICRISAT in lysimeters (Vadez et al., 2011) filled with alfisol (sandy loam soil), which achieved an average HI under drought stress of 27% (range of 0–45%), comparing to 25% in the sandy loam soil treatment and an average of 28% over all soils. We could not find a relationship between grain yield and water use, which was also confirmed by the PCA analysis, but there was a significant correlation between yield and HI (Suppl. Fig. S8). In the screening of 146 genotypes, grain yield was highly variable in both well-watered and water-stressed conditions and similarly poorly related to water availability (Vadez et al., 2011). Residual panicle DW not explained by HI was positive for the landrace IS 8348 on all soils and for IS 12447 on all soil textures except silty clay soil, confirming the already observed trends for these genotypes and indicating that these landraces would have achieved a high panicle DW also without the effect of HI (suppl. Fig. S6). For the control M35–1, it was around 0 on all soils except on sandy soil, where it was very negative. Residual panicle DW not explained by flowering date was positive for the landrace IS 29914 on all soils, negative for the landraces IS 15945 and IS 8348 on all soils except sandy soil, and very positive for IS 12447 in sandy loam soil. It had a great variability for the elite line M35–1 when grown on sandy loam soil. It also shows that when grown in sandy soil, all landraces would have performed even better without the HI effect, while the elite line M35–1 would have performed worse (Suppl. Fig. S6).

In general, the elite line M35–1 showed a strong interaction with the soils and especially the sandy soil. While in silty clay, sandy loam, and loamy sand soil M35–1 was able to extract more water and nutrients than any of the landraces, this was not the case when grown in sandy soil. On the opposite, the landraces IS 8348, IS 29914, and IS 12447 were very stable across all soils and achieved high HI constantly. While these were the earlier flowering genotypes, IS 12447 flowered five days
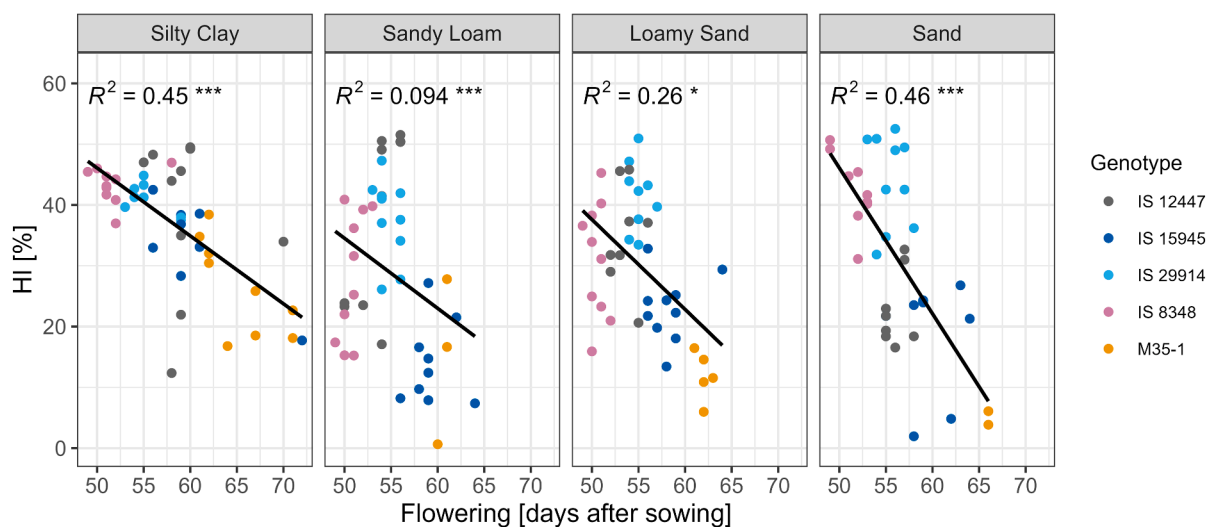

Fig. 9. Harvest Index [%] plotted against flowering date [DAS], showing a significant negative correlation in all soil textures and a pattern in genotype distribution. Points indicate genotypes with colors, black line is a linear correlation across genotypes, R^2 provided, stars indicate p-values ($< 0.001 =$ ***; $<0.01 =$ **; $< 0.05 =$ *).

later when growing in silty clay soil than in the other soils. Overall, the flowering period was about five days longer for sorghum in silty clay soil which may indicate that the higher soil water content relieved plant stress (Table 2). This difference of silty clay soil can also be seen in TE of the landrace IS 29914, which achieved the highest TE in silty clay soil but the lowest in all other soils (Table 1).

In summary, hypothesis 1, stating that landraces under water-limited conditions would achieve higher TE than elite lines (here M35–1), can be rejected. It should be noted though, that not only overall TE itself is an important factor in evaluating drought tolerance (Vadez et al., 2011), but also the distribution of water uptake during the crop cycle is essential (Ahmed et al., 2018). Adapted plants tend to use less water before anthesis and therefore prevent intense drought stress during the grain filling period (Manschadi et al., 2006). However, the second part of hypothesis 1, that landraces achieve higher yields than the elite line was proven here with the support of the residual analysis and seemed not to be related to TE. The landraces could produce yield despite the harsh, early onset drought. The second hypothesis, stating that this is especially pronounced in more water-limited soils such as sand, is also confirmed, as the elite line M35–1 could mostly not even reach the flowering stage in this case.

Conclusion

This study is among few that monitored transpiration efficiency in sorghum over the entire crop cycle when grown on soils of contrasting textures and hence provided insights to the interplay of water use and yield under drought stress conditions. Comparing the genotypes revealed the importance of early flowering under terminal drought conditions, as late flowering was connected with lower HI. Interestingly, both genotypes, which tendentially achieved the highest HI (landraces IS 29914 and IS 8348), performed lowest in TE, underlining the importance of early flowering over TE in this scenario. Indeed, late flowering of the elite line M35–1 caused low yields and HI. The results also highlighted that water conservation is not necessarily correlated with a high TE, but rather with the importance of water extraction during grain filling. Further research will be needed to answer in greater detail how exactly TE is influenced by soil texture, especially under field conditions.

The differences in plant growth between soil texture treatments were probably mostly linked to the hydraulic properties of each soil and therefore total amount of available water and its' extractability in each column. Further, soil texture influenced nutrient availability which led, in total, to plants with higher total transpiration, TE, and HI in plants grown on silty clay soil compared to sandy soil. The difference in plant performance between sorghum grown on sandy loam and loamy sand soil was generally neglectable. The very low resource availability in sand led to a low variation in transpiration and nutrient uptake, but further highlights the differences between genotypes in regard to biomass partitioning and physiology. These results highlight the important and yet neglected role of soil texture on sorghum cultivation, especially under terminal drought.

Overall, this experiment emphasizes the high potential of sorghum landraces with promising breeding opportunities to overcome terminal drought and produce grain even under severe limitations and extreme soils (i.e. sandy texture). While the popularity of M35–1 for post-rainy cultivation in India underpins its strong general performance, this study revealed that it is not well-suited for more extreme climate conditions and water shortages specifically in the regions with early droughts and more sandy soils. Therefore, there is a need for breeding for better adapted cultivars specifically designed to overcome these conditions. Certain traits of the common cultivar M35–1 are desirable, such as high TE and great ability to extract water and nutrients. However, the relatively shorter genotypes which can invest proportionally more resources into roots and grain and are less prone to logging seem to have an advantage on very sandy soils which are sparse in nutrients and

water. At the same time a faster flowering timepoint and maturity seem important to overcome severe, early droughts. The rich genepool of sorghum landraces offers a great opportunity to find the right traits for different stress scenarios.

CRediT authorship contribution statement

A.M. Sauer: Funding acquisition, Investigation, Formal analysis, Writing – original draft, Writing – review & editing. **S. Loftus:** Conceptualization, Investigation, Formal analysis, Writing – original draft, Writing – review & editing. **E.M. Schneider:** Investigation, Writing – review & editing. **K. Sudhabindu:** Investigation, Writing – review & editing. **A. Hajjarpoor:** Formal analysis, Writing – review & editing. **K. Sivasakthi:** Formal analysis, Writing – review & editing. **J. Kholová:** Conceptualization, Funding acquisition, Writing – review & editing. **M.A. Dippold:** Conceptualization, Funding acquisition, Investigation, Writing – review & editing. **M.A. Ahmed:** Conceptualization, Funding acquisition, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.stress.2024.100549.

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