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Yield, transpiration efficiency, and water-use variations and their interrelationships in the sorghum reference collection

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Abstract. Sorghum is well adapted to water-limited conditions, but the traits responsible for this enhanced adaptation under drought conditions remain unclear. In this study, yield, transpiration efficiency (TE) and water extraction were assessed in 149 germplasm entries from the sorghum reference set (plus three control cultivars) using a lysimetric system under terminal water stress and fully irrigated conditions outdoors. A 10-fold range for grain yield and harvest index (HI), 2-fold range for TE and a 1.25-fold variation for water extraction were observed under terminal water stress conditions. Transpiration efficiency and water extraction under water stress related poorly to that under fully irrigated conditions, reflecting a large genotype-by-water treatment interaction. Under drought stress, total water extraction varied by ~3 L plant^{-1} among germplasm. Entries from the Durra race had highest water extraction capacity, whereas Caudatum-Bicolor and Caudatum-Durra intermediate races had poor water extraction. Durra, Caudatum and Caudatum-Guinea races had highest TE, whereas the Guinea race had the lowest. Although yield was closely related to HI, at any level of HI there were substantial yield differences that remained unexplained, and these residual yield variations were closely related to TE ($R^2 = 0.60$). Similarly, substantial yield variations that were still not explained by HI or TE were closely related to the total water extracted under water stress ($R^2 = 0.35$). A multilinear regression analysis confirmed these results and showed the importance of water extraction during grain filling. Therefore, next to HI, the yield differences under terminal drought in sorghum were driven by TE, and then next by water extraction. The large genetic variation for TE and water extraction offer great breeding opportunities and in particular, highlight the Durra race as a critical source of variation.

Additional keywords: germplasm reference set, pre-anthesis water use, roots, water uptake profile.

Introduction

Water deficit is the most important abiotic stress and significantly limits crop production globally, particularly in the Semiarid Tropics. There are different 'patterns' of water stresses depending on the timing, the intensity, and the duration of drought stress (Serraj *et al*. 2005). In the Semiarid Tropics, where the length of the cropping period is limited, sorghum often faces a terminal drought, caused by the cessation of rain towards the end of the rainy season. This is particularly the case for post-rainy (*rabi*) sorghum in India, which is sown at the end of the rainy season to take advantage of the moisture accumulated in the soil profile. Successful crops under terminal drought are those having increased water availability and accessibility during grain filling (Vadez *et al*. 2007*a*). Possible options for increasing water availability post-anthesis are to: (*i*) manage the soil moisture profile in a way that leaves water available for grain filling, including strategies to minimise water use before anthesis (Kholová *et al*. 2010*a*, 2010*b*) or strategies to enhance transpiration efficiency (TE); (*ii*) develop a deeper and/or more profuse rooting system to access extra water from the soil profile.

Having higher TE (in g biomass kg^{-1} water transpired) could contribute to a slower rate of soil moisture depletion. Genotypic differences for TE have been reported in sorghum under well watered conditions (Hammer *et al*. 1997; Xin *et al*. 2009). Few studies have looked at TE under both fully irrigated and water stress conditions (Donatelli *et al*. 1992; Balota *et al*. 2008), with only a limited range of germplasm being assessed. Also, except Balota *et al*. (2008), TE has been measured over relatively limited periods of time. So it is therefore important to assess genetic variation for TE over an entire crop cycle and to determine whether there are large genotype-by-water regime interactions for TE. We used this approach to assess a large and diverse set of germplasm lines from the sorghum reference set (Ramu *et al*., unpubl. data).

Rooting traits have been reported as potentially important for drought adaptation in sorghum (Bhan *et al*. 1973; Mayaki *et al*. 1976; Blum *et al*. 1977; Jordan *et al*. 1979) based on studies involving a limited number of genotypes. In one study, the roots of a drought-tolerant sorghum line grew at least 40-cm deeper than a drought-sensitive one (Salih *et al*. 1999). Yet, root measurements are time consuming and prone to error

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(Vadez *et al*. 2007*a*), and the range of genotypic variation for the capacity to extract water from a soil profile remains unknown. This is critical information to gather since recent simulation and experimental work in wheat shows that each millimetre of water extraction during the grain-filling period contributes to an additional 55 kg ha^{-1} grain yield (Manschadi *et al*. 2006) and 59 kg ha^{-1} grain yield (Kirkegaard *et al*. 2007), respectively. It was also shown that the total water extraction did not differ between the tolerant and the sensitive wheat genotype, but the tolerant line used less water before anthesis and more after anthesis than the sensitive line (Manschadi *et al*. 2006). Here, similar hypotheses are developed in sorghum to assess differences in the total water extraction and the proportion of water being used during the post-anthesis period to service grain filling (Hammer 2006).

Passioura's equation (Passioura 1977) (Y = WU × TE × HI, with Y, WU, TE, and HI standing for yield, water used, transpiration efficiency and harvest index) has been widely used to guide the search for traits contributing to drought adaptation. However, since there was no method to evaluate all components on the same plants with an equal degree of precision, the use of that equation was generally limited to only single components, regardless of the relative importance of other components. For example, the past 20 years of drought research in groundnut has focussed on water-use efficiency (Hubick *et al*. 1986; Wright *et al*. 1994; Udayakumar *et al*. 1998; Nageswara Rao *et al*. 2001; Krishnamurthy *et al*. 2007), often relying on surrogates to estimate trait value. Similarly, rooting traits have been used as surrogates for water extraction (the WU component) (reviewed in Vadez *et al*. 2007*a*). Whether high TE relates to low water use (Blum 2005) or not (Peng and Krieg 1992) is still a matter of debate. Also, it is possible that one of the components of the equation may have, under specific conditions, a greater bearing on yield, thereby obscuring the true contribution of the other components to yield. Here, a method is used (Vadez *et al*. 2008; Ratnakumar *et al*. 2009) to precisely assess all components of Passioura's equation on the same plant and test their relationships using a large set of germplasm.

Sorghum is among the most adapted crops to dryland farming. Yet there is considerable genetic diversity available for adaptation to water deficit (Crasta *et al*. 1999; Harris *et al*. 2006). Recently, a mini core collection of 242 accessions of sorghum germplasm lines representing global diversity in core and entire collections has been developed using data on 21 phenotypic traits (Upadhyaya *et al*. 2009). More recently, a reference set collection based on data from 41 simple sequence repeat markers consisting of 384 entries has been developed (Ramu *et al*., unpubl. data). We assess variation in the traits described above in a subset of the reference set of sorghum which was chosen to limit variation in their time to flowering.

The overall objective of the present study was to assess variation in the sorghum reference collection for traits related to plant water use and hypothesised to be closely related to crop adaptation under terminal drought. We specifically assessed: (*i*) the genotypic differences in water extraction and the pattern of water use before and after anthesis; (*ii*) the genotypic variation in TE; (*iii*) the range of water regime-by-genotype interaction for these traits; (*iv*) the contribution of these traits to grain yield under terminal drought, and (*v*) possible association between specific sorghum races and values of the traits assessed.

Materials and methods

Soil and growth conditions of the lysimeters

Plants were grown in lysimeters, i.e. PVC tubes of 25-cm diameter and 2.0-m length, filled with Alfisol in outdoor conditions, with possibility to cover them with a shelter in case of rain. A PVC end plate was placed on top of four screws at the bottom of the cylinders, 3 cm from the very bottom, to prevent the soil from seeping through. The endplate did not fit the cylinder tightly and allowed water drainage, although drainage was prevented when lysimeter weighing started (see below). Tubes were filled with Alfisol collected from the ICRISAT farm and sieved to particles smaller than 1 cm. This allowed the bulk density of the soil profile to be set at ~1.35 g cm^{-3}, a standard value for Alfisols. Cylinders were filled with soil in three increments of 40 kg of dry soil. After addition of each 40-kg increment, the soil level in several cylinders was checked to ensure they were similar in all tubes. Then each 40 kg of soil added was watered. A previous assessment of the water needed to fill the profile before drainage determined that the soil water-holding capacity of the Alfisol was ~20%. Therefore, 8 L of water were added to each 40-kg increment of soil. After adding/watering 40 kg of soil three times, an additional 15 kg of dry soil was added to each cylinder and watered with 3 L. At that stage, the cylinders were almost filled to the desired level, i.e. ~5 cm from the top. A top-up using dry soil was done to ensure that all cylinders were filled to the same level. This top-up varied between ~1 and 2 kg, i.e. less than 1–2% variation across cylinders. Hence, all the cylinders had a similar bulk density close to 1.35 g cm^{-3}. All cylinders at field capacity weighed between 163 and 165 kg.

The soil in the lysimeters had been fertilised with DAP and muriate of potash, both at a rate of 200 mg kg^{-1} soil. It was also complemented with sieved and sterilised farm manure at a rate of 2 : 50 to prevent micro-nutrient deficiency. Before growing the sorghum crop, the lysimeters were used for a crop of finger millet and foxtail millet, planted sequentially. The foxtail millet crop had received a urea top-dressing of 3 g plant^{-1}. At the end of this crop, only the main root stock from the plants was removed from the top layer of soil by softening the top soil with water and pulling. The soil was then tilled superficially with sickles and limited Alfisol top-up was added so that the surface level was ~5 cm below the lysimeter brim. This created a soil profile that was undisturbed from previous cropping, except for minimum tillage of the surface. The lysimeters were then watered to field capacity, based on their expected weight, and the sorghum crop was planted on a full profile. The crop was top-dressed with 3 g urea plant^{-1} at 4 weeks after sowing.

Space arrangement of the lysimeters and weighing

The top of the cylinders was equipped with a metal collar and rings that allowed them to be lifted. Weighing of the cylinders was done by lifting the cylinders with a block-chained pulley, and an S-type load cell (Mettler-Toledo, Geneva, Switzerland) was inserted between the rings of the cylinder and the pulley.

The scale (200-kg capacity) allowed repeated-measurements with an accuracy of 20 g on each weighing. The lysimeters were separated from one another by a distance of ~5 cm. Thus the sorghum crop was planted at a density of ~11 plants m^{-2}, a plant population similar to typical field plantings at ICRISAT (row-to-row distance of 60 cm and plant-to-plant spacing of 15 cm). This allowed us to accurately assess the water extraction pattern of a crop cultivated in conditions similar to the field. The tubes were arranged in four trenches of 2-m depth and 1.75-m width. Each trench was separated by a 20-cm concrete wall. Possible border effects were expected on the south side of the trenches (these were oriented east–west) and those effects were curbed by bordering the trench with two rows of plants on the south side of the trenches.

Treatments used and traits assessed

The DS (drought stress) treatment received no water from 28 DAS until maturity, except for 2 L that were added to all cylinders at 73 DAS (beginning of grain filling), whereas the WW (well-watered) treatment was irrigated regularly (see below). Four seeds were planted in each cylinder on 20 October 2008 during the *rabi* sorghum season. Plants were thinned to two seedlings per cylinder at 14 days after sowing (DAS) and then to one plant per cylinder at 21 DAS. Disturbance to remaining plant was avoided by clipping the thinned plant below the collar. All plants were fully irrigated until 28 DAS. This involved cylinders receiving 500 mL twice a week for the first 2 weeks after sowing, and then on alternate days until 28 DAS. At 28 DAS, the cylinders were covered with a 2-cm layer of low density polyethylene beads to prevent soil evaporation. Preliminary testing indicated that the beads prevented more than 90% of the soil evaporation, so that differences in mass primarily reflected plant transpiration (data not shown). Biomass increase between weighing was negligible compared with plant water use. Weighing of the cylinders was done at 30 DAS for the first time and then subsequently every 2 weeks. This gave a total of five weights until harvest for the DS plants and six weights for the WW plants. The first weighing at 30 DAS gave the field capacity weight of each cylinder. The cylinders were distributed in four trenches and the weighing of one trench per day was done. The same sequence of weighing was used for each trench so that the time intervals between weighing were the same in all cylinders.

To keep the WW plants sufficiently wet for optimum growth and to avoid water drainage after irrigation, the WW plants were watered when the cylinder weight, at the time of weighing, had fallen below 2 L from the weight at field capacity. This prevented drainage at the bottom. The watering was done every week. The week that plants were not weighted, the water addition of the previous week was used for watering the WW plants.

Flowering time (days) was recorded on a plant basis. Transpiration was calculated at ~2-weekly intervals between 31 DAS (the time at which weighing started) and maturity. Daily transpiration values were calculated for each plant by dividing the transpiration for each time interval between weighing by the number of days in each interval. Pre-anthesis transpiration was the sum of the daily transpiration values until anthesis, plus water used in the first 28 DAS, which was estimated to be 1.5 L for all genotypes. This was based on dry biomass estimates of 15 g at 28 DAS and on the assumption of a TE of 10 g kg^{-1} water transpired at such an early stage (our unpublished observations). The post-anthesis water use was the sum of the daily transpiration values from anthesis until maturity. Harvest was done over a period of 4 days. Leaf, stem (including sheath) and panicle masses were recorded after drying for 3 days in a forced-air oven set at 70°C. Panicles were then subsequently threshed to determine grain yield. The HI was calculated as the ratio of grain yield divided by the total aboveground biomass (the aggregated mass of stems, leaves, and panicles). Transpiration efficiency was calculated as the ratio of the total aboveground biomass divided by the sum of transpiration values between 30 DAS and maturity. The initial biomass at the time of initiating the transpiration measurements was not taken into account, assuming that biomass differences between genotypes at that stage were negligible. This would have led to a slight overestimation of TE.

Plant material

The flowering time of 384 lines belonging to the sorghum reference set had been determined under field conditions in 2008–09 (H. D. Upadhayaya, pers. comm.). Based on these data, 149 reference set entries and three control cultivars, IS 2205, IS 18758, and IS 33844, varying in flowering time between 70 and 85 DAS, were selected. IS 2205 is a Durra-Bicolor landrace resistant to shoot fly and stem borer. IS 18758 is a Guinea-Caudatum landrace, released as E 35–1 in Burkina Faso in 1983 and as Gambella 1107 in Burundi in 1990. IS 33844 is a Durra landrace released in India as Parbhani Moti in 2002. The 149 reference set lines represented 30 out of 44 countries in the entire reference set. Race-wise composition was Caudatum (31), Durra (18), Bicolor (17 accessions), Guinea (14), Kafir (6), Guinea-Caudatum (24), Caudatum-Bicolor (14), Durra-Caudatum (13), Durra-Bicolor (3), Kafir-Bicolor (1), and Kafir-Caudatum (1). An accession each of *aethiopicuum* and *virgatum*, two accessions of *drummondii*, and three of *verticilliflorum* were also part of the 149 reference set material.

In addition to the DS and WW sets of plants used above, a third set of plants was sown at the same time in an area adjacent to the trenches. Plants were grown in 25-cm pots filled with 11 kg of the same Alfisol. Previous experiments in sorghum using these pots showed no signs of growth restriction due to pot size up to anthesis. The same planting procedures were used and plants were kept well watered until harvest. This set was harvested at flowering and its purpose was to evaluate leaf area and tillering characteristics of the different genotypes at that stage.

Data analysis

The experiment design was an Alpha lattice with 19 blocks of eight entries within each block. There were three replications and two water regimes (WW and DS). The Residual Maximum Likelihood method of GENSTAT was used to obtain the unbiased estimate of the variance components and the best linear unbiased predictions for the different parameters measured within each treatment, considering genotypes as random and replications as fixed effects. The significance of the genetic variability among accessions within treatment was assessed from the standard

error of the estimate of genetic variance σ^2_g. Analysis was also performed to assess the effect of genotype, water treatment and genotype-by-water treatment (G × T) interaction for the different traits measured. In this case, genotype and G × T were considered as random effects whereas treatment and replication were considered as fixed effects. The significance of genetic variability across treatments or of the G × T interaction effect was assessed in a manner similar to the above. The significance of the fixed effect of the treatment was assessed using the Wald statistic that asymptotically follows a χ^2 distribution.

For the multilinear regression analysis, a multilinear model was used in the software STATA (Stata Corp., College Station, TX, USA), where yield was taken as an additive function of HI, TE, total water extraction, water extracted in the post-anthesis period, water extracted in the 45–59 DAS and 59–78 DAS period, days to flowering, and a constant. The same multilinear model was used to assess the residual yield variations not explained by HI (see below), therefore excluding HI from the list of explanatory variables.

Results

Yield and biomass components

Grain yield varied significantly between genotypes under DS conditions, ranging from 0.3 to 36.6 g plant^{-1} (Fig. 1*a*). Overall, the mean yield of 20.6 g plant^{-1} under DS conditions was ~50% of the yield mean under WW conditions (42.0), indicating that the stress imposed was neither too severe nor too mild (Table 1). Under WW conditions, grain yield varied from 2.1 to 82.8 g plant^{-1}. Grain yield under WW and DS conditions were poorly related ($R^2 = 0.10$), which also reflected the large G × T interaction for grain yield (Table 1).

Harvest index also varied significantly between genotypes under DS conditions, ranging from 0.05 to 0.52 (Fig. 1*b*), except for two genotypes that did not produce any grains. The overall mean HI of 0.27 under DS was only slightly smaller than the mean HI under WW conditions (0.33). The HI also varied considerably under WW conditions, ranging from 0.21 to 0.53, except for five genotypes that had a poor HI lower than 0.15. Contrary to the grain yield data, the HI under DS conditions was better related to the HI under WW conditions ($R^2 = 0.33$) (Fig. 1*b*), although HI also displayed a significant G × T interaction (Table 1). The total plant biomass varied largely between entries. Under DS conditions, there was a 2-fold

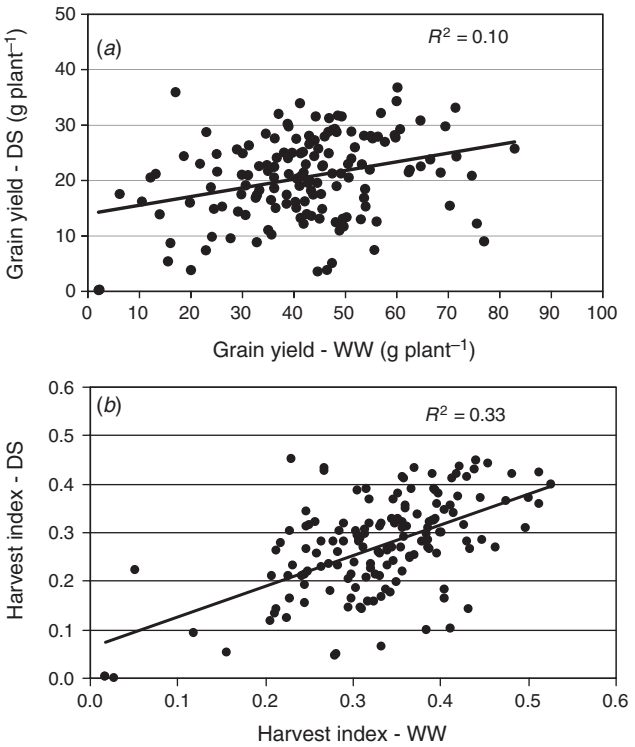

Fig. 1. Relationship between grain yield under terminal water stress (DS, g plant^{-1}) and grain yield under well watered conditions (WW, g plant^{-1}) (*a*), and relationship between harvest index under DS and harvest index under WW (*b*) in 152 germplasm entries. Data are the mean of three replicated lysimeter-grown plants per genotype.

Table 1. Trial means, range of expected means, genetic variance estimate and standard error of estimate, standard error of differences (s.e.d.) within treatment, and Wald statistics and *F*-probability for genotype effect, treatment effect and genotype-by-treatment (G × T) interaction related to time to flowering (day), grain dry mass (g plant^{-1}), total dry mass (g plant^{-1}), harvest index (HI), transpiration efficiency (TE, g kg^{-1}) and panicle harvest index (PNHI, i.e. the ratio of the grain weight by the panicle weight)

WW, Well-watered; DS, drought stress

		50% Fl		Grain yield		Total DW		HI		TE		PNHI	
		WW	DS	WW	DS	WW	DS	WW	DS	WW	DS	WW	DS
Mean		57	56	41.97	20.59	126.94	67.05	0.33	0.27	4.38	4.82	0.75	0.70
Min.		46	44	2.06	0.23	34.01	41.75	0.02	0.00	2.95	3.21	0.26	0.00
Max.		67	72	82.83	36.76	193.29	88.47	0.53	0.45	5.59	6.09	0.89	0.89
σ^2_g		13.1	17.6	166.0	38.69	664.6	43.47	0.06173	0.00584	0.162	0.162	0.005493	0.00623
s.e.		1.9	2.3	28.2	6.53	106.3	8.89	0.00098	0.00095	0.054	0.038	0.00099	0.00118
s.e.d.		2.14	2.02	10.07	4.80	18.83	5.99	0.057	0.056	0.45	0.39	0.061	0.067
G	σ^2_g	15.0		41.6		113.2		0.00496		0.113		0.005677	
	s.e.	1.94		12.5		40.7		0.00080		0.032		0.000942	
T	Wald	14.6		325		731.6		56.5		78.4		33.1	
	Prob.	0.001		0.001		0.001		0.001		0.01		0.001	
G × T	σ^2_{gxT}	0.65		61.1		236.7		0.001342		0.049		0.001065	
	s.e.	0.42		12.4		43.7		0.000433		0.032		0.000540	

difference between the minimum and the maximum value, whereas under WW conditions these differences were about 4-fold. This reflects in part genotypic differences in plant size and tillering, which became larger under WW conditions. Since the genotypes were randomised in the different replications, it is also a possibility that dwarf germplasm may have suffered from shading from tall germplasm in the WW conditions. This possibility is, however, quite unlikely under DS conditions, where the range of total biomass was smaller than under WW conditions, and also where total biomass differences also reflected large differences in grain yield.

Total water extraction

Total water extracted under DS conditions varied significantly ($P < 0.001$) among the 149 entries, ranging from 10 600 to 15 200 g plant^{-1} (Table 2). Noticeably, a low coefficient of variation of only 6% was obtained for the total water extraction in the lysimetric system. Under fully irrigated conditions, the water extracted by the plants also varied significantly, ranging from 10 500 to 42 300 g plant^{-1}. Besides an expected treatment effect, the total water extracted showed a large G × T interaction effect, whereas the genotypic effect was non-significant. In fact, the water extracted under WW and DS conditions showed a poor relationship ($R^2 = 0.08$). Total water uptake under DS conditions was assessed for each individual race. The Durra race had the highest total water uptake (14 120 g plant^{-1}, $n = 20$) (Fig. 2). The Durra-Caudatum race had, on average, the lowest total water uptake (13 570 g plant^{-1}, $n = 12$), followed by the Caudatum-Bicolor accessions (13 800 g plant^{-1}, $n = 14$).

The first two water-use measurements for the 31–45 DAS and 45–59 DAS time intervals were similar in WW and DS plants (Fig. 3), although there was a significant, but minor, treatment effect on the water extraction in the 45–59 DAS interval (Table 2). Indeed, the water used under DS in the 45–59 DAS period was above 70% of that under WW conditions, except for 18 lines where water used was 50–70% of that under WW. This indicated that for the 29 days following the last irrigation in the

Table 2. Trial means, range of expected means, genetic variance estimate and standard error of estimate, standard error of differences (s.e.d) within treatment, and Wald statistics and *F*-probability for genotype effect, treatment effect and genotype-by-treatment (G × T) interaction related to total water use (g plant^{-1}), pre-anthesis water use (g plant^{-1}), post-anthesis water use (g plant^{-1}), and water used in the 45–59 days after sowing (DAS) (g plant^{-1} day^{-1}), 59–78 DAS (g plant^{-1} day^{-1}) and 78–94 DAS (g plant^{-1} day^{-1}) periods

Water use		Total		Pre-anthesis		Post-anthesis		45–59 DAS		59–78 DAS		78–94 DAS	
		WW	DS	WW	DS	WW	DS	WW	DS	WW	DS	WW	DS
Mean		28 856	13 908	9383	8956	20 727	6452	358	344	401	180	368	112
Min.		10 500	10 620	5406	4493	5854	2439	141	162	114	70	99	58
Max.		42 320	15 240	15 493	13 628	35 018	10 917	556	668	598	279	630	229
σ_g^2		27 908 726	158 959	3 641 052	1 731 958	22 464 015	1 982 010	4528	1452	4482	677	7954	334
s.e.		4 141 939	50 275	535 809	285 982	3 435 089	301 436	759	969	838	260	1164	76.7
s.e.d.		3467	436	1147	999	3053	961	52	49	57	30	57	18
G	σ_g^2	1 124 515		2 183 060		1 452 707		2641		974		75	
	s.e.	1 456 941		328 263		1 238 507		600		375		430	
T	Wald	1017		8.95		1132		4.19		702		953	
	Prob.	0.001		0.003		0.001		0.04		0.001		0.001	
G × T	σ_{gxT}^2	12 814 903		365 709		10 488 093		247		3509		4187	
	s.e.	1 939 986		144 457		1 572 411		53.9		641		620	

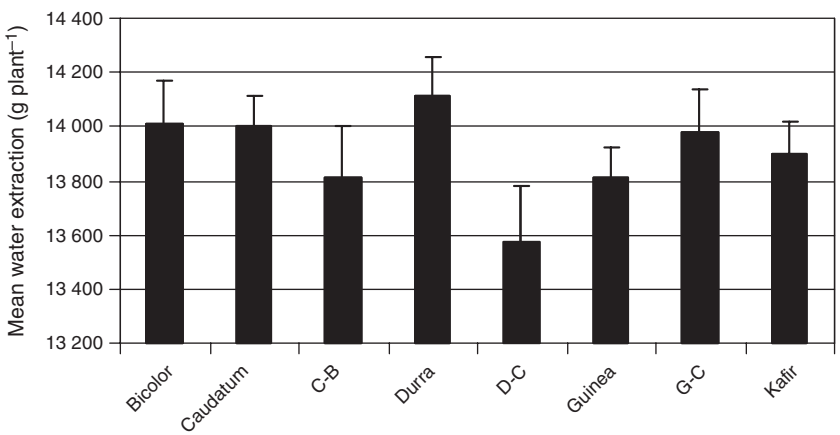

Fig. 2. Total water extracted from the lysimeter soil profile (g plant^{-1}) under terminal water stress conditions in the different sorghum races. Data are the mean of the average transpiration values within each race [Bicolor, $n = 17$; Caudatum, $n = 31$; Caudatum-Bicolor (C-B), $n = 14$; Durra, $n = 18$; Durra-Caudatum (D-C), $n = 13$; Guinea, $n = 14$; Guinea-Caudatum (G-C), $n = 24$; Kafir, $n = 6$].

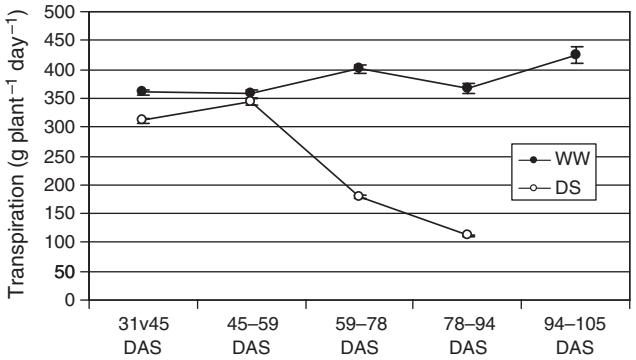

Fig. 3. Profile of transpiration (g plant^{-1}) as a function of time after sowing. Last irrigation was applied at 30 days after sowing (DAS) in plants exposed to terminal water stress (DS, open symbols) and well watered conditions (WW, closed symbols). Data are the mean (±s.e.) of the average transpiration values for 152 germplasm entries. For the DS and WW plants, five and six lysimeter weighings, respectively, were done, giving four and five transpiration intervals.

DS treatment, DS plants extracted similar amounts of water to WW plants. Water uptake in the 59–78 DAS interval showed a large treatment effect on water extraction, and large and significant genotype and G × T effects, the latter being more important than the genotype effect. Water uptake in the 78–94 DAS interval also showed large treatment and G × T effects, and no significant genotype effect. By 59 DAS, 125 out of 152 entries had flowered and all the others flowered by 65 DAS.

Summarising, the large variation in water extraction capacity under DS conditions, with a tendency to have higher water extraction in the Durra race than in the Durra-Caudatum race, resulted from specific adaptation of genotypes to the stress conditions, and the temporal pattern of water use indicated that stress occurred after flowering for most lines.

Relationships between water extracted before and after anthesis

The pre-anthesis water use varied by 9 L plant^{-1} among genotypes (5–14 L plant^{-1} range). These differences were, in part, explained by the flowering time ($R^2 = 0.70$, data not shown) although large variations in pre-anthesis water use per day, which removes the differences due to flowering time, remained (101–205 g water per day). Pre-anthesis water use was also significantly correlated with the leaf area at anthesis ($R^2 = 0.18$, data not shown). Pre-anthesis water use under DS was also predominantly determined by genetic effects (Table 2). The post-anthesis water used ranged from ~2 to 10 L plant^{-1} among genotypes. Post-anthesis water use under DS was correlated with flowering time ($R^2 = 0.73$) but not to the post-anthesis water use of WW plants. Pre- and post-anthesis water use showed a close negative correlation ($R^2 = 0.83$) (Fig. 4). Post-anthesis water use was also predominantly determined by G × T interaction effects, whereas the genotype effects were not significant (Table 2). Post-anthesis water use was also negatively correlated with the leaf area at anthesis ($R^2 = 0.17$). These data indicate that despite flowering time determining about two-thirds of the variation in pre- and post-anthesis water use, there was still a large range of variation in pre- and post-anthesis water use at any level of flowering time.

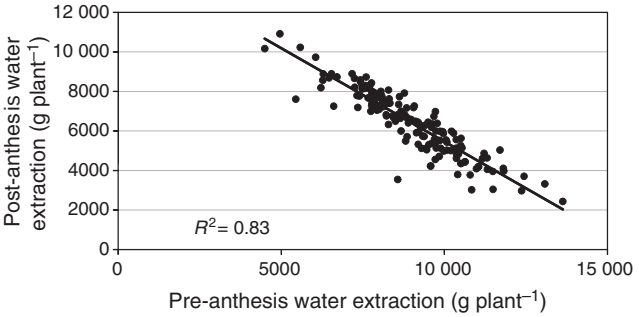

Fig. 4. Relationship between the pre-anthesis water use (g plant^{-1}) and the post-anthesis water use (g plant^{-1}) in 152 germplasm entries. Data are the mean of three replicated lysimeter-grown plants per genotype.

Transpiration efficiency

Transpiration efficiency varied largely among entries, ranging from 3.21 to 6.09 g kg^{-1} water transpired under DS conditions. The coefficient of variation was only 13.6%. Under fully irrigated conditions, TE also varied significantly, ranging from 2.95 and 5.59 g kg^{-1} (Table 1). The grand mean of 4.30 g kg^{-1} was lower than under DS conditions (4.82 g kg^{-1}). TE under DS and WW conditions were correlated but the correlation coefficient was weak ($R^2 = 0.13$, data not shown). Besides a strong treatment effect on TE, genotype and G × T interaction effects were both significant although the magnitude of the G effects was slightly higher. Transpiration efficiency was assessed for each individual race under DS conditions. The Guinea race exhibited the lowest mean TE values (4.29 g kg^{-1}, $n = 13$), followed by the Kafir (4.58 g kg^{-1}, $n = 6$), whereas the Guinea-Caudatum, Durra and Caudatum races had the highest mean TE values (5.09, 5.05 and 4.98 g kg^{-1}, $n = 25$, 20 and 32, respectively) (Fig. 5). In summary, TE was mostly driven by genotypic effects rather than by G × T interactions, and high TE variants were identified, especially in the Guinea-Caudatum, Durra and Caudatum races.

Relationships between water extraction, TE, HI, and yield

Regression analyses were conducted between grain yield and water used, TE, and HI. The relationship between grain yield and water used was significant under fully irrigated conditions only ($R^2 = 0.33$), but not under DS conditions (data not shown). Similarly, grain yield was significantly related to TE under WW conditions ($R^2 = 0.35$) and, although the relationship was significant under DS conditions, the correlation coefficient was weak ($R^2 = 0.07$) (data not shown).

Therefore, individually, neither the total water used nor TE had any substantial bearing on yield under DS conditions. This was because the relationship between yield and HI was highly significant, and more so under DS conditions ($R^2 = 0.88$) than under WW conditions ($R^2 = 0.53$) (Fig. 6*a*). However, for any given HI level, Fig. 6*a* indicates clearly that substantial variation in yield remained unexplained by HI, especially at HI levels above 0.30. These residual yield variations unexplained by HI were calculated by subtracting the yield predicted by the