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Mid-Season water stress on yield and water use of millet *(Panicum miliaceum)* and sorghum (*Sorghum bicolour* L. Moench)

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Abstract

In water-limited environments, plant productivity is determined jointly by the amount of water available and the water use or evapotranspiration efficiency (WUE or ETE). Mid-season water deficit can lead to a halving of yield. Some genotypes of Millet (*Panicum miliaceum*) and of Sorghum [*Sorghum bicolor* (L.) Moench] with different maturity status (Early; E, Middle; M, and Late; L) were cultivated in sand/nutrient media in a greenhouse. Control plants were maintained at field capacity. The mid-season water stress was imposed at 50% flowering for ten consecutive days, followed by re-irrigation to field capacity until harvest. Yield reductions by water stress averaged 77% in millet and 37% in sorghum and these differences were substantiated when genotypes of the same maturity were compared. This is pointing to a higher stress susceptibility of millet, particularly in M and L genotypes. Evapotranspiration efficiency, ETE, showed genotypic variation in well-watered plants and tended to be higher in sorghum. Evapotranspiration efficiency was generally raised by stress, however, difference between genotypes and crops were almost quenched at maturity. Nevertheless, water use efficiency, WUE differed significantly among genotypes in each crop and each water regime, but changes in rankings of genotypes gave evidence of some interactions with water regimes. In both crops WUE was correlated to its components ETE and HI (harvest index) under well-watered conditions, but only to HI under stress condition. Negative correlations of WUE with CID (carbon-13-isotope discrimination) were weak to poor and some conflicting results with regard to genotypic ranking were observed. These outcomes show the worth of continuous attention to harvest index in breeding for improved water use efficiency in C_4 crops.

Keywords: Carbon isotope discrimination; Evapotranspiration efficiency; Harvest index; Maturity groups; and Water use efficiency.
Abbreviations: CID-Carbon isotope discrimination; ETE-Evapotranspiration efficiency; HI- Harvest index; WUE- Water use efficiency.

Introduction

Scenarios for global environmental change predict increases in aridity and in the frequency of extreme events in many areas of the earth (IPCC, 2001). Today, with more than 70% of global available water been employed in agriculture, the use of appropriate crops and irrigation is an important issue particularly in drought prone areas. In recent decades, physiological, morphological, and molecular bases for plant responses to drought, and concurrent stresses, such as high temperature and irradiance, have been the subjects of intense research (Chaves et al., 2003: Flexas et al., 2004). Plant response to water deficit or drought spells depends on the timing, intensity, and duration of the stress episodes; and it reflects the integration of stress effects and responses to all underlying levels of organization over space and time (Blum, 1996). As conventional breeding and biotechnology makes headways into the development of drought-resistant cultivars, the conceptual framework of what actually constitutes a viable target for selection in this respect is not always clear (Blum, 2005). There is a constant debate of “putative” drought resistance mechanisms, water-use efficiency, and their interrelationship and associations with yield potential. Sorghum and the Millet are ranked fifth and sixth, respectively, in the world production of cereals. They are crucial to the world food economy because they contribute to household food security in many of the world’s poorest and most food-insecure regions. In the main production regions in Africa and Asia, more than 70% of the Sorghum crop and over 95% of the Millet crop are consumed as staple food. Their cultivation in areas with very low annual rainfall is attributed to their relatively low transpiration coefficient (i.e. water transpired per unit of total dry matter produced, Briggs and Shantz, 1913; Shantz and Piemeisel, 1927) compared to other cereals. The preferential selection of sorghum and millet landraces for cultivation in these drought-prone areas has mostly relied on the farmer's intuition rather than scientific information. There is a general believe that maize is a successful crop of humid areas and sorghum grows best in semi-arid regions with good distribution of rainfall or availability of irrigation water, while millet is preferred when the water supply is inadequate for maize and sorghum (Pai and Hukkeri, 1979). However, there is insufficient scientific evidence to support this view (Bishnoi and Bishnoi, 1986; Singh and Singh, 1988). To understand the physiological responses of water deficit in Sorghum and Millet, investigation of concurrent effects on soil-plant water relations is essential. In the present study, the effects of water deficit applied at flowering on the water relations of different maturity groups of both crops were tested.

Table 1. Effect of irrigation (well watered; ww and water stressed; ws) on cumulative evapotranspiration efficiency (ETE; g/l) of different Millet and Sorghum maturity taking on three sampling dates (before stress; bs, stress end; se, and maturity; fm).

	Early		Middle		Late	
Millet	ww	ws	ww	ws	ww	ws
bs	2.8 a	-	4.1 b	-	3.6 b	-
se	2.8 aA	4.5 bB	3.4 bA	4.1 bB	3.1 ab	3.4 a
fm	2.8 a	2.7 a	2.9 a	2.8 a	3.2 a	3.3 b
Sorghum						
bs	3.5 a	-	3.7 a	-	4.7 b	-
se	3.3 a	2.9 a	4.6 bA	5.6 bB	5.3 cA	6.5 cB
fm	2.5 a	2.8 a	3.0 aA	4.0 bB	2.7 a	2.8 a

Small letters (a, b, and c) indicates maturity differences (Tukey HSD test, P≤0.05), and capital letters (A and B) indicates difference (T-test; α=0.05) between treatments.

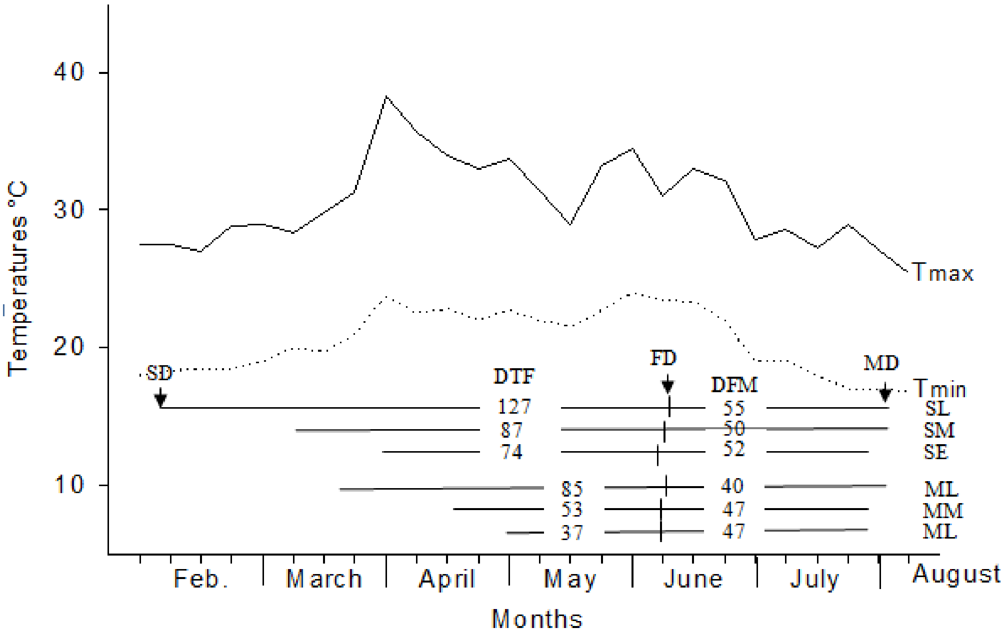

Fig 1. Growth cycles of genotypes and maximum (T_{max}) and minimum (T_{min}) temperatures in the greenhouse. Maturity (Mat.) group of Millet (M): E=Körnberger, M=Capatobckoe 10, and L=IPm2501; Sorghum (S): E=Sc.1790, M=ICSV273, L=S35. SD: Sowing date, FD: Flowering date, MD: Maturity date, DTF: Days to flowering, and DFM: Days from flowering to maturity

The objectives of this experiment were to (1) determine if mid-season water stress affects crop and maturity differences in water use and yield and (2) compare methods in determining WUE directly or indirectly by the ^{13}C-discrimination.

Results

Grain yield

As expected, mean yield of well-watered plants (Fig. 2) was lower for millet than that for sorghum (11.5 vs 26.4 g.); and generally, late genotypes were superior to medium ones. However, relative performance of the early ones was different in millet (ranking, E≈M<L) and sorghum (ranking, E>M≤L). Yields were significantly ($P \leq 0.05$) reduced by water stress (ws) across maturity groups in both crops, more so in Millet (77%) than Sorghum (37%). A higher stress susceptibility of millet compared to sorghum was also reflected in relative yield reductions of each genotype (E: 56 vs. 52%; M: 70 vs. 22%; L: 81 vs. 29%). Interaction of water stress and maturity are evident by the different rankings of stressed genotypes in millet (E~M~ L) and sorghum (E~M< L) compared to their well-watered counterparts, indicating that, within millet the late one was most affected compared to the early and middle one, whereas within sorghum the reverse was true.

Harvest index

Mean harvest index (HI) of non-stressed plants was higher in Millet than Sorghum (Fig. 3), but both crops showed similar differences among maturity groups (E≈M>L). Water stress strongly reduced HI in all maturity groups in both crops, except in the late sorghum (reduction not significant). The genotypic rankings of HI in non-stressed and stressed plants differed markedly, indicating a lower stress effect in early millet and in late sorghum compared to the other genotypes in each crop. Mean relative effect was stronger in millet (58%) than in sorghum (38%), which was mainly due to the late genotypes (E: 30 vs.37%; M: 62 vs. 60%; L: 79 vs. 28%)

Table 2. Correlation coefficients of WUE with other parameters in well-watered (ww) and stressed (ws) plants of millet and sorghum.

Correlations		Millet		Sorghum	
		ww	ws	ww	ws
(a) across genotypes[2]					
	WUE-ETE	0,56**	ns	0,64**	ns
	WUE-HI	0,33**	0,97**	0,70**	0,80**
	WUE-GY	ns	0,70**	ns	ns
(b) WUE-CID[3]					
	E	-0,84*	-0,94*	-0,98*	-0,93*
	M	-0,98*	-0,92*	-0,95*	-0,95*
	L	-0,90*	-0,98*	-0,98*	-0,96*

[1]ns,*, ** not significant/significant at P = 0.05/0.01, respectively, [2]N=24 (millet) and N=15 (sorghum), respectively. [3]within each genotype, N=4 (millet and sorghum)

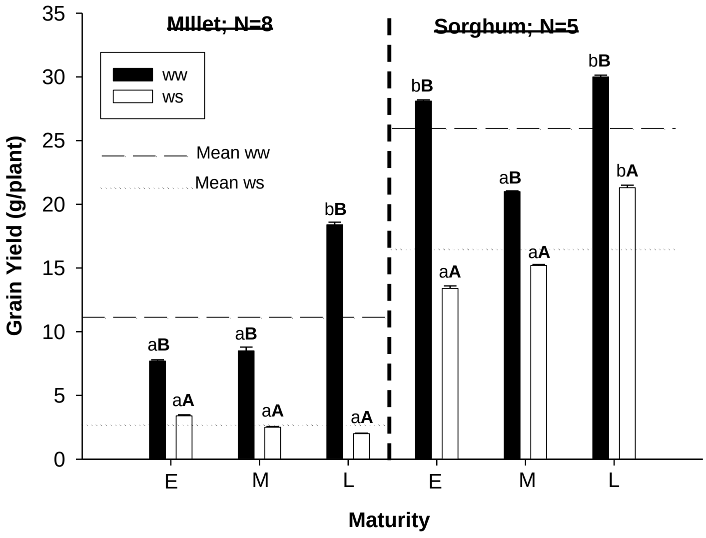

Fig 2. Effect of water stress on grain yield of different maturity (E, early, M; middle, and L; late) genotypes of Millet and Sorghum grown under glasshouse conditions. Small letters (a, b, and c) indicates maturity differences (Tukey HSD test, P≤0.05), while capital letters (A and B) indicates differences *(T-test; α=0.05)* between treatments (ww; well watered, and ws; water-stressed).

Evapotranspiration efficiency

Before stress (bs) (Table 1); while rankings for evapotranspiration efficiency (ETE; g/l) differed in millet (E<M≈L) and sorghum (E≈M<L), mean ETE was similar in millet (4.0g/l) and sorghum (3.5g/l). At stress end (se), well-watered treatment rankings were inconsistent in both crops. However, water stress significantly increased the ETE except for late millet and early sorghum, with lower mean ETE value in millet (4.0g/l) than in sorghum (5.0g/l). Rankings at full maturity (fm) under well-watered treatment were similar (E≈M≈L) in both crops, and only the water stressed treatment of the middle maturity sorghum maintained a significantly higher ETE value compared to its control treatment. End mean ETE values decreased (2.96 vs 2.73 and 2.93 vs 3.20) for millet vs sorghum under well-watered and water-stressed treatments, respectively.

Water use efficiency

In non-stressed plants of both crops, WUE showed similar maturity differences (E≈M>L) as HI, though mean WUE (Fig. 4) was higher in millet (1.03g/l) than sorghum (0.78g/l). While water stress significantly reduced WUE in all millet maturity groups without relevant changes of the genotypic ranking (E≥M>L), only the middle (M) maturity of sorghum (E≈M≈L) experienced a significant reduction. Relative reduction by stress was stronger in millet (58%) than sorghum (38%).

Carbon isotope discrimination (CID)

Numerous studies have concluded that CID could be used to select cereals for water use efficiency because of the significant and negative correlations exhibited by both parameters under control or water deficit conditions.

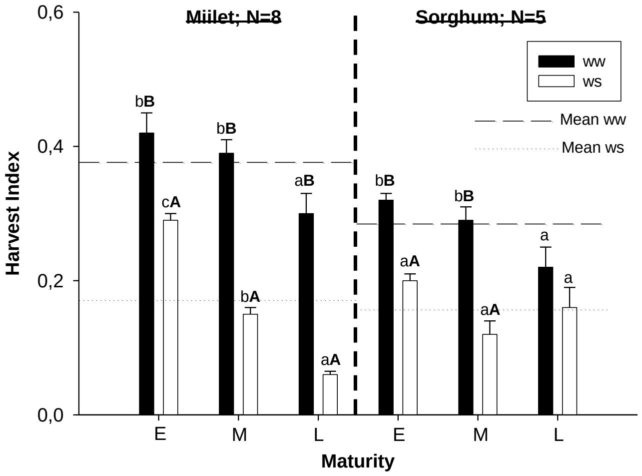

Fig 3. Effect of water stress on harvest index (HI) of different maturity (E, early, M; middle, and L; late) genotypes of millet and sorghum grown under glasshouse conditions. Small letters (a, b, and c) indicates maturity differences (Tukey HSD test, P≤0.05), and capital letters (A and B) indicates difference (T-test; α=0.05) between treatments (ww; well watered, and ws; water-stressed).

While a CID-WUE linkage was evident across well-watered (ww) and stressed (ws) genotypes of millet, it was fairly weak within sorghum (Fig. 5). CID-values showed similar rankings in ww and ws plants of millet (E, M, L: a, a, b and A, AB, B, respectively) and of sorghum (E, M, L: a, b, b and A, B, B, respectively). However, no marked effects of stress on CID were observed. WUE–rankings of ww and ws genotypes (Fig. 4 and 5) showed similar trends in millet (E, M, L: b, b, a and c, b, a, respectively.) and in sorghum (a, b, a and a, a, a, respectively). Stress considerably reduced WUE-values and displayed some interaction with genotypes (see E in millet and M in sorghum). Assuming a negative correlation of CID and WUE within a species, both methods led to consistent genotypic efficiencies in millet with E being better than M, and M being intermediary, whereas in sorghum consistency existed just for a low efficiency in L under ww, and in both L and M under ws.

Correlations

Correlations between WUE and its components ETE and HI are of some interest for breeding (Table 2). Under well-watered conditions (ww), each component correlated with WUE in both crops, while under stress (ws) just HI showed a significant correlation with WUE. Negative correlations between WUE and CID existed in each crop as expected, if calculated across genotypes and water regimes (Fig 5) and if each genotype and each regime was separately considered (Table 2b). However, no correlations were established if calculation was made across genotypes for one water regime (Table 2a).

Discussion

Since grain yield under water stress depends on phenological, morphological, and physiological characters of the crop (Ludlow and Muchow, 1990), we used different maturity groups of both millet and sorghum (both C4 crops), to allow a certain comparison between these crops regarding their yield performance under stress and water use condition. However, stress effects on growth and yield depends on its timing (Craufurd and Peacock, 1993; Mahalakshimi et al., 1987). Timing of water supply may even have a larger effect on grain yield than the total water used (Shaw, 1988). Statements of these authors are in accordance with those from Garrity et al. (1983) and Hattendorf et al. (1988) that reported millet and grain sorghum are most sensitive to water stress during flowering and grain filling. Hence, a prerequisite in our experiment was that water stress for each genotype /crop must be with the same strength and (ca. -40KPa), duration (14 days), begin at the same developmental stage (onset of flowering) and take place under the same environment (temperature, radiation, relative humidity). This was achieved by an almost simultaneous flowering of all genotypes due to differential sowing dates (Fig 1). Yield per plant (GY) was significantly reduced across all genotypes in both crops, more in millet than sorghum. A higher stress susceptibility of millet was also recorded in comparison with its respective counterpart of sorghum. This may be ascribed to a less drought-prone origin of millet which extends from mountainous regions near Mongolia to the Southern steppes of Russia (3000-5000 BC, Vavilov, 1987), whereas archaeological findings of grains from ancestors of sorghum points its origin in the semi-arid North-Eastern quadrant of Africa (about 5000 BC, Dogget, 1965). Harvest index (HI), was significantly lowered by water deficit stress in each genotype and crop as well. Because the genotypic ranking of HI within each species was changed due to stress, no consistent association with yield per plant was observed across well-watered or stressed genotypes of either crop. Differences of evapotranspiration efficiency (ETE) were detected among genotypes within each species before stress and at stress end, but rank orders among genotypes were affected to a degree by water regimes. Such interaction between genotype and environment on ETE matched the observations in 6 wheat cultivars in 2 years (Foulkes et al., 2001). At stress end, ETE was generally increased by water stress in both species indicating that stress impeded the dry matter production less than water uptake (Emendack, 2007). That stressed plants could not profit from the lowered water uptake later on. This might be attributed to an optimum irrigation of plants after stress end (ψ_{soil}= ca -0.008 MPa), which at maturity quench off the previous stress-improved ETE. In well-watered plants, WUE showed considerable genotypic variation in millet as well as in sorghum, and stress

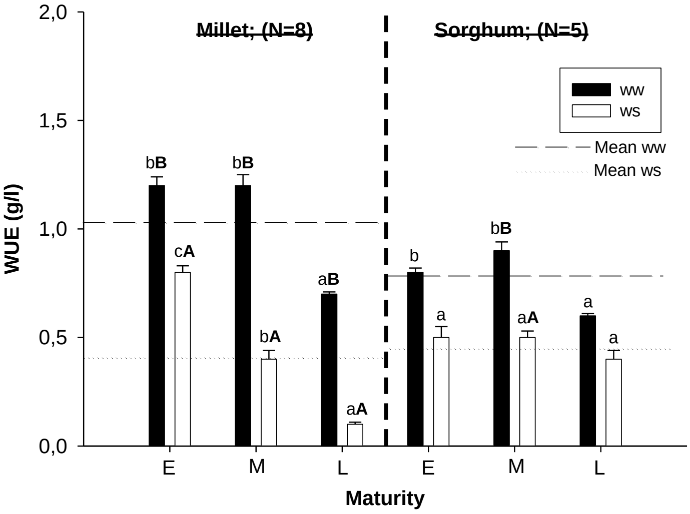

Fig 4. Effect of water stress on Water Use Efficiency of different maturity (E, early, M; middle, and L; late) genotypes of Millet and Sorghum grown under glasshouse conditions. Small letters (a, b, and c) indicates maturity differences (Tukey HSD test, P≤0.05), and capital letters (A and B) indicates difference (T-test; α=0.05) between treatments (ww; well watered, and ws; water-stress).

markedly reduced it, but just slightly changed the ranking among genotypes. Since correlation between WUE and grain yield was not detected (or very weak) in stressed millet, therefore breeding for a higher WUE that saves water and contributes to an improved crop performance under late season drought seems promising. Interestingly, WUE in both crops correlated with both of its components, ETE and HI under well-watered conditions, but did so just with HI under stress. Thus, it is worth to pay more attention to HI in breeding of improved WUE. Negative correlations between CID and WUE were weak to poor (non-existing) within millet and sorghum (Fig. 5). Similar inconsistent CID-WUE correlations were also found using both crops (Emendack, 2007) and also in several other crops such as wheat, peanut and sorghum under milder stress intensities (Farquhar and Richards, 1984; Wright et al., 1988; Henderson et al., 1998). These inconsistencies are theoretically common in C4 crops, where the CO_2 concentrating mechanism might mask the potentially high discriminative effects of Rubisco. Therefore, utility of CID as a feasible selection tool for greater water use efficiency is less clear in C4 crops. Though, significant negative CID-WUE correlations were found within each genotype in all cases (Table 2b), and stress expectedly exerted opposite effects on the two parameters. There were some obvious conflicting results at least in sorghum: (1) under ww conditions, genotype E had lower WUE and CID than M; (2) under ws, no significant genotypic differences in WUE were obtained though CID in E was significantly lower than in M and L genotypes. These findings cast doubts on the usefulness of CID as a selection tool for improve water use efficiency, at least in C4-crops like sorghum.

Materials and methods

Plant materials

Three genotypes representing different maturity groups (early; E, middle; M, and late; L) of *Panicum miliaceum* (E: Körnberger Mittelfruehe, Austria; M: Capatobckoe 10, Belarus; L: IPm2501; India, ICRSAT) and *Sorghum bicolor* L. (E: Sc.1790, USA, TAMU, M: ICSV273, India, ICRISAT; L: S35, Cameroon/Chad, ICRISAT) were germinated on moistened filter paper in a glasshouse. Genotypes were sown on different dates according to their maturity, so that flowering coincided in all genotypes **(**Fig 1**)**. Following germinations, seedlings of each genotype were transferred to a “coarse sand + plant nutrient” media homogenously filled in a 13.5 l volume PVC tube (height; 50 cm, diameter; 16 cm). Coarse sand constituted of 78% sand, 16.4% fine sand, and 4.2 % gravels (Anyia, 2002), and the nutrients were 70% inorganic (Hoffmann-Bahnsen, 1996) and 30% organic matters from BIO-GARTEN-AZET by NEUDORF.

Growth conditions

Study was carried out in the spring-summer months of 2005 in a Glasshouse at the department of Crop Science in the Tropics and Subtropics of the Humboldt university of Berlin; Germany. Variation of humidity was between 35-45% during the day and 60-70% during the night over the entire experimental period. Bulbs (POWERSTAR Son-T AGRO 400W DAYLIGHT by OSRAM, Germany) were used to provide additional lightening when necessary to have at least 12 hours of daylight. The temperature and growth cycles of the genotypes during the experiment is shown in Fig 1.

Experimental set up

Design was split-split plot, with treatments (well-watered; ww and water-stressed; ws) as main plots, crop types (sorghum and millet; both C4 crops) as subplot, and maturity groups (early; E, middle; M, and late; L) as sub-subplot. Each sub-subplot had eight replications or tubes. An irrometer electronically linked to an automatic irrigation system (Hoffmann-Bahnsen, 1996) was randomly inserted at 20 cm depth in a tube of every sub-subplot to monitor the soil water potential (SWP). Time Domain Reflectometry (TDR) probe was inserted at 15 cm depth in the remaining seven tubes to monitor soil water content (SWC). Tubes were suspended with collection pan placed beneath each to take care of any drained water. Evaporation was minimised by covering the surface of the soil in each tube with 2 cm layer of quartz. At

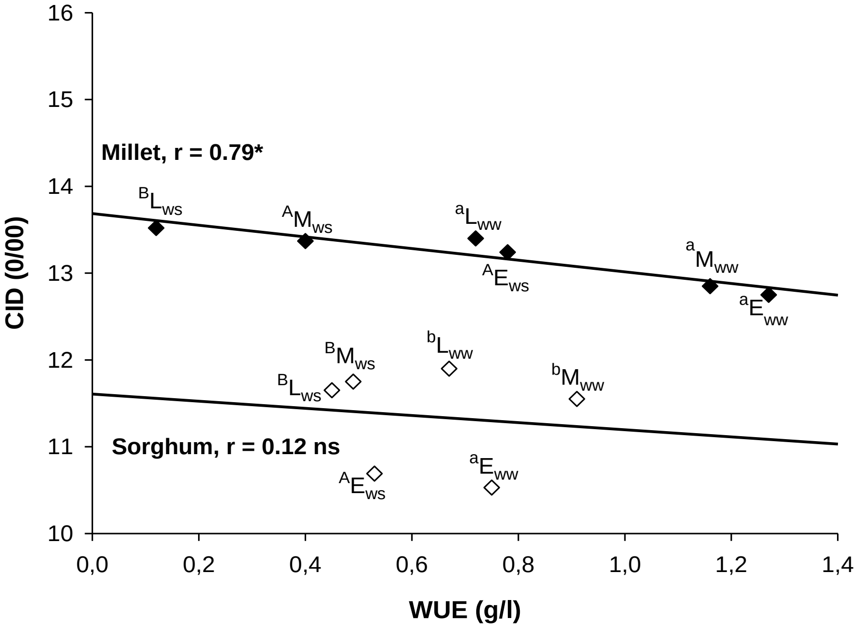

Fig 5. Effect of water stress on the relation between water use efficiency and carbon isotope discrimination of millet (◆) and sorghum (◇) genotypes (E, early, M; middle, and L; late). Small letters (superscripts; a and b) indicate CID-differences between well-watered plants (ww) and capital letters (superscripts; A and B) indicate differences between stressed plants (ws) (Tukey HSD test, P≤0.05, ns/* non/significant Pearson correlation, r).

50% flowering (June 7±2 days) in all the genotypes (see FD; flowering dates in Fig 1), stress was imposed on plants by withholding water supply until the soil water potential dropped to – 0.04MPa, and then maintaining it for 10 consecutive days. Stressed plants were then re-irrigated to control level (field capacity of –0.006 to –0.008MPa) until physiological maturity.

Yield and water relation parameters assessed

At physiological maturity, crops were harvested; panicles, main shoot, and tillers separated and oven dried at 70°C for 48 hours. Panicles were then thrashed and grain yield (gram per plant) recorded. Harvest index was determined as the ratio of grain yield to total above ground biomass.

Evapotranspiration efficiency (ETE) was calculated cumulatively at three sampling dates: before stress (bs), at the end of stress (se), and at full maturity (fm). It was determined as the amount of dry biomass produced per unit of water (Loomis and Connor, 1998) used from sowing to the defined sampling date. Water use efficiency (WUE) is defined as the product of three components (Ehdaie, 1995):

$$WUE\ (g/l) = U/U_o \times ETE \times HI$$

where, U is water uptake by plants, and U_o is water supplied to plants. ETE was defined as the ratio of the total aerial biomass to the water use. WUE determined as the ratio of the grain yield to total water use, up to maturity; and HI as the ratio of grain yield to total aerial biomass. In this study, since an automatic irrigation and drainage system based on desired soil water potential was used, the ratio of U/U_0 is unitary. Thus WUE was the product of ETE and HI. Carbon isotope discrimination (CID) was determined from oven-dried finely ground (mesh diameter 0.5 mm) seeds using an isotope mass spectrometer (Tracer mass 20-20, SerCon, Crewe, UK) operated in continuous flow mode.

Statistical analysis

The analysis of variance between mean values of the different maturity groups per crop type was compared using Tukey HSD test at P ≤ 0.05 and 0.01. Differences between treatments were analyzed using the student T-test at α = 0.05. Differences between crop types were compared based on relative reductions (stress versus control mean values) of assessed parameters. Statistical soft wares used were SPSS version 11.0, Sigma Plot 9.0, and Sigma Stat 3.1.

Conclusions

Yield reductions by water stress were stronger in millet than sorghum genotypes, especially in M and L groups. Similar trends were observed respect to reductions in HI and WUE by water stress. Thus, millet does not have the potential of being used as a substitute for grain sorghum especially when faces with a severe mid-season drought. Since association between grain yield and WUE among genotypes were not evident (weak in stressed millet), separate selection for improved WUE seems possible and HI may play an important role. Nevertheless, high ETE up to the early grain filling (here; stress end) may help to save water for the later yield formation.

Acknowledgements

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