

Growth and physiological response of two biomass sorghum (*Sorghum bicolor* (L.) Moench) genotypes bred for different environments, to contrasting levels of soil moisture

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Abstract

A better understanding of plant mechanisms in response to drought is a strong premise to achieving high yields while saving unnecessary water. This is especially true in the case of biomass crops for non-food uses (energy, fibre and forage), grown with limited water supply. In this frame, we investigated growth and physiological response of two genotypes of biomass sorghum (*Sorghum bicolor* (L.) Moench) to contrasting levels of soil moisture in a pot experiment carried out in a greenhouse. Two water regimes (high and low water, corresponding to 70% and 30% field capacity) were applied to JS-2002 and Trudan-8 sorghum genotypes, respectively bred for dry sub-tropical and mild temperate conditions. Two harvests were carried out at 73 and 105 days after seeding. Physiological traits (transpiration, photosynthesis and stomatal conductance) were assessed in four dates during growth. Leaf water potential, its components and relative water content were determined at the two harvests. Low watering curbed plant height and aboveground biomass to a similar extent (ca. 70%) in both genotypes. JS-2002 exhibited a higher proportion of belowground to aboveground

biomass, *i.e.*, a morphology better suited to withstand drought. Despite this, JS-2002 was more affected by low water in terms of physiology: during the growing season, the average ratio in transpiration, photosynthesis and stomatal conductance between droughty and well watered plants was, respectively, 0.82, 0.80 and 0.79 in JS-2002; 1.05, 1.08 and 1.03 in Trudan-8. Hence Trudan-8 evidenced a ca. 20% advantage in the three traits. In addition, Trudan-8 could better exploit abundant moisture (70% field capacity), increasing aboveground biomass and water use efficiency. In both genotypes, drought led to very low levels of leaf water potential and relative water content, still supporting photosynthesis. Hence, both morphological and physiological characteristics of sorghum were involved in plant adaptation to drought, in accordance with previous results. Conversely, the common assumption that genotypes best performing under wet conditions are less suited to face drought was contradicted by the results of the two genotypes in our experiment. This discloses a potential to be further exploited in programmes of biomass utilization for various end uses, although further evidence at greenhouse and field level is needed to corroborate this finding.

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Introduction

Sorghum (*Sorghum bicolor* (L.) Moench) is the fifth most important world crop grown for food, feed and industrial uses. It is the major crop for millions of people in the semi-arid tropics, and is extensively grown in Africa, China, USA, Mexico and India (Surwenshi *et al.*, 2010), where water availability is a major constraint to crop production.

Water shortage is one of the most important limiting factors in crop production at world level (Umar, 2006). Drought is a multidimensional stress affecting crop plants at various stages of their development (Blum, 1996), and is generally acknowledged as the foremost abiotic stress (Quarrie *et al.*, 1999). Even intermittent water deficit at critical stages of cereal crops may reduce yield (Ludlow and Muchow, 1990), and in high rainfall (>800 mm) areas, short periods of water stress are known to significantly affect yield. Drought imposes many adverse effects on plants, resulting in decreased growth and yield (Yadav *et al.*, 1999). Under water shortage, water has to be spared in order to be used at critical growth stages (Stewart *et al.*, 1975). In such condition, one of the main goals in breeding is the release of genotypes maintaining good yield under dry conditions (Richards *et al.*, 2002).

Effects of water deficit on plants have been extensively studied and include osmotic, biochemical and physiological effects. Water deficit affects nearly all growth processes; however, the stress response depends upon intensity, rate and duration of the stress phase, as well as plant stage development (Brar *et al.*, 1990; Sinaki *et al.*, 2007).

Soil moisture is crucial to growth and development of sorghum

plants. Under stress conditions, root water uptake may be insufficient to meet evapotranspiration potential. In sorghum, drought response has been related to two distinct stages: pre-flowering and post-flowering (Rosenow and Clark, 1981; Tuinstra *et al.*, 1997). Resistance to drought at both stages has been reported in all the existing germplasm. However, many genotypes with a high level of resistance at either stage are more susceptible at the other stage (Walulu, 1994).

The sorghum plant can avoid dehydration by enhanced water uptake through deeper and more extensive root system than maize, and can tolerate dehydration by osmotic regulation (Wright and Smith, 1983; Singh, 1989). Sorghum's ability to enhance tillering can offer yield compensation when the main culm is damaged by water stress, providing yield stability in dry environments (Mahalakshmi and Bidinger, 1986; Richards, 1987). In addition, sorghum can reduce transpirational loss of water through upright leaf habit (Begg, 1980).

Despite these mechanisms, limited water availability determines stress, affecting various metabolic processes. Experimental evidence shows that soil moisture deficit causes disturbance in the photosynthetic process, reflecting on growth and final crop yield. Among plant processes, leaf water potential, net photosynthesis and stomatal conductance were shown to be significantly affected by moisture stress in sorghum (Singh and Singh, 1992).

In sweet sorghum that is a sub-type of biomass sorghum, serious drought stress determined photo-inhibition and low water use efficiency (Tingting *et al.*, 2010). In unstressed conditions, photo-inhibition could be avoided but water use efficiency remained sub-optimal. Thus, moderate stress determined the highest water use efficiency in sweet sorghum (Tingting *et al.*, 2010).

Given the uncertainties still surrounding sorghum behaviour in response to drought, especially as it concerns biomass genotypes, the present study was planned to investigate growth and physiological response of two genotypes to contrasting levels of soil moisture. Based on the wide diffusion of biomass sorghum in mild temperate to dry sub-tropical areas of the world, one representative genotype from each of these two areas was selected for the study. Hence, the experiment was intended as something not yet echoed in the literature on biomass sorghum: a showcase comparing genotypes bred for different environmental conditions, as it concerns their performance under limiting *vs* non-limiting moisture. This was ultimately aimed at discovering whether differences of behaviour could provide the grounds for differential crop management in the areas where such genotypes are currently used.

Materials and methods

Experimental set up

During May to September 2011, the proposed study was conducted in a glasshouse at the Department of Agricultural Sciences, University of Bologna, Italy (44° 29' N, 11° 20' E; 32 m asl). Ambient conditions during the experiment were: minima and maxima temperatures, 17.8±2.4°C and 33.6±3.6°C, respectively; relative humidity, 58.1±6.7%.

Two genotypes of biomass sorghum bred in different ambient conditions, dry sub-tropical (JS-2002) *vs* mild temperate (Trudan-8), were used in the experiment. These were commercial hybrids whose seeds were supplied by their respective breeders, the Fodder Research Institute, Sargodha, Pakistan, and Syngenta Seeds, Casalmorano (CR), Italy. They are both thin-stemmed, highly tillering sorghum genotypes, considered among top biomass producers in their respective environments. The two genotypes were sown on May 31 in 36 pots filled with 7 kg of soil on oven dry basis. Eight seeds of either sorghum genotype

were sown in each pot. Seedling emergence was recorded on June 6; thereafter, 21 days after seeding (DAS), seedlings were thinned to two plants per pot. One plant per pot was harvested on August 12; the other on September 13; therefore, sorghum growth extended for a total of 105 DAS.

The soil was collected at the Research Farm, University of Bologna in Cadriano (Italy). Before filling the pots, the soil was air-dried and ground to pass a 2 nm sieve. Residual moisture was determined at 105°C until constant weight, and the following physical-chemical traits were assessed, according to standard procedures (Italian Regulation, 1999): particle size distribution (sand, silt and clay, 500, 330 and 170 mg g⁻¹, respectively); pH (8.1; soil to water ratio, 1:2.5); total and active limestone (71.2 and 17.5 mg g⁻¹, respectively); cation exchange capacity (17.2 cmol_c kg⁻¹); total organic carbon and total Kjeldahl nitrogen (6.82 and 0.76 mg g⁻¹, respectively); available phosphorus (Olsen) and exchangeable potassium (14 and 101 mg kg⁻¹, respectively). The volumetric water content of soil at field capacity and wilting point (Richards' apparatus) were 26.9% and 12.7%, respectively.

Experimental design and treatments

The two genotypes were cross combined with the two watering regimes and two harvest times in a completely randomized factorial design arranged in four replications. Thirteen days after sowing, high and low water regime (70 and 30% of the water holding capacity, respectively) were differentiated by adding the amount of water determined by the volumetric method. In the high water regime, water was added almost every day after the first weeks of the experiment. Soil moisture was monitored using the gravimetric method three times a week, in order to maintain the required amount of water. Extra pots were set up and harvested during the experiment, to account for the increase of pot weight due to plant growth. In addition, recommended doses of fertilizers were applied at appropriate time.

Plant morphology and growth

After thinning, sorghum growth was assessed on a tagged plant in each pot at fourteen-day intervals by means of allometric measurements: plant height was measured at the ligule of top leaf using a ruler.

The fresh weight of green and dead leaves, stems, panicles and their sum and the total fresh weight were recorded from a single plant pot⁻¹ in two destructive harvests (August 12 and September 13), aimed for the boot and soft dough stage of sorghum, respectively. Plant components were oven dried (105°C) until constant weight, and the respective dry weights were determined. Green leaf area (LA) was recorded by means of a LI 3001 leaf area meter (LI-COR, Lincoln, NE, USA). Water use efficiency (WUE; g L⁻¹) was assessed as the ratio between total dry weight and the supply of water (Passioura, 1977).

At the second harvest, root dry weight was also determined, by collecting, washing and oven drying (105°C) the root apparatus retrieved from each pot. Based on this data and total dry weight (TDW), the root to shoot (R:S) ratio was calculated.

Physiological traits and leaf water status

A CIRAS-2 (PP Systems, Amesbury, MA, USA) infrared gas analyser was used to determine leaf transpiration, photosynthesis and stomatal conductance. To assure uniform levels of photosynthetically active radiation (PAR) in the glasshouse during measurements, an internal PAR setting at 1800 μmol m⁻² s⁻¹ in the cuvette was used as non-limiting in the assessment of photosynthetic traits. Measurements were taken at mid length of the top, fully developed leaf, in the central hours of the day (10.00 to 16.00 h).

On the two harvest dates, leaf water potential (LWP) was measured on the 3rd fully developed leaf using a WP4-T dew point potentiometer

apparatus (Decagon Devices, Pullman, WA, USA) in two dates (August 11 and 31). After freezing and subsequent thawing, the measurement was repeated on the same samples to determine osmotic potential (OP). Thereafter, turgor potential (TP) was assessed as the difference between LWP and OP, considering equivalent to nil the matric potential (De Pascale *et al.*, 2003).

In the second harvest, relative water content (RWC; %) was determined in the same leaves used to measure leaf water potential. A small disc was cut from a fresh leaf, placed in a 15 mL vial and the fresh weight (FW) was measured. Then the same leaf was put in distilled water in the dark and after 4 h, the turgid leaf weight (TW) was measured. After leaf drying at 80°C for 24 h, the final dry weight (DW) was assessed. The relative water content was calculated according to Smart and Bingham (1974):

$$RWC = \frac{(FW - DW)}{(TW - DW)} \times 100 \quad (1)$$

In the second harvest, osmotic adjustment (OA) in the high water regime was also determined as:

$$OA = (RWC_H \times OA_H) - (RWC_L \times OA_L) \quad (2)$$

where RWC_H , RWC_L , OA_H and OA_L indicate RWC and OA at high (H) and low (L) water regime, respectively.

Statistical analysis

Normal distribution and equal variance of data were controlled through the Kolmogorov-Smirnov and Bartlett test, respectively. The dataset was then submitted to the analysis of variance (ANOVA) through the CoStat 6.3 software (CoHort Software, Monterey, CA, USA): the significance of the investigated sources (cultivars, moisture levels and their interaction) was investigated at each specific date, and indicated through the symbols ns, * and **, representing non significant and significant differences at $P \leq 0.05$ and $P \leq 0.01$, respectively.

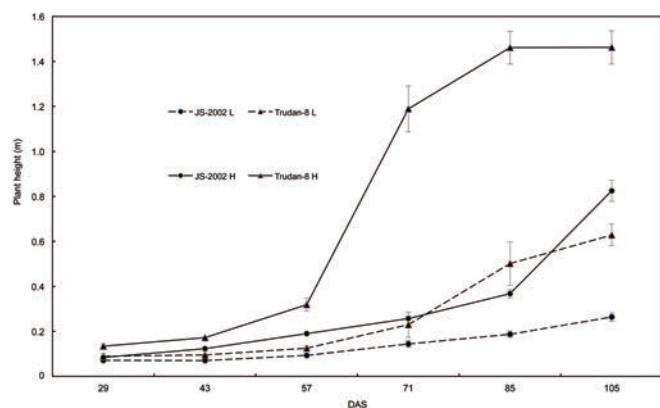


Figure 1. Plant height in six dates with two sorghum genotypes subjected to low (L) and high (H) water supply. Vertical bars, \pm standard error ($n=4$). DAS, days after seeding.

Results

Plant morphology and growth

During the 105-day experiment, plant height was remarkably influenced by genotype (G) and water regime (Figure 1): at the end of growth, Trudan-8 rose to almost 1.5 m with high water supply; to only 0.6 m with low water supply. JS-2002 showed a similar relationship between well watered and stressed plants, attaining ca. 0.8 and 0.3 m with the two respective regimes.

Total dry weight outlined a similar behaviour (Figure 2A): in the first harvest (DAS 73), both genotypes exhibited large TDW gains with H vs

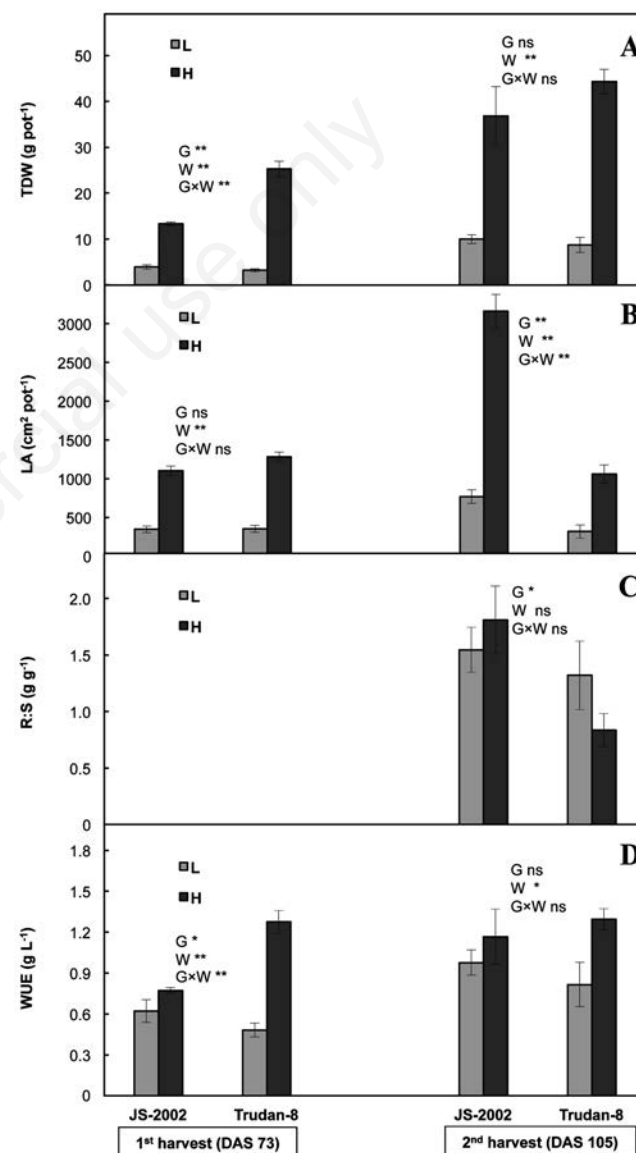


Figure 2. A) Total dry weight (TDW), B) leaf area (LA), C) root to shoot ratio (R:S) and D) water use efficiency (WUE) in two harvests with two sorghum genotypes subjected to low (L) and high (H) water supply. Vertical bars, \pm standard error ($n=4$). In each harvest, ns, * and ** mean not significant and significant at $P \leq 0.05$ and 0.01 , respectively. DAS, days after seeding; G, genotype; W, water supply.

L water. However, Trudan-8 cumulated more TDW than JS-2002 at high water supply, not at low water supply. The same pattern was shown in the second harvest (DAS 105), although the gap between Trudan-8 H and JS-2002 H was slightly reduced with respect to the first harvest. Green leaf area was consistent with TDW at DAS 73, whereas at DAS 105 Trudan-8 was already senescing and its LA was declining in both water levels, compared to JS-2002 (Figure 2B). This is supported by the fact that Trudan-8 showed panicles representing an average 37% of TDW at DAS 105 (data not shown), whereas JS-2002, having been bred for a warmer environment, at that time was not yet in the reproductive stage. Root dry weight at the end of the experiment (DAS 105) featured higher values, on average, than TDW (31 vs 25 g pot⁻¹ in the two respective traits; data not shown). However, in Trudan-8 high water supply determined a stronger increase in above- than belowground biomass, and the R:S ratio declined to less than 1. Conversely, in JS-2002 the two-biomass portions increased to a similar extent under high water supply, and the R:S ratio remained above 1.5 (Figure 2C).

Water use efficiency improved under well watered vs drought conditions (Figure 2D). At low water supply, JS-2002 appeared slightly more efficient than Trudan-8 in both harvests, while at high water supply Trudan-8 passed JS-2002, especially in the first harvest. As a result, JS-2002 maintained a similar ratio in the WUE of stressed to unstressed plants (average, 0.84), whereas Trudan-8 showed stronger WUE reductions under drought conditions, especially in the first harvest (WUE ratio, 0.39 and 0.63 at DAS 73 and 105, respectively).

Physiological traits

Leaf transpiration (EVP) increased, then decreased during plant growth (Figure 3A). At the time of peak leaf transpiration (EVP) levels (DAS 78), the difference between high and low water supply was enhanced in both genotypes. In this date, Trudan-8 showed a significantly higher EVP than JS-2002 under drought conditions. In this date, the G×W interaction was almost significant ($P \leq 0.10$), suggesting that the higher performance of Trudan-8 vs JS-2002 was mainly associated with the low water supply. Also photosynthesis (PN) depicted an increasing, then decreasing trend during plant growth. Peak PN levels were registered at both DAS 65 and DAS 78 (Figure 3B). However, the difference between high and low water supply was enhanced at DAS 78, when also the difference between Trudan-8 and JS-2002 became remarkable, especially under drought conditions.

At last, stomatal conductance (GS) depicted the same trend as the previous two traits, attaining top levels in the two intermediate dates (DAS 65 and 78) (Figure 3C). At DAS 78, GS displayed a large difference between the two water regimes as well as the two genotypes. As a result, Trudan-8 under low water supply achieved slightly higher GS values than JS-2002 under high water supply.

Leaf water status

At the first harvest (DAS 73), modest differences were observed in leaf water potential between genotypes and water regimes (Figure 4A). LWP averaged -1.08 MPa, as the result of its contrasting components: OP showing an average -2.77 MPa (Figure 4B); TP, 1.69 MPa (Figure 4C). Compared to this, in the second harvest (DAS 105) LWP was remarkably influenced by water supply (Figure 4A): a difference of more than 1 MPa was shown between well watered and droughty plants, these latter falling to LWP values as low as -2.97 MPa (average of the two genotypes). In both water regimes, LWP data were mainly driven by the OP component (Figure 4B), while TP was weaker than in the first harvest, especially in the high water regime (Figure 4C). In the second harvest, OA played a significant role in well watered plants, showing an average 0.66 MPa with no significant difference between genotypes (Table 1).

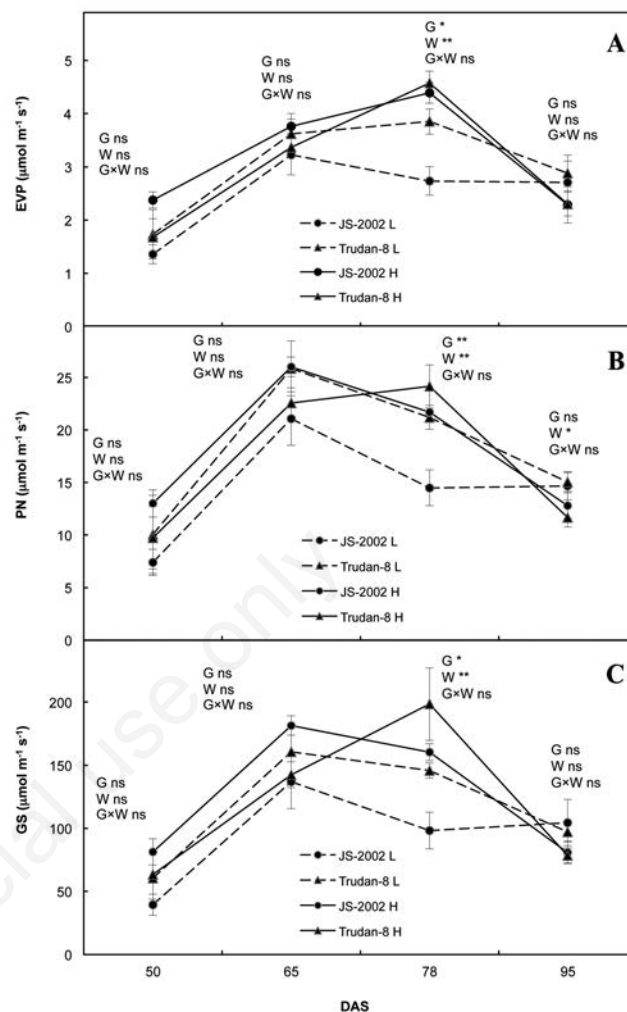


Figure 3. A) Leaf transpiration (EVP), B) photosynthesis (PN) and C) stomatal conductance (GS) in four dates with two sorghum genotypes subjected to low (L) and high (H) water supply. Vertical bars, \pm standard error ($n=4$). In each date, ns, * and ** mean not significant and significant at $P \leq 0.05$ and 0.01 , respectively. DAS, days after seeding; G, genotype; W, water supply.

Table 1. Relative water content and osmotic adjustment at the second harvest (105 days after seeding) in two sorghum genotypes subjected to low and high water supply.

Genotype (G)	Water supply (W)	RWC (%)	OA (MPa)
JS-2002	Low	77.0	-
Trudan-8	Low	72.4	-
JS-2002	High	89.1	0.68
Trudan-8	High	86.4	0.65
ANOVA sources			
G	ns	ns	
W	**	-	
G×W	ns	-	

RWC, relative water content; OA, osmotic adjustment; ANOVA, analysis of variance. ns, * and ** mean not significant and significant at $P \leq 0.05$ and 0.01 , respectively.

Relative water content in the second harvest was consistent with LWP data at the same time (Table 1): quite lower RWC data were recorded in plants at low *vs* high water supply, indicating a loss of turgor as clear consequence of drought. Conversely, no substantial difference was found between the two genotypes. Therefore it appears that the prolonged drought (DAS 105) exerted a strong effect on leaf water status, decreasing the moisture and increasing the strength (*i.e.*, decreasing the potential) at which water was held by the leaf.

Discussion

Plant morphology and growth

Plant height epitomizes growth and structural changes of biomass sorghum under drought conditions. In our experiment, the ratio in plant height between droughty and well-watered plants decreased during growth as the effect of cumulated stress (Figure 1). However, plant height at mid growth (DAS 57) was significantly correlated with TDW at DAS 105 ($r=0.79^{**}$), as in previous works of ours' (Sher *et al.*, 2011, 2013), and in other literary sources (Saeed and El-Nadi, 1998). It appears, therefore, that plant height at mid growth could be used to assist sorghum yield predictions under large-scale farming.

The root to shoot ratio (Figure 2C) featured high values compared to similar works in the literature (Younis *et al.*, 2000; Zegada-Lizarazu *et al.*, 2012; Sher *et al.*, 2013). In the cited sources, the R:S ratio was seen to increase with the decrease in soil moisture, which is consistent with the enhanced role of the root apparatus under moisture deficit. In our experiment, this behaviour was shown by Trudan-8: an 80% TDW decrease under drought was accompanied by a weaker reduction in RDW (data not shown), and the R:S ratio increased. Conversely, in JS-2002 the decrease of RDW under drought was similar to that of TDW, leading to no significant variation in the R:S ratio. Hence, it could be argued that JS-2002 owns a better attitude to withstand drought thanks to a higher R:S ratio, but a lower ability to exploit abundant moisture by partitioning more assimilates to the above ground organs.

Water use efficiency (Figure 2D) is a focal trait in studies on plant behaviour under water deficit. In sorghum, a species at C₄ photosynthetic pathway, WUE has a potential of 7-8 g TDW L⁻¹ in field plots (Saeed and El-Nadi, 1998; Aishah *et al.*, 2011), although in the special conditions of pots (Sher *et al.*, 2013) and sometimes also in plots (Singh and Singh, 1995; Farré and Faci, 2006), lower WUE's are often recorded. In our experiment, drought determined a reduction in WUE that is echoed in several works (Saeed and El-Nadi, 1998; Farré and Faci, 2006; Ahmed *et al.*, 2007; Sher *et al.*, 2013), whereas in other sources drought involved an increase in WUE (Singh and Singh, 1995; Abdel-Motagally, 2010; Aishah *et al.*, 2011). This diverging behaviour has already been discussed (Sher *et al.*, 2013), and credited to the fact that, as long as the restriction of moisture is moderate, sorghum can make a more efficient use of water and enhance WUE. Once the restriction gets severe, yield falls and WUE declines. In our experiment, the latter condition apparently occurred, especially in Trudan-8 (Figure 2D): this genotype made a more efficient use of water at high moisture, in exchange for a steeper drop of WUE at low moisture.

Physiological traits

Leaf transpiration, photosynthesis and stomatal conductance displayed a similar behaviour (Figure 3), and were highly correlated during sorghum growth season (r among them ranging between 0.92^{**} and 0.97^{**}). Differences between genotypes and water regimes became more relevant in the second part of the season, which is consistent with the effect of cumulated drought. In the literature, sorghum

has always been shown better suited to face drought than maize, also in terms of physiological traits (Singh and Singh, 1995; Allen *et al.*, 2011; Zegada-Lizarazu *et al.*, 2012; Takele and Farrant, 2013). In sorghum, drought affects photosynthesis to an extent depending on plant stage, intensity and duration of the dry period, and ambient conditions. Therefore, constraints to the assimilation process either show up only after some time (Tsuji *et al.*, 2003; Tingting *et al.*, 2010; Zegada-Lizarazu *et al.*, 2012), as in our experiment, or are reversed in case of transient drought periods (Takele and Farrant, 2013).

However, in our experiment differences between the two genotypes were noticeable: during the growing season, the average ratios in EVP, PN and GS between droughty and well watered plants were 0.82, 0.80 and 0.79 in JS-2002; 1.05, 1.08 and 1.03 in Trudan-8. Therefore, it results a ca. 20% gap in the three physiological traits, to the advantage of Trudan-8. The mild constraint generally suffered by this genotype is amenable to the loss of leaf area at the end of the season: when Trudan-8 entered the reproductive stage, plants in the low water regime underwent a faster senescence (Figure 2B), involving a faster loss of basal leaves. This could have helped the upper fully developed leaf to sustain

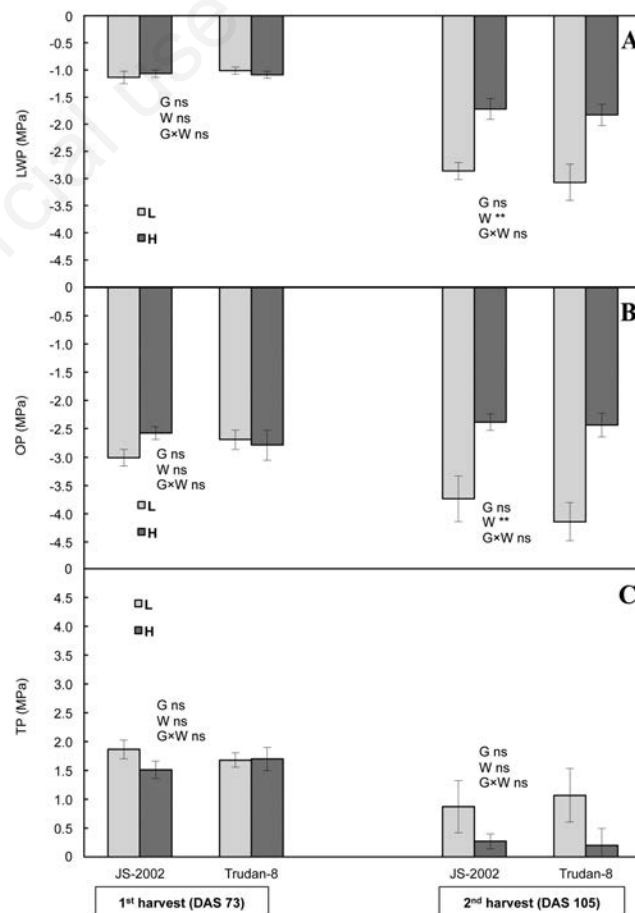


Figure 4. A) Leaf water potential (LWP), B) osmotic potential (OP) and C) turgor potential (TP) in two harvests with two sorghum genotypes subjected to low (L) and high (H) water supply. Vertical bars, \pm standard error ($n=4$). In each harvest, ns, * and ** mean not significant and significant at $P \leq 0.05$ and 0.01, respectively. DAS, days after seeding; G, genotype; W, water supply.

photosynthesis at a similar level as in well watered plants (Figure 3). Nevertheless, differences in photosynthetic traits among genotypes of grain sorghum (Tsuji *et al.*, 2003; Surwenshi *et al.*, 2010) as well as biomass sorghum (Massacci *et al.*, 1996) are reported in the literature, indicating that a sizeable variation may be exploited to improve this species' performance under drought conditions.

At peak time in our experiment (DAS 78), transpiration, photosynthesis and stomatal conductance were curbed by 23%, 19% and 30%, respectively (average of the two genotypes) (Figure 3), with 30% *vs* 70% field capacity. In comparable cases, PN was reduced by 24% in grain sorghum with a 30% *vs* 60% restoration of evapotranspiration (Singh and Singh, 1995); EVP, PN and GS were curbed by a respective 43%, 54% and 34% in grain sorghum during the vegetative stage, after a long withholding of irrigation (29 days) (Tsuji *et al.*, 2003); EVP and PN decreased by ca. 33% and 40%, respectively, with 30% *vs* 70% field capacity in biomass sorghum at jointing (Tingting *et al.*, 2010). Stronger restrictions (>50%) of the three parameters were observed when sorghum was exposed to drought stress in sand pots (Cechin, 1998). However, weaker reductions in the three parameters were also observed than in our experiment (Allen *et al.*, 2011; Zegada-Lizarazu *et al.*, 2012), suggesting a variation in the results depending on a vast array of physiological, ontological and experimental conditions.

Leaf water status

Leaf water potential and relative water content best express plant response to water deficit (Brown, 1995). Leaf water potential and osmotic potential, its major component in our experiment, were only affected in the second harvest (DAS 105), whereas in the first harvest (DAS 73) LWP data were quite high and undifferentiated (Figure 4). This indicates a modest effect exerted by drought on leaf potential at DAS 73, despite the differences in physiological traits recorded some time later (DAS 78) (Figure 3).

LWP data at DAS 105 depict a condition of high water tension in leaf tissues, associated with a strong dehydration of this organ (Table 1). In fact, LWP, OP and RWC values as low as -3.0 MPa, -3.9 MPa and 75%, respectively (average of the two genotypes under stress at DAS 105), have hardly been observed in the scientific literature on this species. In grain sorghum, LWP and OP values as low as -2.8 and -3 MPa were observed at peak time with a stronger restriction of water supply (15% restoration of evapotranspiration) than in our experiment (Singh and Singh, 1995). In biomass sorghum subjected to the same moisture restriction as in our experiment (30% *vs* 70% field capacity), a similar decline of RWC (from 92% to 78%) was associated with a modest loss of LWP (from -0.85 to -1.42 MPa) (Tingting *et al.*, 2010). The rest of sources consulted also for the photosynthetic traits showed quite lower reductions in leaf water status, with the only exception of Takele and Farrant (2013), who found RWC values below 50% in grain sorghum pots after 20 days without irrigation.

Lastly, a significant correlation was observed between RWC and OP at DAS 105 in our experiment ($r=0.84^{**}$), and, to a lesser extent, between RWC, on one side, and LWP and TP, on the other side ($r=0.55^*$ with LWP and 0.59^* with TP). Hence, the osmotic component is evidenced as that most strongly associated with sorghum ability to maintain LWP at levels still supporting physiological processes.

Conclusions

Two genotypes of biomass sorghum bred in dry sub-tropical (JS-2002) and mild temperate (Trudan-8) conditions staged a similar response to drought, as it concerns plant morphology and growth. JS-

2002 outlined a higher suitability to withstand drought in morphological terms, thanks to a higher proportion of belowground to aboveground biomass. In exchange for this, Trudan-8 showed a lower constraint exerted by low water on photosynthesis, and a better ability to exploit abundant moisture, resulting in higher WUE and aboveground biomass. In both genotypes, prolonged drought led to very low levels of leaf water potential and relative water content, still supporting photosynthesis.

Biomass sorghum was once more proven a valuable crop under limited water supply. The mechanisms of plant adaptation to the drought stress vary according to genotype morphological and physiological characteristics. The common assumption that genotypes best performing under wet conditions are less suited to face drought was contradicted by the results of the two genotypes in our experiment. However, further evidence at greenhouse and field level on a wider number of genotypes is needed to corroborate this finding.

Thereby, it may be concluded that the genotype bred for mild temperate conditions (Trudan-8) actually benefited from adequate water supply that is likely to occur in those areas, whereas the genotype bred for dry sub-tropical conditions (JS-2002) proved able to withstand drought that consistently occurs in those regions. However, Trudan-8 demonstrated to be a suitable genotype also in case of drought, whereas JS-2002 should better be replaced by a more performing genotype, under wet conditions.

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