Growth and gas exchange of three sorghum cultivars under drought stress

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Abstract

A field study was conducted to evaluate the drought tolerance of three sorghum [*Sorghum bicolor* (L.) Moench] cultivars, Gadambalia, Arous elRimal and Tabat, and quantify the physiological bases for differences in their drought tolerance. Water stress reduced shoot dry mass of Gadambalia, Arous elRimal and Tabat by 43, 46 and 58 %, respectively. The respective reduction in leaf area of the three cultivars was 28, 54 and 63 %. The reduction in net photosynthetic rate, stomatal conductance and transpiration rate due to water stress was lowest in Gadambalia and highest in Tabat. The leaf water potentials and relative water contents of Gadambalia under wet and dry treatments were similar, while those of Tabat were significantly reduced by water stress. The lowest and highest liquid water flow conductance was displayed by Tabat and Gadambalia, respectively. Drought tolerance in Gadambalia is associated with its smaller leaf area, higher liquid water flow conductance, and ability to maintain high leaf water potential, relative water content, stomatal conductance, transpiration rate and photosynthetic rate under drought stress.

Additional key words: liquid water flow conductance, drought tolerance, leaf water potential, photosynthesis, relative water content, *Sorghum bicolor*, stomatal conductance, transpiration.

Introduction

Sorghum is characterized by its ability to tolerate and survive under conditions of continuous or intermittent drought (Hulse *et al.* 1980). Drought resistance in sorghum has been attributed to a dense and prolific root system (Bloodworth *et al.* 1958, Mayaki *et al.* 1976, Jordan and Miller 1980), an ability to maintain stomatal opening at low leaf water potential (Glover 1959, Sánchez-Diaz and Kramer 1971, Beadle *et al.* 1973, Turner 1974) possibly through osmotic adjustment (Jones and Turner 1978, Fereres *et al.* 1978, Wright *et al.* 1983, Ludlow *et al.* 1990), and an ability to delay reproductive development (Hsiao *et al.* 1976).

Drought stress decreases photosynthesis, stomatal conductance and transpiration in sorghum (Premachandra *et al.* 1994, Massacci *et al.* 1996). Net photosynthetic rate and stomatal conductance of sorghum declined with decrease in leaf water potential (Ackerson *et al.* 1980, Garrity *et al.* 1984, Massacci *et al.* 1996). A positive correlation has been found between leaf photosynthesis, total biomass and grain production of sorghum under both well-watered and water-limited conditions (Peng *et al.* 1991). A drought-tolerant grain sorghum line has been found to maintain significantly higher leaf relative water content, osmotic potential and pressure potential than a drought-susceptible line (Premachandra *et al.* 1995).

In a previous study, Salih *et al.* (1999) reported that drought tolerance in sorghum cv. Gadambalia is associated with higher water extraction efficiency, fewer nodal roots per plant, fewer late metaxylem vessels per nodal root, a smaller leaf area, and a well developed sclerenchyma. The present study was undertaken to evaluate the drought tolerance of three sorghum cultivars and quantify the physiological bases for differences in their drought tolerance.

Received 22 March 2002, *accepted* 22 August 2002.

Abbreviations: E - transpiration rate; g_s - stomatal conductance; LA - leaf area; L_p - liquid water flow conductance; P_N - net photosynthetic rate; RS - reproductive stage; RWC - relative water content; SDM - shoot dry mass; VS - vegetative stage.

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Materials and methods

Experimental site, treatments and experimental design: A field experiment was conducted in a sandy soil at the Arid Land Research Center, Tottori University, Tottori, Japan during August - December 2001. The experimental area (210 m^2) was covered with transparent plastic that was permeable to more than 95 % of incident solar radiation. Treatments consisted of three sorghum [*Sorghum bicolor* (L.) Moench] cultivars and two irrigation treatments (wet and dry). The six treatments were arranged in a split-plot design with three replications. The three sorghum cultivars, Gadambalia, Arous elRimal and Tabat, used in this study were brought from Sudan. Gadamblia is a local drought-resistant cultivar, while Arous elRimal and Tabat are improved cultivars released for the rainfed and irrigated areas, respectively. A compound fertilizer at a rate of 7.8 g(N) m^{-2}, 7.8 g(P_2O_5) m^{-2} and 9.6 g(K_2O) m^{-2} was incorporated into the soil prior to planting. Five seeds per hole were sown on 16 August in rows 0.7 m apart at intra-row spacing of 0.15 m. At the four-leaf stage, the seedlings were thinned to one seedling per hill. Irrigation water was applied through perforated plastic pipes laid uniformly in the plots. All treatments continued to receive water at a rate of 0.01 m^3 m^{-2} every two days up to 32 d after planting. After that, the wet treatment continued to receive the same amount of water every two days, while the dry treatment was not watered up to 118 d after sowing.

At vegetative and reproductive stage, soil samples were taken using an auger between rows in each sub-plot at 0.1 m interval to a depth of 1 m and 1.5 m, respectively. After fresh mass of the soil samples was determined, the samples were dried in an oven at 105 °C for 24 h and weighed. Soil water potential was calculated according to the method used by Inoue and Nomura (1983).

Shoot measurements: Net photosynthetic rate (P_N), stomatal conductance (g_s) and transpiration rate (E) were measured on the upper-most fully expanded leaves at late vegetative [61 d after sowing (DAS)] and reproductive stage (90 DAS) using a portable photosynthesis system (*LI-6400, LI-COR Inc.*, Lincoln, Nebraska, USA). These measurements were accomplished on clear sunny days between 10:00 and 15:00. Leaf water potential (Ψ_l) was measured with a pressure chamber (*Model 1000, PMS Instrument Co.*, Corvallis, Oregon, USA) on the same leaves used for measuring P_N, g_s and E. Leaf relative water content (RWC) was determined at the reproductive stage (97 DAS) according to the method used by Wright *et al.* (1983).

Liquid water flow conductance (L_p) was calculated according to the equation $L_p = E / (\Psi_s - \Psi_l)$ which was converted from the equation $R = (\Psi_s - \Psi_l) / E$ (Hirasawa and Ishihara 1991), where R is resistance to water flow, Ψ_s is the average of soil water potential values higher than the permanent wilting point, Ψ_l is leaf water potential and E is transpiration rate.

At the end of the experiment (118 DAS), five random plants in each sub-plot were cut at ground level for leaf area and shoot dry mass determination. Leaf area was measured with an optical area meter (*LI-3050A, LI-COR Inc.*). After leaf area was measured, the plants were dried in an oven at 80 °C for 72 h for shoot dry mass determination. Leaf area and shoot dry mass data were reported on per plant basis.

Statistical analysis: All data were subjected to analysis of variance using the *MSTAT-C Statistical Package* developed by Michigan State University. The least significant difference (LSD) test was used for comparing treatments' means.

Results

Shoot dry mass (SDM) of the three sorghum cultivars was significantly ($P < 0.05$) reduced by drought stress (Table 1). The reduction in SDM of Gadambalia, Arous elRimal and Tabat was 43, 46 and 58 %, respectively. Drought stress also significantly reduced leaf area (LA) of the three sorghum cultivars (Table 1). Although Gadambalia and Arous elRimal had significantly smaller LA than Tabat under both wet and dry treatments, the reduction in LA of Gadambalia, Arous elRimal and Tabat due to water stress was 28, 54 and 63 %, respectively.

At late vegetative stage (61 DAS), there were no significant differences in net photosynthetic rate (P_N) among the three cultivars under wet treatment (Table 2). However, under dry treatment, Gadambalia had significantly higher P_N than the other two cultivars. Drought stress decreased P_N of Gadambalia, Arous elRimal and Tabat by 34, 65, and 80 %, respectively. At reproductive stage (90 DAS), the decrease in P_N for Gadambalia, Arous elRimal and Tabat was 31, 44 and 78 %, respectively (Table 2).

At late vegetative stage (61 DAS), the decrease in stomatal conductance (g_s) of Gadambalia, Arous elRimal and Tabat as a result of drought stress was 54, 86 and 88 %, respectively. At reproductive stage (90 DAS), drought stress decreased g_s of Gadambalia, Arous elRimal and Tabat by 52, 54 and 72 %, respectively.

At late vegetative stage (61 DAS), the decrease in transpiration rate (E) of Gadambalia, Arous elRimal and Tabat was 43, 62 and 78 %, respectively. At reproductive stage (90 DAS), on the other hand, the three cultivars had

Table 1. Shoot dry mass, SDM [g plant^{-1}] and leaf area, LA [cm^2 plant^{-1}] of three sorghum cultivars grown under wet and dry soil conditions. SDM and LA was determined 118 d after sowing. Means ± SE, n = 3. Values within a column followed by the same letter are not significantly different according to LSD test at the 5 % probability level.

Cultivar	Soil	SDM	LA
Gadambalia	Wet	48.7 ± 2.3^b	526.5 ± 58.1^c
	Dry	27.5 ± 0.2^d	380.0 ± 35.9^d
Arous elRimal	Wet	38.1 ± 0.6^c	776.0 ± 2.4^b
	Dry	20.5 ± 0.4^e	357.8 ± 28.0^d
Tabat	Wet	54.3 ± 1.8^a	1695.0 ± 8.7^a
	Dry	22.9 ± 0.0^{de}	628.7 ± 13.3^c
$LSD_{0.05}$		5.3	110.8

comparable E under wet treatment, whereas under dry treatment, Gadambalia and Arous elRimal had significantly higher E than Tabat. Drought stress decreased E of Gadambalia, Arous elRimal and Tabat by 44, 47 and 82 %, respectively.

At late vegetative stage (61 DAS), Gadambalia had similar leaf water potential (Ψ_l) under both wet and dry treatments (Table 3). However, Arous elRimal and Tabat had significantly lower Ψ_l under dry than under wet treatment. At reproductive stage (90 DAS), similar Ψ_l under wet and dry treatments were recorded for both Gadambalia and Arous elRimal (Table 3). On the other hand, Tabat had significantly lower Ψ_l under dry than under wet treatment.

Under wet treatment, the leaf relative water content (RWC) of Tabat was significantly higher than that of Gadambalia and comparable to that of Arous elRimal (Table 3). Gadambalia had similar RWC under wet and dry treatments, while RWC of Arous elRimal and Tabat were significantly decreased by water stress. The decrease in RWC for Gadambalia, Arous elRimal and Tabat was 5, 14 and 24 %, respectively.

At vegetative stage, liquid water flow conductance (L_p) in the three cultivars was similar under wet treatment, while under dry treatment it was significantly higher in Gadambalia than in both Arous elRimal and Tabat (Table 3). Moreover, under dry treatment L_p in Arous elRimal and Tabat was similar. At reproductive stage, the relative decrease in L_p for Gadambalia, Arous elRimal and Tabat due to water stress was 71, 53, and 28 %, respectively.

Table 2. Photosynthetic rate, P_N [μmol m^{-2} s^{-1}], stomatal conductance, g_s [mol m^{-2} s^{-1}] and transpiration rate, E [mmol m^{-2} s^{-1}] at late vegetative (VS) and reproductive (RS) stages of three sorghum cultivars grown under wet and dry soil conditions. Means ± SE, n = 3. Values within a column followed by the same letter are not significantly different according to LSD test at the 5 % probability level.

Cultivar	Soil	P_N at VS	P_N at RS	g_s at VS	g_s at RS	E at VS	E at RS
Gadambalia	Wet	24.89 ± 2.64^a	12.45 ± 0.69	0.191 ± 0.013	0.085 ± 0.001	3.174 ± 0.289	2.089 ± 0.007^a
	Dry	16.35 ± 1.36^b	8.64 ± 1.99	0.088 ± 0.003	0.041 ± 0.009	1.801 ± 0.130	1.110 ± 0.190^b
Arous elRimal	Wet	22.55 ± 2.08^a	11.74 ± 0.90	0.139 ± 0.005	0.083 ± 0.005	2.360 ± 0.361	1.926 ± 0.088^a
	Dry	7.83 ± 2.47^c	6.58 ± 0.43	0.020 ± 0.002	0.038 ± 0.004	0.888 ± 0.337	1.071 ± 0.087^b
Tabat	Wet	24.33 ± 0.77^a	16.45 ± 0.37	0.131 ± 0.004	0.087 ± 0.004	2.541 ± 0.225	2.119 ± 0.208^a
	Dry	4.80 ± 1.99^c	3.67 ± 1.32	0.016 ± 0.001	0.024 ± 0.004	0.565 ± 0.114	0.373 ± 0.104^c

Table 3. Leaf water potential, Ψ_l [MPa] and liquid water flow conductance, Lp [10^4 cm MPa^{-1} s^{-1}] at late vegetative (VS) and reproductive (RS) stages, and leaf relative water content (RWC) at RS of three sorghum cultivars grown under wet and dry soil conditions. Means ± SE, n = 3. Values within a column followed by the same letter are not significantly different according to LSD test at the 5 % probability level.

Cultivar	Soil	Ψ_l at VS	Ψ_l at RS	RWC at RS	Lp at VS	Lp at RS
Gadambalia	Wet	-2.12 ± 0.09^b	-1.84 ± 0.07^{abc}	0.80 ± 0.01^{bc}	1.52 ± 0.19^a	1.19 ± 0.02
	Dry	-2.00 ± 0.08^b	-1.63 ± 0.22^{ab}	0.76 ± 0.04^{cd}	0.95 ± 0.07^b	0.84 ± 0.14
Arous elRimal	Wet	-1.54 ± 0.05^a	-1.59 ± 0.04^{ab}	0.84 ± 0.01^{ab}	1.56 ± 0.27^a	1.24 ± 0.08
	Dry	-1.96 ± 0.11^b	-1.90 ± 0.09^{bc}	0.72 ± 0.01^{de}	0.42 ± 0.11^c	0.66 ± 0.10
Tabat	Wet	-1.35 ± 0.08^a	-1.43 ± 0.04^a	0.90 ± 0.01^a	1.90 ± 0.17^a	1.49 ± 0.08
	Dry	-2.25 ± 0.05^b	-2.12 ± 0.14^c	0.68 ± 0.04^e	0.26 ± 0.05^c	0.42 ± 0.12

Discussion

SDM of each of the three sorghum cultivars was significantly reduced by water stress (Table 1), however, the reduction was most pronounced for Tabat than for Gadambalia and Arous elRimal. Differences in LA are consistent with those of SDM (Table 1). A similar response in LA for Tabat and Gadambalia has been reported (Salih *et al.* 1999). The differences in water stress level and soil type may account for the higher reduction in LA obtained in the present study than in that reported by Salih *et al.* (1999).

At vegetative and reproductive stages, P_N of the three cultivars was significantly decreased by water stress (Table 2). These results are consistent with those for SDM. A positive correlation between leaf photosynthesis and total biomass under both well- watered and water-limited conditions has been reported (Peng *et al.* 1991). The results of P_N are consistent with those of g_s and E (Table 2). Similar results were reported previously (Premachandra *et al.* 1994, Massacci *et al.* 1996).

At both vegetative and reproductive stages, Ψ_l of Gadambalia under wet and dry treatments were similar, while that of Tabat was significantly decreased by water stress (Table 3). At vegetative stage, Ψ_l of Arous elRimal was significantly decreased by water stress, whereas at reproductive stage, it maintained comparable Ψ_l under wet and dry treatments. The leaf RWC of Gadambalia under wet and dry treatments were also similar, while those of Arous elRimal and Tabat were significantly decreased by water stress (Table 3). Similar differences in Ψ_l and RWC between a drought-tolerant and a drought-susceptible sorghum line have been reported (Premachandra *et al.* 1995). The high photosynthetic capacity of Gadambalia under dry treatment is probably associated with its ability to maintain higher g_s due to its higher Ψ_l and RWC (Ackerson *et al.* 1980, Garrity *et al.* 1984, Massacci *et al.* 1996).

At vegetative stage, the three cultivars had comparable L_p under wet treatment, whereas under dry treatment Gadambalia had significantly higher L_p than both Arous elRimal and Tabat (Table 3). Arous elRimal, on the other hand, showed similar L_p with Tabat. A similar tendency was also observed at reproductive stage. The lack of significant differences in total area and capacity of late metaxylem vessels in roots of Gadambalia between wet and dry treatments, and the significant reduction in these two parameters in Tabat under drought stress (Salih *et al.* 1999) may explain the higher and lower L_p exhibited by Gadambalia and Tabat, respectively, under water stress.

The results of SDM, LA and physiological responses clearly demonstrated the drought tolerance of Gadambalia and susceptibility of Tabat. Arous elRimal, however, displayed moderate tolerance to water stress. Drought tolerance in Gadambalia is associated with its smaller LA, higher L_p, and ability to maintain high Ψ_l, RWC, g_s, E and P_N under drought stress.

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