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Mechanism of Interspecific Differences among Four Gramineous Crops in Growth Response to Soil Drying*

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Abstract : Drought tolerance is an important crop characteristic for maintenance of productivity under water deficit conditions. Interspecific differences among four gramineous crops (barnyard millet, maize, pearl millet and sorghum) in growth response to soil drying were studied. Seeds were sown in a sandy soil. Irrigation was stopped in some plots 16 days after sowing and was continued in others. Stopping irrigation increased resistance to water flow to between 2- and 21-fold. However, it decreased the soil water potential by -0.004 to -12.7 MPa, the relative growth rate (RGR) by 15 to 27%, the net assimilation rate (NAR) by 17 to 34% and the photosynthetic rate by 16 to 45%, respectively. Pearl millet and sorghum, which were identified as drought tolerant, displayed the lowest reductions in RGR. RGR was predominantly limited by NAR in all crops. The photosynthetic rate was preponderantly limited by stomatal conductance. Stomatal conductance correlated with leaf xylem water potential significantly. Pearl millet and sourghum showed the highest leaf water status. Root systems of all crops reached 140 cm soil depth. Under water stress, total root length was significantly reduced in maize, was not affected in barnyard millet, and was significantly increased in sorghum and pearl millet. Drought toleranace in sorghum and pearl millet was assoicated with sustained water uptake ability by increasing total root length and maintenance of high leaf water status under soil drying conditions at the vegetative growth stage.
Key words : Drought tolerance, *Echinochloa framentacea* Link., *Pennisetum typhoideum* Rich., Root, *Sorghum bicolor* Moench., Water stress, Water uptake ability, *Zea mays* L.

イネ科作物4種の土壌乾燥に対する生長反応における種間差の機構 : 松浦朝奈・稲永　忍・杉本幸裕（鳥取大学乾燥地研究センター）

要　旨 : 水分欠乏下で作物生産を実現するための基礎として作物の耐乾性機構を解明する必要がある. 4種のイネ科作物（ソルガム，トウモロコシ，ヒエおよびパールミレット）における土壌乾燥に対する成長反応における種間差を検討した. 4作物を夏季にビニルハウス内の砂土に播種し，播種後16日に灌水を停止した乾燥区と適宜灌水した湿潤区を設けた. 灌水停止により，植物体の通水抵抗は2から21倍に増加した. 一方，それは土壌の水ポテンシャルを -0.004 から -12.7 MPa，相対生長率（RGR） を15から27%，純同化率（NAR）を17から34%および光合成速度を16から45%，それぞれ低下させた. RGRの低下はソルガムとパールミレットの方が軽度であったことから耐乾性の強い作物であることが示された. 乾燥処理によるRGRの低下は主にNARの減少によるものであり，光合成速度の低下には概して気孔伝導度が関与することが判明した. 気孔伝導度と葉身木部の水ポテンシャルとの間には，全作物において有意な相関関係が認められた. 日中の葉身の水分状態は，パールミレットとソルガムでは高く維持された. 根系は4作物共に140 cmまで到達していた. 全根長は乾燥処理によりヒエでは変化せず，ソルガムとパールミレットではそれぞれ有意に増加し，トウモロコシでは有意に減少した. 以上のことから，栄養成長期においてパールミレットとソルガムが強い耐乾性を示す理由は，根長を増大させて吸水能力を維持することにより，日中の葉内水分の低下を軽減し，光合成やRGRを比較的高く保つことにあるといえる.
キーワード : 吸水能力，ソルガム，耐乾性，トウモロコシ，根，パールミレット，ヒエ，水ストレス.

Breeding and introduction of drought tolerant crops are important measures to maintain productivity under water deficit. Plants ability to maintain adequate water uptake plays an important role in drought tolerance[11]. Taylor[23] working on cotton and soybean concluded that transpiration rate, axial resistance to water flow along the xylem elements, radial resistance to water flow from soil to the xylem elements, total root length, energy status and quantity of water in soil around the roots are the most important factors controlling water uptake by plants. Turner[25] considered depth and density of roots and the hydraulic resistance to water flow to be the determinant factors. Passioura[18] pointed out that root density and longitudinal resistance to water flow are the most crucial.

It is thus evident that available information

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indicates the importance of resistance to water flow from soil to shoot, depth of root system and root length (root length density or total root length) as the main factors that control water uptake. Many studies on interspecific differences in drought tolerance between plants focused on, only one or two of these aspects[2,4,14,19]. The studies reported in this paper were designed to ascertain the role of these factors and their relative preponderance in determining drought tolerance among four gramineous crops.

Materials and Methods

1. Plant materials and culture conditions

The experiment was undertaken in the field during summer season at the Arid Land Research Center in Tottori Japan where soils are very light with more than 90% sand content[7]. The experimental area ($70m^2$), placed under a vinyl shed, was divided into three equal major plots separated by plastic wave plates buried to a depth of 90 cm. Each major plot was further subdivided into 12 small sub-plots. Each sub-plot (1.2×1.5m) was lined with plastic wave plates to a 60 cm depth to prevent intermingling of roots from neighbouring sub-plots. Seeds of Barnyard millet (*Echinochloa framentacea* Link. cv. Hidashirobie), grain sorghum (*Sorghum bicolor* Moench. cv. Feterita pergamino 1430), pearl millet (*Pennisetum typhoideum* Rich.) and maize (*Zea mays* L. cv. P3352) were planted, in August, each in a sub-plot in rows 60 cm apart at a spacing of 30 cm within rows. Individual species were planted in three replicates within each major plot. At planting a compound fertilizer (N-P_2O_5-K_2O, 15-15-12%), dolomite and a magnesium sulfate fertilizer (soluble Mg, 14%) were applied basically at the rates of 60, 40 and 40 g m^{-2}, respectively. Sufficient watering of all plots was maintained during the first 16 days after sowing. Thereafter, plants from one major plot were harvested for initial measurements. Of the remaining two major plots watering was discontinued on one (dry plot) and continued on the other (wet plot) for an additional period of 24 days. The experiment was concluded 40 days after initiation. All measurements were made during vegetative growth.

2. Growth measurements

Shoot dry weight and leaf area were measured twice, initially at the set on of soil drying stress and 24 days later. Roots were sampled over plants, between plants and between rows by extracting cylindrical cores (ϕ=5.0 cm) at 10 cm increments, down the profile, to 140 cm soil depth. The root samples were washed free from soil and stored in FAA solution (formalin : acetic acid : 50% ethanol, 1 : 1 : 18, v/v). Root length was determined, after staining with 1% crystal violet solution, by the image analysis method[16]. The root samples were then dried at 80°C for 72 hours and weighed. Root length density per plant in each soil layer was calculated as average for the three sampling locations ; over the plants, between the plants and between the rows. Root dry weight and total root length per plant were estimated as the sum of individual measurements across the three locations. Specific root length per plant was calculated by dividing total root length by root dry weight. Relative growth rate (RGR), net assimilation rate (NAR) and leaf area ratio (LAR) were calculated from shoot dry weight, leaf area and root dry weigth. Relative leaf growth rate (RLGR) was calculated from leaf area.

3. Leaf water status and gas exchange rate measurement

All measurements were undertaken at daytime (1000~1500), 19 days after soil drying stress was implemented, using the second or third expanded leaf from the top. Leaf water potential (Ψ_l) was measured with a pressure chamber (PMS Inc., 1002) and relative water content (RWC) was determined as described by Kobata[10]. Photosynthetic rate, transpiration rate, stomatal conductance (g_s) and intercellular CO_2 concentration (Ci) were measured with a portable photosynthesis system (LI-COR Inc., LI-6200).

4. Soil water potential measurement

Soil samples were taken between the rows to a depth of 140 cm using a 1.65 m boring stick (Daiki Rika Kogyo Co., Ltd., DIK-1641, $10\times$ 300 mm). Sampling was done twice, initially at the set on of the drying period and 20~21 days later. Soil moisture was measured gravimetrically and then volumetric water content was calculated assuming a 1.5 g cm^{-3} [8] as mean dry bulk density before converting into soil water potential (Ψ_S) using the standard soil water characteristic curve[7] for Tottori sandy soils.

5. Resistance to water flow

Resistance to water flow throuth the plant was estimated from equation (1)[3],

$$R = \Delta (\Psi_c - \Psi_l) / \Delta T \quad (1)$$

where R (MPa s cm^{-1}) is the resistance to water flow through the plant, Ψ_c (MPa) is the mean soil water potential where soil water content was above permanent wilting point and T (mg m^{-2} s^{-1}) is the transpiration rate. R was calculated from the slope of the regression line between ($\Psi_c - \Psi_l$) and T. Ψ_c was calculated from equation (2)

$$\Psi_c = \sum_{Z_m}^{140} (\Psi_s \times RL/RL_t) \quad (2)$$

where RL (cm) is the root length in each soil layer, RL_t (cm) is the sum of root length in the soil layers where Ψ_s is higher than the permanent wilting point, Z_m (cm) is the minimum (shallowest) soil depth where Ψ_s is higher than the permanent wilting point.

Results

There were no significant interspecific differences in soil water potenitial in the wet plot. All values of Ψ_s, across the 140 cm profile, were around field capacity (Fig. 1). In the dry plot, Ψ_s decreased in the top 20 cm and was lowest in sub-plots cropped to pearl millet (Fig. 1). RGR, NAR and RLGR were, invariably, reduced by moisture stress (Table 1). The reductions of RGR in pearl millet and sorghum were significantly lower than those in barnyard millet and maize ($p<0.01$). Multiple regression analysis showed that, under soil drying stress, NAR dominantly limited RGR in the four crops (Table 1). LAR of stressed plants significantly increased for barnyard millet, but not for the other crops (Table 1). Photosynthetic rate was, invariably, decreased by soil moisture stress (Table 2). The reductions of photosynthetic rate in pearl millet and sorghum were smaller than those in barnyard millet and maize. Results of multiple regression analysis showed that photosynthetic rate in sorghum was limited by g_s and intercellular CO_2 concentration. However, in the other crops g_s was the main limiting factor.

Soil moisture stress decreased both Ψ_l and g_s in all crops. Among the four crops, Ψ_l and g_s in pearl millet and sorghum were the least affected (Table 3 and Fig. 2). Both Ψ_l and g_s varied with time, and were significantly correlated ($p<0.05$) (Fig. 2). Soil moisture stress did not reduce leaf RWC in pearl millet and sorghum, but a slight and a considerable reductions were inflicted on barnyard millet and maize, respectively on 12 days after the stress was started (Table 3).

There were significant correlations between leaf xylem water potential difference, ($\Psi_c -$

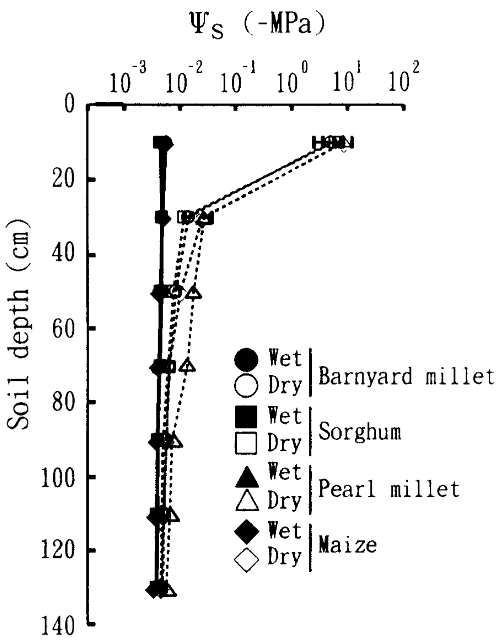

Fig. 1. Soil water potential (Ψ_s) at different depths.

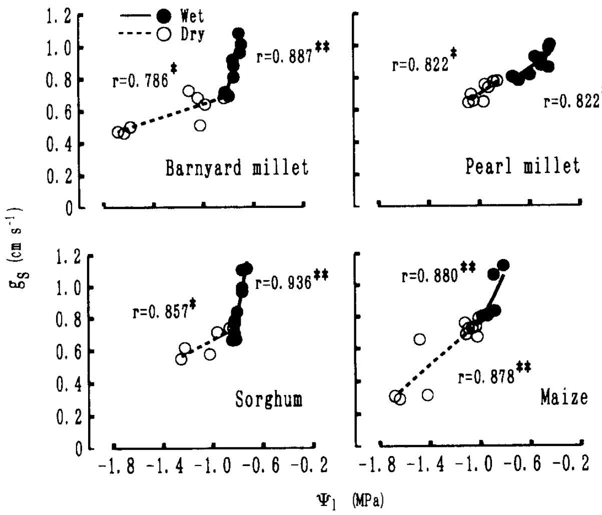

Fig. 2. Relationships between stomatal conductance (g_s) and leaf xylem water potential (Ψ_l) at midday for four crops at 19 days after soil drying stress was started.
* = significant at 5% level, ** = significant at 1% level.

Table 1. Relative growth rate (RGR), net assimilation rate (NAR), leaf area ratio (LAR) and relative leaf growth rate (RLGR) of four crops during soil drying stress.

		RGR ($g\ g^{-1}\ day^{-1}$)		NAR ($g\ m^{-2}\ day^{-1}$)		LAR ($cm^2\ g^{-1}$)		RLGR ($cm\ cm^{-1}\ day^{-1}$)	
Barnyard millet	Wet	0.225	(100)[1)]	14.2	(100)	159	(100)	0.167	(100)
	Dry	0.165**	(73)[c]	9.4**	(66)	176*	(111)	0.108**	(65)
Sorghum	Wet	0.183	(100)	9.2	(100)	198	(100)	0.154	(100)
	Dry	0.146**	(80)[b]	6.6**	(72)	220 NS	(111)	0.122**	(79)
Pearl millet	Wet	0.222	(100)	11.4	(100)	195	(100)	0.175	(100)
	Dry	0.188*	(85)[a]	9.4*	(83)	201 NS	(103)	0.141*	(81)
Maize	Wet	0.154	(100)	7.4	(100)	207	(100)	0.118	(100)
	Dry	0.117**	(76)[c]	5.4**	(73)	217*	(105)	0.081**	(69)

		SPRC[2)]		AMC[3)]	F[4)]
		NAR	LAR		
Barnyard millet	Wet / Dry	1.33	0.36	1.00	911
Sorghum	Wet / Dry	1.46	0.62	0.99	163
Pearl millet	Wet / Dry	1.57	0.85	0.89	10
Maize	Wet / Dry	1.14	0.25	1.00	3280

1) Percentage to wet. 2) Standardized partial regression coefficient. 3) Adjusted multiple correlation. 4) F value at 1% level.

Probability of the differences between wet and dry means: ** = significant at 1% level, * = significant at 5% level, NS = not significant.

The ratio of dry to wet followed by different at 1% level.

Table 2. Contribution of stomatal conductance (g_s) and intercellular CO_2 concentration (Ci) to photosynthesis rate (P) of four crops at 19 days after treatment.

		P ($\mu mol\ m^{-2}\ s^{-1}$)		g_s ($cm\ s^{-1}$)		Ci (ppm)		SPRC[2)]		AMC[3)]	F[4)]
								g_s	C_i		
Barnyard millet	Wet	32.6	(100)[1)]	0.88	(100)	142	(100)	0.94	0.03	0.93	49
	Dry	20.7**	(64)	0.57**	(65)	145 NS	(101)				
Sorghum	Wet	34.0	(100)	0.86	(100)	121	(100)	0.50	0.41	0.86	22
	Dry	28.6**	(84)	0.66**	(77)	96**	(79)				
Pearl millet	Wet	32.3	(100)	0.87	(100)	134	(100)	0.85	0.08	0.83	20
	Dry	27.1**	(84)	0.70*	(81)	104**	(78)				
Maize	Wet	34.3	(100)	0.94	(100)	101	(100)	0.70	−0.41	0.94	61
	Dry	19.0**	(55)	0.60**	(64)	144**	(142)				

1) Percentage to wet. 2) Standardized partial regression coefficient. 3) Adjusted multiple correlation. 4) F value at 1% level.

Probability of the differences between wet and dry means: ** = significant at 1% level, * = significant at 5% level, NS = not significant.

Photosynthetic photon flux density was $1263 \pm 23\ \mu mol\ m^{-2}\ s^{-1}$, air temperature was 36.7 ± 0.3°C and relative humidity was 48.8 ± 0.4%

Ψ_l), and transpiration rate for all of the crops (Fig. 3). Soil drying stress increased resistance to water flow through the plant (R) and there were significant interspecific differences. R in water stressed sorghum, barnyard millet, maize and pearl millet was increased to 21, 14, 4 and 2-fold, respectively (Table 4).

The root systems of all crops reached 140

Table 3. Leaf xylem water potential (Ψ_l) and relative water cotent (RWC) of leaf at midday among four crops at 19 days after treatment.

		Ψ_l (MPa)		RWC (%)	
Barnyard millet	Wet	−0.78	±0.02	95.2	±2.2
	Dry	−1.61**	±0.03	82.5*	±1.1
Sorghum	Wet	−0.77	±0.02	90.3	±0.3
	Dry	−1.24**	±0.01	87.9 NS	±0.8
Pearl millet	Wet	−0.47	±0.04	93.5	±0.6
	Dry	−0.96*	±0.08	88.1 NS	±0.9
Maize	Wet	−0.88	±0.07	90.6	±1.3
	Dry	−1.49*	±0.09	70.1*	±0.7

Probability of the differences between wet and dry means : **= significant at 1% level, *=significant at 5% level, NS=not significant.

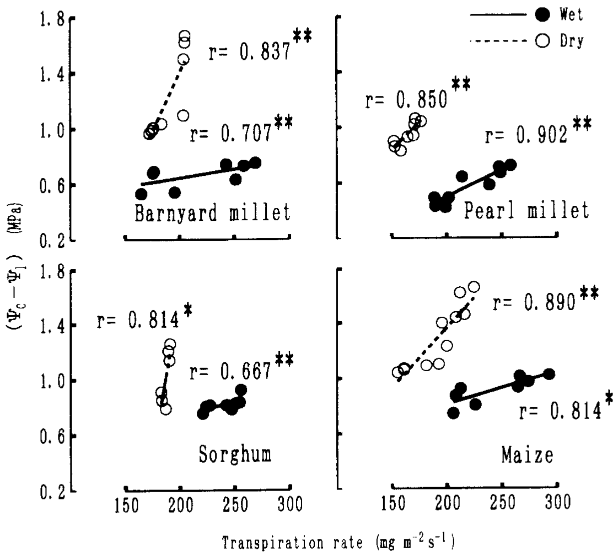

Fig. 3. Relationships between transpiration rate and ($\Psi_c - \Psi_l$) in four crops during soil drying stress.
*=significant at 5% level, **=significant at 1% level.

Table 4. Resistance to water flow(R) among four crops during soil drying stress.

	R(×10^{-4}MPa s cm^{-1})	
	Wet	Dry
Barnyard millet	1.2	16.7** (13.5)[1)]
Sorghum	2.2	45.6** (20.7)
Pearl millet	3.9	7.9** (2.0)
Maize	2.4	8.7** (3.7)

1) Ratio of dry to wet.
Probability of the differences between wet and dry means ; **=significant at 1% level, *=significant at 5% level, NS=not significant.

cm soil depth and there were no significant interspecific differences (Fig. 4). Root length density in stressed plants increased in deeper soils for all crops. Root length in pearl millet displayed a considerable increase at 80∼100 cm depth (Fig. 4). Total root length was considerably reduced, by water stress, in maize, but was not affected in barnyard millet and was substantially increased in sorghum and pearl millet (Fig. 4). Water stress decreased root dry weight in barnyard millet and maize, but not in sorghum and pearl millet (Table 5). Specific root length of water stressed plants was not changed in maize, but was considerably increased in the other three species (Table 5). The leaf area/total root length ratio (LA/TRL) was significantly decreased under soil drying stress (Table 6). Resutls of multiple regression analysis showed that LA/TRL in barnyard millet and maize was limited by LA while in sorghum and pearl millet it was limited by both LA and TRL (Table 6).

Discussion

The results of growth analysis (Table 1) indicated that pearl millet and sorghum were drought tolerant crops rather than barnyard millet and maize. Furthermore, sorghum and pearl millet had higher photosynthetic rate and leaf water status than the other two crops under soil drying stress (Table 2 and 3).

Under water deficit conditions, photosynthetic rate is limited by either chloroplastic activity or CO_2 supply. Some researchers reported preponderance of stomatal conductan-

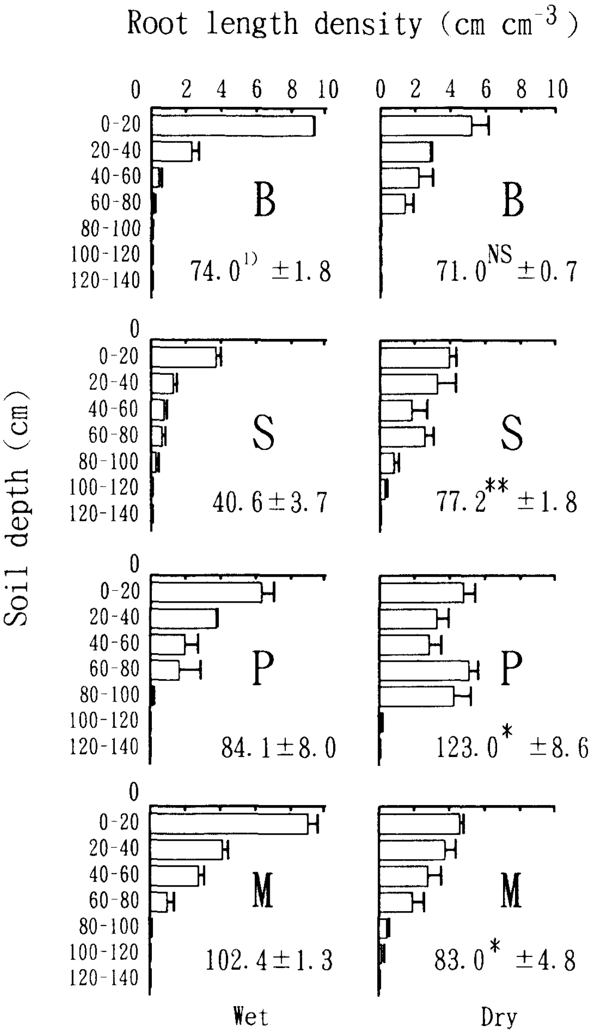

Fig. 4. Root length density at different depths among four crops (B : Barnyard millet, S : Sorghum, P : Pearl millet and M : Maize) during soil drying stress.
1) Total root length (m). Probability of the difference between wet and dry means ; * = significant at 5 % level, ** = significant at 1 % level, NS = not significant.

ce (g_s) as a limiting factor in photosynthesis[22]. However, others emphasized the importance of CO_2 fixation as a determinant factor[12,26]. Hirasawa et al.[6] showed that the relative importance of g_s and CO_2 fixation, as limiting factors in photosynthesis, varied with leaf xylem water potential. Stomatal conductance dominates at a relatively high leaf water potential, while CO_2 fixation activity preponderates at a relatively low leaf xylem water potential. In this study g_s had a significant correlation with Ψ_l ($p<0.05$). Similar findings were reported with various plant species[1,5,9,13]. Thus, the preceeding results suggest that water stressed sorghum and pearl millet had high photosynthetic rate because of their ability to maintain high leaf water status.

Assuming that water uptake and leaf water conditions are closely related, could be argued that resistance to water flow through the plant (R), depth of the root system and amount and spatial distribution of the roots, which are determinant factors in water uptake, also affect leaf water status and consequently photosynthetic rate and drought tolerance. R was increased by soil drying in all crops. A similar increase in R under water deficit conditions, was reported for several plant species including rice[24]. Results from pot and water culture experiments associated drought tolerance with low resistance to water flow through the plant[20,21]. However, our results, which are based on field experiment, showed that the values of R were not consistent with the interspecific difference of leaf water conditions in the four crops. Water stressed sorghum and pearl millet, which displayed the lowest reductions in leaf water status, had the highest and lowest R, respectively (Table 3 and 4). The observed inconsistency suggests that R was not the sole factor limiting water uptake in all four crops and that more subtle differences were involved. The disparity between our results, obtained from field grown plants, and those reported from experiments involving pots and water culture could be due to restriction of root growth in the latter two media[20,21]. However, the exact reason remains unclear.

This study revealed no significant interspecific differences in root depth between the four crops. However, the data (Fig. 4) showed that there were significant interspecific differences in spatial distribution of the roots and total root length. These findings strongly suggest that the interspecific differences in water upteke ability between the four crops were more related to the total root length rather than to R or to the depth of the root systems. Root growth response, generally, demonstrates interspecific differences under water stress and it is likely that a vigorous root system is beneficial for extracting water and nutrients[4,17,19]. Robertson et al.[19] investigated the influence of water stress on root length density and yields of maize, soybeans and

Table 5. Root dry weight and specific root length among four crops during soil drying rtress.

		Root dry weight (g)		Specific root length (m g^{-1})	
Barnyard millet	Wet	0.56	(100)[1)]	133	(100)
	Dry	0.43*	(76)	166*	(125)
Sorghum	Wet	0.90	(100)	46	(100)
	Dry	0.84 NS	(93)	97*	(212)
Pearl millet	Wet	1.67	(100)	50	(100)
	Dry	1.38 NS	(83)	90*	(179)
Maize	Wet	2.34	(100)	44	(100)
	Dry	1.74*	(74)	49 NS	(112)

1) Percentage to wet.
Probability of the differences between wet and dry means :
** = significant at 1% level, * = significant at 5% level, NS = not significant.

Table 6. Contribution of leaf area (LA) and total root length (TRL) to leaf area/total root length (LA/TRL) in four crops during soil drying stress.

		LA/TRL	LA (dm^2)	TRL (m)	SPRC[2)]		AMC[3)]	F[4)]
					LA	TRL		
Barnyard millet	Wet	0.14	10.6	74.0	1.06	−0.09	1.00	4519
	Dry	0.04**	2.6**	71.0 NS				
Sorghum	Wet	0.32	12.8	40.6	0.43	−0.60	0.99	237
	Dry	0.08**	5.9**	77.2**				
Pearl millet	Wet	0.28	23.5	84.1	0.54	−0.49	0.98	188
	Dry	0.09**	10.5**	123.0*				
Maize	Wet	0.30	31.0	102.4	1.42	−0.44	0.99	791
	Dry	0.16**	12.8**	83.0*				

1) Percentage to wet. 2) Standardized partial regression coefficient. 3) Adjusted multiple correlation. 4) F value at 1% level.
Probability of the differences between wet and dry means : ** = significant at 1% level, * = significant at 5% level, NS = not significant.

peanuts. They concluded that limited rooting of maize under water stress very likely decreased the efficiency of water and fertilizer use and consequently reduced yield. In conformity with Robertson et al.[19)], our study showed that total root length of maize decreased under soil drying stress. However, in contrast, soil drying stress increased total and specific root length in sorghum and pearl millet. An increase in total and specific root length enhanced water uptake, improved leaf water status, and consequently maintained high photosynthetic rate and RGR. An increase in total and specific root length, in sorghum and pearl millet, is thus an important adaptive response to maintain dry matter production under water deficit conditions.

The increase in specific root length indicated production and development of more lateral roots. Development of more lateral roots is expected to decrease radial resistance to water flow from the soil into the root and increase axial resistance along the xylem elements and hence facilitates water uptake.

Precise estimate of the contribution of the root resistance to R can not be made as the former was not measured in this study. However, the presence of regions of high resistance, hydraulic safety zones, between branches and main root xylem systems have been reported[15)]. This suggest that root length and branching may be closely related to R. Further detailed studies on the relationship between root growth and R are therefore pertinent.

In conclusion, pearl millet and sorghum were identified as drought tolerant crops compared to barnyard millet and maize. Drought tolerance in sorghum and pearl millet was associated with increased total root length and maintenance of high leaf water status and consequently high photosynthetic rate and RGR during their vegetative growth. LA/TRL was, invariably, reduced by water stress. A decrease in LA was the main causative factor in barnyard millet and maize. However in sorghum and pearl millet the reduction in LA/TRL was effected by both a decrease in LA and an increase in TRL.

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