

# Deep Root Water Uptake Ability and Water Use Efficiency of Pearl Millet in Comparison to Other Millet Species

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**Abstract** : Pearl millet is better adapted to hot and semi-arid conditions than most other major cereals. The objective of this study was to compare the deep water uptake ability and water use efficiency (WUE) of pearl millet among millet species. First, the WUE of six millet species was evaluated in pots under waterlogging, well-watered (control), and drought conditions. Secondly, the water uptake from deep soil layers by pearl millet and barnyard millet, which showed the highest drought and waterlogging tolerance, respectively, was compared in long tubes which consisted of three parts (two loose soil layers separated by a hardpan and a Vaseline layer). Soil moisture was adjusted to well-watered and drought conditions in the upper (topsoil) layer, while the lower (deep) layer was always kept wet. WUE was significantly reduced in all millet species by waterlogging but not by drought. The ratio of WUE to the control condition indicated that pearl millet had the highest and lowest resistances to drought and waterlogging conditions, respectively, while barnyard millet was the most stable under both conditions. The deuterium concentration in xylem sap water, relative water uptake from deep soil layers, and water uptake efficiency of deep roots were significantly increased in barnyard millet but not in pearl millet by drought in topsoil layers. In conclusion, the drought resistance of pearl millet is explained by higher WUE but not by increased water uptake efficiency in deep soil layers as compared to barnyard millet, another drought-resistant millet species.

**Key words** : Deep root, Deuterium, Drought, Heavy water, Stable Isotope, Transpiration, Waterlogging, Water source.

Due to the undulating topography of semi-arid areas (e.g., Sudanian and Sahelian zones), large amounts of water are accumulated in deep layers of lower slopes or lowlands (Van Staveren and Stoop, 1985). Despite being severely stressed, many crops appear to under-utilise these potential sources of water (Passioura, 1983). The effective utilisation of these deep-water sources is of particular interest in millet-growing areas. Pearl millet is one of the most important cereal species in semi-arid areas that are too hot, too dry, or too low in soil fertility for maize or sorghum production (Zaongo et al., 1994; Singh and Singh, 1995). The productivity of pearl millet under these conditions, however, is seriously affected by severe drought, especially when it occurs during panicle initiation and/or during flowering, in which case, it may lead to complete crop failure (De Rouw and Winkel, 1998).

The magnitude of the impacts of water stress may vary with the millet species according to the nature of their physiological and morphological traits. The plant growth analysis by Matsuura et al. (1996) indicated that the drought resistance of pearl millet is higher than those of barnyard millet and maize. One of the characteristics of a drought-resistant plant is the deep, wide-spreading, branching root system. Deep rooting

of annual food crop species has been extensively studied before (Araki and Iijima, 1998; 2001; Araki et al., 2000). In pearl millet, root elongation in deep soil layers has also been investigated in semi-arid environments (Sivakumar and Salaam, 1994; Zaongo et al., 1994; Bruck et al., 2003); however, the function of deep roots, such as water uptake, is not well documented. In our previous investigation, the deuterium labelling of deep soil water provided evidence that finger millet, Job's tears, and barnyard millet increased their water extraction from deep wet layers when topsoil was subjected to drought stress, but common millet, pearl millet, and foxtail millet did not (Zegada-Lizarazu and Iijima, 2004). Further study on the deep-water uptake ability of pearl millet is required to elucidate the drought tolerance of pearl millet.

Water use efficiency (WUE), i.e., the biomass produced per unit of water transpired, is one of the criteria to evaluate drought resistance in plants, and is a useful criterion in drought selection (Ibrahim et al., 1986). Under drought conditions, the main concern is the production per unit of applied water rather than the absolute production. Singh and Singh (1995) found that pearl millet had the highest WUE among maize and sorghum species under severely drought-

Table 1. Water use efficiency of six millet species grown in pots under different water regimes. Different letters within a row indicate significant differences among water treatments at 5% level of probability (Duncan's multiple range test). Values are means of four replications.

Species	Water use efficiency (g Kg <sup>-1</sup> )			Ratio to well-watered plants	
	Waterlogged	Well-watered	Drought	Waterlogged	Drought
Finger millet	2.32 b	3.00 a	2.82 a	0.77	0.94
Job's tears	2.21 b	2.82 a	1.90 c	0.78	0.67
Barnyard millet	2.85 c	3.30 b	3.49 a	0.86	1.06
Common millet	2.14 b	2.88 a	2.95 a	0.74	1.03
Pearl millet	2.77 b	3.91 a	4.19 a	0.71	1.07
Foxtail millet	1.96 b	2.73 a	2.59 a	0.72	0.95

stressed conditions. Since the ability to take up water from deep soil layers and WUE seem to operate largely independently on drought tolerance (Passioura, 1983), drought-tolerant millet species may have either one or both of these traits but not necessarily both of them. Many studies have stressed the ability of pearl millet to avoid drought stress by phenological, physiological, and morphological characteristics at the canopy level (Singh and Singh, 1995; Do et al., 1996; Levy et al., 1997; Winkel et al., 1997; 2001), but only a few investigated the ability of pearl millet to take up water from the whole soil profile (Zaongo et al., 1994; McIntyre et al., 1995). There is no quantitative information on the ability of the deep roots of pearl millet to extract water from wet subsoil layers when topsoil is prone to drought.

Lately, the use of stable isotopes has acquired preponderancy in the evaluation of water sources, especially, in forestry systems (Dawson, 1993; Schwinning et al., 2002) and in some crop species (Araki and Iijima, 2004; Sekiya and Yano, 2004; Zegada-Lizarazu and Iijima, 2004). Deuterium labelling is a powerful tool in assessing water sources and water uptake and can be used to study the ability of deep-rooted crops to withdraw water from wet subsoil layers. Araki and Iijima (2004) quantified the water uptake ability of deep roots of upland rice using the hydrogen stable isotope method. In this study, we employed this technique to evaluate the deep-water uptake ability of pearl millet and barnyard millet, which is another drought-tolerant millet species. The aim of this study was to compare the deep water uptake ability and WUE of pearl millet with those of other millet species to acquire further knowledge of pearl millet drought tolerance.

#### Materials and methods

A series of experiments was conducted to evaluate the WUE of several millet species (Exp. 1) and the water uptake ability of the deep roots of pearl millet and barnyard millet (Exp. 2). In Exp. 1, the WUE of six

millet species was compared under three different soil moisture regimes. In Exp. 2, the ability of pearl millet to withdraw water from wet subsoil was compared to that of barnyard millet in long tubes emulating field conditions in which there was a hardpan (a compact soil layer) just above a water table and the topsoil was prone to drought. In both experiments, the plants were grown in a greenhouse.

#### 1. Water use efficiency (Experiment 1)

The WUE can be based on either transpiration or evapotranspiration and on grain yield or above-ground biomass (Passioura, 1983). In this experiment, the WUE was calculated as the above-ground biomass produced per unit cumulative water transpired by the plant. The experiment was conducted in a greenhouse with average minimum and maximum temperatures of 25 and 37 °C, respectively. Six millet species [finger millet (*Eleusine coracana* (L.) Gaertn.; cv. Gifu, local), Job's tears (*Coix lacryma-jobi* L.; cv. Kyoto, local), barnyard millet (*Echinochloa utilis* Ohwi et Yabuno.; cv. Okayama, local), common millet (*Panicum miliaceum* L.; cv. Saitama, local), pearl millet (*Pennisetum typhoideum* Rich.; cv. Okashana, local), and foxtail millet (*Setaria italica* (L.) Beauv.; cv. Saitama, local)] were grown in pots of 113 mm in diameter and 135 mm in height. The total number of pots used was 78 {three water treatments x six species x four replications, plus six additional pots without plants (three water treatments x two replicates)}. A powdered compound synthetic fertilizer (N: 12 %, P<sub>2</sub>O<sub>5</sub>: 16 %, K<sub>2</sub>O: 14 %) was mixed into the soil at a rate of 0.4 g Kg<sup>-1</sup>. Pots were loosely filled with sandy loam soil with a bulk density of 1.33 Mg m<sup>-3</sup>. Three seeds of each species were planted at the centre of each pot. At five days after planting, seedlings were thinned to one per pot. From the 25<sup>th</sup> day after planting, the soil water content (gravimetric basis) was adjusted every other day to saturation, 25% ( $\psi = -7$  kPa), and 8% ( $\psi = -280$  kPa) in the waterlogged, well-watered (control), and drought treatments, respectively. The shoot biomass was sampled between

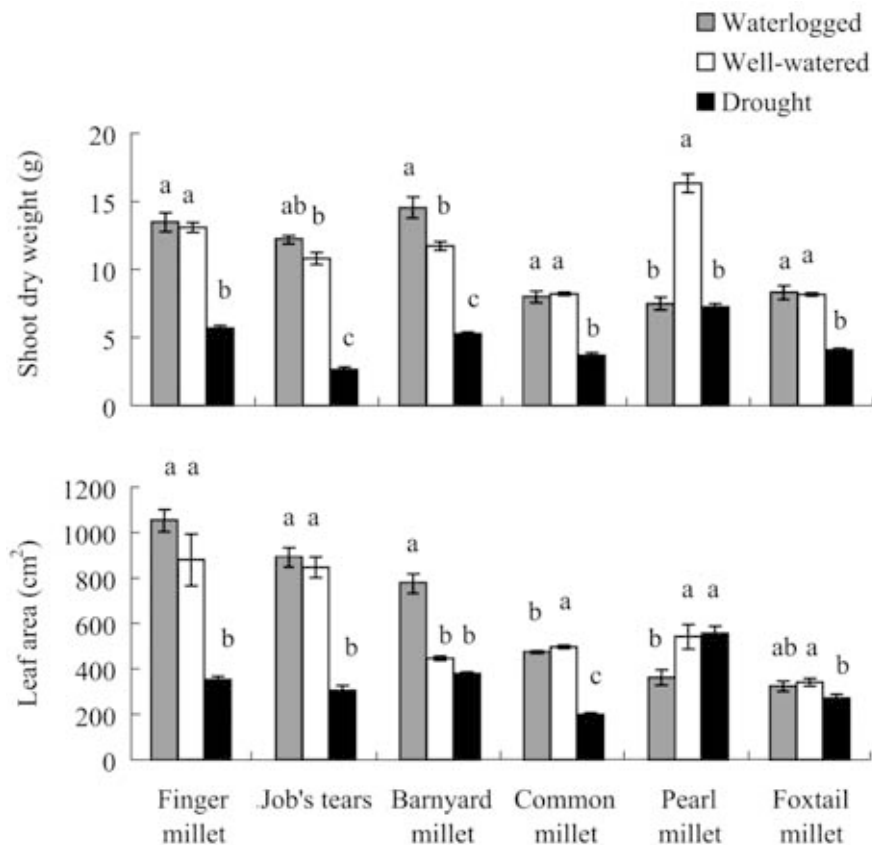


Fig. 1. Shoot dry weight (upper) and leaf area (lower) of six millet species grown in pots under different water regimes. The same letters within species indicate not significant differences among water treatments at 5% level of probability (Duncan's multiple range test). Values are means of four replications  $\pm$  SE.

60 and 65 days after planting just after the heading or booting was started. Shoot samples were oven dried at 80 °C for three days and then shoot dry weight was determined. Together with soil water adjustments, daily transpiration was accurately determined by weighing the pots. Transpiration was calculated as the difference between the weights of pots with and without plants, in each treatment. The leaf area was measured with a Li-Cor leaf area meter (LI-COR, Inc., USA, LI-3100).

## 2. Water uptake from deep soil layers (Experiment 2)

The water uptake from deep soil layers by pearl millet and barnyard millet was evaluated in long pots (75 mm in diameter and 500 mm deep) with two compartments, similar to those used by Araki and Iijima (2004) and Zegada-Lizarazu and Iijima (2004). The total number of pots used was 20 (two water treatments  $\times$  two species  $\times$  five replications). Each of the compartments in the pots was 250 mm high; the upper (topsoil) and lower (deep) compartments were separated by a Vaseline layer (2 - 3 mm thick), which prevented water movement between the two parts. The lower compartments were loosely filled with loamy sand soil with a bulk density of 1.33 Mg

m<sup>-3</sup>. In the upper compartments, a compact soil layer (hardpan) with a bulk density of 1.50 Mg m<sup>-3</sup> was formed at a depth between 180 and 250 mm, and the rest of the compartment was loosely filled with soil. Five seeds of each species were planted at the centre of each pot. After one week, the number of seedlings was reduced to one per pot. The lower compartments were always kept wet (average 30%;  $\psi = -5.5$  kPa), while soil moisture in the upper ones (shallow layer) was adjusted every other day to 25% ( $\psi = -7$  kPa) and 8% ( $\psi = -280$  kPa) in the well-watered and drought treatments, respectively. The drought treatment was started at 25 days after planting. Until then, plants were grown under well-watered conditions. To prevent evaporation, each pot was covered with a vinyl sheet. Daily transpiration was determined gravimetrically. Plants were harvested at 60 days after planting, and the shoot dry weight was measured as in Exp. 1. The root length in the deep layers was measured according to the procedure described by Kimura et al. (1999) and Kimura and Yamasaki (2001). Deuterated water (1 atom % D<sub>2</sub>O; about 17–50 mL depending on the amount of transpiration on the previous day) was applied to the deep soil layers during the drought

Table 2. Deuterium enrichment in xylem sap water, water uptake from deep soil layers (25-50 cm depth) and water uptake efficiency of deep roots of millets grown in long pots under different soil moisture conditions. \* indicates significant difference between treatments at 5% level of probability. Topsoil layer was well-watered or drought stressed, but deep soil layer was always kept wet. A Vaseline layer prevented water movement between topsoil and deep soil layers. Deuterated water was applied to deep soil layers. Values are means of three replications  $\pm$  SE.

	Deuterium concentration in xylem sap (atom % excess)		Water uptake from deep soil (%)		Water uptake efficiency (mg water root cm <sup>-1</sup> )	
	Well-watered	Drought	Well-watered	Drought	Well-watered	Drought
Barnyard millet	0.14 $\pm$ 0.02	0.35 $\pm$ 0.02 *	25.2 $\pm$ 4.4	53.9 $\pm$ 7.5 *	1.97 $\pm$ 0.3	8.78 $\pm$ 1.7 *
Pearl millet	0.16 $\pm$ 0.07	0.33 $\pm$ 0.04 ns	20.1 $\pm$ 7.6	37.0 $\pm$ 3.9 ns	2.45 $\pm$ 0.5	2.28 $\pm$ 0.4 ns

period. At harvest, xylem sap was collected by the method of Zegada-Lizarazu and Iijima (2004). Because of the high fluctuation in shoot growth, the xylem sap of three replicates showing average shoot growth was collected for the hydrogen stable isotope analysis. The deuterium concentration in xylem sap and soil water were determined and used to calculate the percentage of water taken up from the deep soil layers. The percentage of water taken up from deep wet soil layers was calculated according to Araki and Iijima (2004) as follows:

$$(C_D \text{ up}/100)*n+(C_D \text{ low}/100)*(1-n)=(C_D \text{ trans}/100),$$

where  $n$  ( $0 \leq n \leq 1$ ) and  $1-n$  ( $0 \leq 1-n \leq 1$ ) are the fractions of water transpired from the upper (0 to 250 mm depth) and lower (250 to 500 mm depth) compartments, respectively. The total water uptake in the pots is  $1 = n + (1 - n)$ .  $C_D$  up and  $C_D$  low are the concentrations of heavy water included in the soil sampled from the upper and lower compartments, respectively.  $C_D$  trans is the concentration in transpired water. Further details for the procedures of xylem sap and soil water sampling and the determination of their deuterium concentrations are given in Zegada-Lizarazu and Iijima (2004). The water uptake efficiency of deep roots was expressed as the water used (calculated from the percentage of water taken from deep layers and plant transpiration) per unit root length in the deep layers.

### 3. Statistical analysis

In both experiments, the pots were arranged in a completely randomised design, with four and five replicates for Exp.1 and Exp. 2, respectively. One-way analysis of variance (ANOVA) and Duncan's multiple range tests were used for the comparison of all the parameters measured between water treatments and species.

## Results

### 1. Water use efficiency, dry matter production, and leaf area (Exp. 1.)

Table 1 shows the WUE of six millet species grown under waterlogged, well-watered (control), and drought conditions. As compared with that in

the control treatment, the WUE was significantly reduced in all millet species by waterlogging but not by drought. Only Job's tears showed a significant reduction under the drought condition. Barnyard millet even increased its WUE under drought. The ratio to the control conditions indicated that pearl millet had the highest and lowest resistances to drought and waterlogging conditions, respectively, while barnyard millet was the most stable under both soil conditions. Waterlogging reduced the WUE of pearl millet by 29% but only by 14% in the case of barnyard millet. On the other hand, the WUE was not reduced in either species by the drought treatment as compared with the control conditions (Table 1).

Most of the millets showed a significant reduction in shoot dry weight and leaf area by drought but not by waterlogging conditions as compared with the control treatment (Fig. 1). Pearl millet and barnyard millet were the exception to this pattern. The leaf area was not reduced in either species by the drought treatment. Barnyard millet showed a significantly higher leaf area and shoot dry weight under waterlogging than under control and drought conditions. The ratio of leaf area to control conditions followed the same pattern as WUE. The highest reduction under waterlogging conditions was found in pearl millet (33 %) while the leaf area of barnyard millet was increased by 75 %. Among the six millet species barnyard millet showed the best performance under waterlogging conditions in terms of biomass production; the ratio to control conditions shows a 24 % increase. In contrast, only pearl millet showed a significant reduction in shoot dry weight under the waterlogging condition (54%) which was the lowest performance among the millet species.

### 2. Water uptake from deep soil layers, transpiration rate, and plant growth characteristics (Exp. 2)

The result of Exp. 1 indicated that pearl millet and barnyard millet were the highest drought-resistant and waterlogging-resistant species among the six millet species, respectively. Barnyard millet also showed similar high drought resistance as pearl millet. Therefore, the water uptake ability of the deep roots of

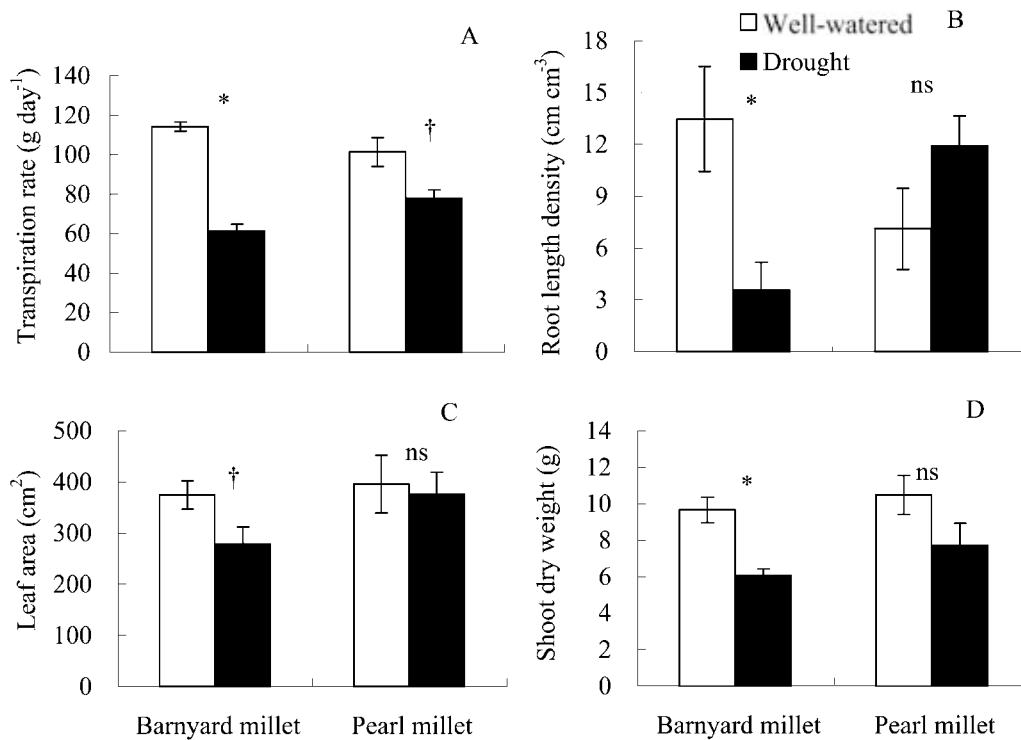


Fig. 2. Transpiration rate (A), root length density in the deep soil layer [(25-50 cm depth); (B)], leaf area (C) and shoot dry weight (D) of millets grown in long pots under different soil moisture conditions. \* and † indicates 5 and 10 % level of significance for differences between treatments. Values are means of three to five replications  $\pm$  SE.

pearl millet was compared with that of barnyard millet. In Table 2, the effects of drought in the topsoil layers on the deep water uptake characteristics of the two species are presented. The deuterium concentration in xylem sap water and the relative water uptake from deep soil layers were significantly increased in barnyard millet, but not in pearl millet, by drought imposed on topsoil layers. The deuterium concentration in xylem sap of barnyard millet rose up to 0.35 atom % excess, and its relative water uptake from the deep layers rose up to 54%. In pearl millet, although the drought treatment increased the relative water uptake and deuterium values, these values were not statistically different due to the high genetic variation [because pearl millet is cross-pollinated (De Rouw and Winkel, 1998)] among the replicate plants. The water uptake efficiency of the deep roots of barnyard millet was also significantly increased (4.5 times) by drought in topsoil layers, but it was not in pearl millet (0.9 times).

The water use and plant growth characteristics of the two species are presented in Fig. 2. The transpiration rate was significantly reduced by the drought treatment compared with the well-watered control in both millet species. Drought stress reduced the transpiration rate by 46% in barnyard millet but only by 23% in pearl millet. It reduced both the leaf area and shoot dry weight significantly in barnyard millet but not in pearl millet. In terms of absolute values pearl millet showed

a reduction in dry matter production as in Exp. 1, but the difference was not significant. Only in Exp. 1 this reduction was significant. The always wet conditions of the deep layers in Exp. 2 caused the different response of pearl millet. The root length density in deep soil layers was greatly decreased (74 %) by the drought treatment in barnyard millet, but was increased (67 %) in pearl millet though not significantly. This difference was reflected in the different trend of water uptake efficiency of deep roots between pearl millet and barnyard millet shown in Table 2.

### Discussion

Increased water uptake from deep soil layers may help plants to improve their leaf water status and to maintain transpiration rates and dry matter production. In this study, water uptake from deep soil layer was evaluated by the hydrogen stable isotope method (Araki and Iijima, 2004; Zegada-Lizarazu and Iijima, 2004) to clarify whether or not deep roots subjected to waterlogging conditions play a major role in the drought-resistance strategy of pearl millet. In pearl millet, the water extraction from wet subsoil layers was increased by drought stress imposed on the topsoil layer, but not significantly (Table 2). The high variation among the replicate plants caused non-significant differences between the treatments. In pearl millet, there is often high variability in plant growth

under field conditions; therefore, sub-populations of early-, intermediate-, and late-flowering plants can be found in a group of plants (De Rouw and Winkel, 1998). Moreover, the soil water potential in the deep layers was around -5.5 kPa, which would be a partly anaerobic condition for pearl millet. Although the root length density in the deep layer was increased by the drought treatment, the deep roots of some pearl millet plants might not function well under the wet conditions.

By contrast, water uptake from deep soil in barnyard millet was significantly increased by the drought stress imposed on the topsoil layer, probably because deep roots were well adapted to the anaerobic condition. In barnyard millet, however, increased water uptake from the deep layer (Table 2) was not enough to sustain the transpiration rate and dry matter production under drought condition due to the reduced root development (root length density) in deep soil layer (Fig. 2). On the other hand, in pearl millet, shoot dry weight was not statistically reduced by drought stress even though the deep root water uptake efficiency was not increased. Therefore, the sustained dry matter production of pearl millet under drying topsoil layers is better explained by the higher WUE rather than by increased water uptake efficiency from wet subsoil layers. Singh and Singh (1995) indicated that the higher adaptation of pearl millet to drought conditions in comparison to other crop species, such as sorghum and maize, is more related to its greater ground cover (senesced leaves and tillers acting as mulch), higher degree of leaf rolling, pubescent leaves, and relative low transmission of radiation through canopy due to higher leaf area than to water extraction from the whole soil profile. Moreover, Inada et al. (1992) indicated that pearl millet can maintain high relative water content under drought stress due to its solid leaf cell walls, which prevent water losses. Therefore, these characteristics may help pearl millet to reduce plant transpiration, which, in turn, would result in higher WUE and drought resistance.

The other reasons for the difference in deep root water uptake between pearl millet and barnyard millet would be related to the ability of roots to penetrate the deep soil layer. In this experiment, roots had to grow through a compact soil layer (hardpan), which prevented root elongation before the roots could reach and exploit the deep moist soil layers. As indicated by Iijima and Kono (1991 and 1993) and Iijima et al. (1991), root elongation is usually reduced in compact soil layers, and the reduction rates differ significantly among crop species. Drought stress must have caused higher soil mechanical resistance of the compact soil layer. Most of the roots of barnyard millet could not penetrate this layer well under the drought condition. This limited volume of roots in deep soil layer would have caused the enhanced water uptake efficiency

observed in this study. In contrast, pearl millet roots could penetrate this layer well even under the drought condition, which did not cause the enhancement of root activity. Furthermore, pearl millet and barnyard millet have different protection mechanisms against waterlogging conditions. Galamay et al. (1992) found out that acropetal lignification in protective tissues of nodal roots is enhanced by waterlogging conditions in barnyard millet but not in pearl millet. Therefore, these factors may affect the ability of the roots of pearl millet to take up water from deep wet soil layers.

WUE is a useful criterion for plant screening under drought conditions (Ibrahim et al., 1986). Under stress conditions, the main concern is the production per unit of applied water rather than absolute production. In the present study, the WUE was significantly reduced in all millet species by waterlogging but not by drought (Table 1), which is an indication of the adaptation of these millet species to drought stress conditions. Similar results were reported by Kono et al. (1987), who conducted a series of pot experiments. Although their study showed a similar trend, it did not include statistical analysis. In the present study, the ratio to the control conditions (Table 1) indicated that pearl millet had the highest and lowest resistances to the drought and waterlogging conditions, respectively, while barnyard millet was the most stable under both soil conditions. The higher resistance to drought stress of pearl millet and barnyard millet, as compared to the other millet species, is also reflected in their sustained leaf area (Fig. 1). Leaf area development is the most important factor controlling the WUE in drought-prone environments (Passioura, 1996). In our study, the leaf area of pearl millet and barnyard millet was not reduced by the drought treatment (Fig. 1). In a field experiment, Matsuura et al. (1996) found similar leaf area ratios for drought-stressed and well-watered pearl millet plants, but in their experiment drought stress significantly increased the leaf area of barnyard millet, which did not agree with our results. The relatively small leaf area of well-watered pearl millet and barnyard millet in relation to their shoot dry weight (Fig. 1) might be related to the inferior production and development of tillers under the present experimental conditions.

In summary, the drought resistance of pearl millet is explained by higher WUE but not by increased water uptake efficiency in deep layers as compared to barnyard millet, another drought-resistant millet species.

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