Effect of Pre- and Post-heading Water Deficit on Growth and Grain Yield of Four Millets

Asana Matsuura¹, Wataru Tsuji², Ping An³, Shinobu Inanaga⁴,⁵ and Kouhei Murata¹

(¹School of Agriculture, Tokai University, Kumamoto 869-1404, Japan; ²Faculty of Agriculture, Tottori University, Tottori 680-0001, Japan; ³Arid Land Research Center, Tottori University, Tottori 680-0001, Japan; ⁴Toell Co., Ltd., Kanagawa 223-8510, Japan; ⁵Institute of Technologists, Saitama 361-0038, Japan)

Abstract: Seeds of Panicum miliaceum, P. sumatrense, Setaria glauca and S. italica were raised in polyvinylchloride (PVC) tubes filled with sandy soil in a greenhouse to determine the effect of pre- and post-heading water deficit on growth and grain yield. Water stress treatment was initiated 25 days after sowing. The grain yield of S. italica and S. glauca decreased 80 and 70%, respectively, under water stress; and that of P. miliaceum and P. sumatrense decreased 36 and 20%, respectively. The reductions were ascribed to smaller number of grains per panicle, smaller number of panicles and lighter total dry weight. The grain yield decreased when water stress was imposed before heading in S. italica and S. glauca, but both before and after heading in P. miliaceum and P. sumatrense. Mild water stress decreased the leaf water potential of all millets. Osmotic adjustment of the leaf could not explain the interspecific difference in drought tolerance. Water stress increased the root growth of S. italica, S. glauca and P. sumatrense at deeper soil layers at heading. At harvest, it also increased root growth at deeper soil layers in S. italica and S. glauca. There was a significant correlation between grain yield and root dry weight among the millets except S. italica. The drought tolerant millet showed greater drought tolerance to water deficit not only at the vegetative stages but also at the reproductive stages than two susceptible millets.

Key words: Drought tolerance, Grain yield, Millet, Osmotic adjustment, Root growth.

Water stress may occur at any time during the growing season because of variable climatic changes associated with global warming and this may lead to a profound decrease in yield (Parry et al., 1999). Breeding drought tolerant crops is one way to increase grain yield, but, progress has been slow during the past decades due to lack of understanding of the traits and mechanisms of drought tolerance (Bernier et al., 2009). It is important to identify the critical period and responses to water deficit among crops. Decreases in grain yield following water deficit stress occur during early reproductive development rather than other growth stages in most crops, because the irreversibility of the early events was especially damaging; for example, grain yield decreased as the number of kernels decreased in maize (Boyer and Westgate, 2004; Ribaut et al., 1997). In rice, the reproductive stage is more susceptible to water deficit (Cruz and O’Toole, 1984; Lilly and Fukai, 1994) and reduction in spikelet fertility due to water deficit during flowering caused yield losses (Liu et al., 2006). A reduction in grain size by water stress during grain filling also decreased the grain yield of wheat (Kobata et al., 1992).

Millet is an important genetic resource that conducts C₄ photosynthesis and requires less water. Setaria italica, foxtail millet, is an annual crop that originated from S. viridis (L.) P.Beaup. (Kihara and Kishimoto, 1942) in Central Asia between Trukistan and the Northwestern Indian subcontinent. This millet has been cultivated through Eurasia since about 5000 B.C. (Sakamoto, 1987). In Japan, S. italica might have been cultivated for as long as rice. The mean grain yield of S. italica is around 150 kg 10a⁻¹ and is mainly cultured on hilly and mountainous areas in Japan. Setaria glauca, yellow foxtail millet, is an annual weed that grows along the roadside and elsewhere but it is an

Received 8 December 2011. Accepted 3 April 2012. Corresponding author: A. Matsuura (asana@agri.u-tokai.ac.jp fax +81-967-6-2659. Present address: Department of Plant Science, Faculty of agriculture, Tokai University, Minamiaso, Kumamoto 869-1404, Japan). This research was supported in part by a Grant-in-Aid to the Arid Land Research Centre, Tottori University. Abbreviations: DSI, drought susceptibility index; LA, leaf area; MLA, mean leaf area; NAR, net assimilation rate; OA, osmotic adjustment; PGR, plant growth rate; PVC, polyvinyl chloride; RDW, root dry weight; RDWD, root dry weight density.
important food crop often cultivated with *Panicum sumatrense*, little millet, in South India (Kimata et al., 2000). Farmers in India believe that *S. glauca* provides a reasonable harvest while *P. sumatrense* might fail completely in severe drought (Kimata et al., 2000). However, the reason for *S. glauca* being more drought tolerant than *P. sumatrense* is not clear. *Panicum miliaceum*, common millet, is one of the early maturing among these species and is well known for its drought tolerance. The origin of *P. miliaceum* is not known. The yield of *P. miliaceum* is around 120 kg 10a⁻¹ and is mainly cultivated on hilly and mountainous areas in Japan; it is susceptible to damage by birds. During heading, rainfall was an important factor influencing the yield of common millet in Russia (Pul’man, 1909). Tulaikov (1929) showed that the largest consumption of water by common millet was during flowering. These findings suggest the relationship between the response to water stress at heading and flowering.

Rice with large and deep roots had high grain yields under water stress (Mambani and Lai, 1983; Jordan et al., 1983). A physiological understanding has resulted in higher yielding or more productive germplasm as shown by increased axial resistance in wheat (Passioura, 1972; Richards and Passioura, 1989), osmotic adjustment in *S. italica* (Karyudi and Fletcher, 2003), wheat (Morgan, 1991; 2000) and sorghum (Ludlow et al., 1990; Santamaria et al., 1990) and stay-green in sorghum (Rosenow et al., 1983; Borrell and Hammer, 2000).

Some millets with vigorous root development at a deeper soil layer showed more drought tolerance at the vegetative growth stage (Matsuura et al., 1996), but the relationship between root growth and grain yield in millets is still not clear. Little research has been conducted on millets under water stress from the viewpoint of crop science and eco-physiology (Karyudi and Fletcher, 2003; Kono et al., 1987; Parasuraman and Mani, 2001; Pul’man, 1909).

In this study, we determined the most susceptible growth stage to water deficit and the limiting factor for grain yield in *Setaria* and *Panicum* species under conditions in which the available water exists in deeper soil layers.

### Materials and Methods

#### 1. Plant materials and culture

Common millet (*Panicum miliaceum* L.), foxtail millet (*Setaria italica* L. P.Beauv.), little millet (*P. sumatrense* Roth.), and yellow foxtail millet (*S. glauca* L. P.Beauv.) were used. Seeds of each species were sown in polyvinyl chloride (PVC) tubes (7.5 cm in inner diameter; 70 cm in height) filled with a sandy soil on 9 July 2007 and the cylinders were submerged in half-strength Hoagland and Arnon’s nutrient solution with double concentration of Fe (EDTA-Fe; 90.4 mg l⁻¹) to 25 cm from the bottom. The plants in PVC tubes were grown in a greenhouse at Tokai University, Kumamoto, Japan. From 25 days after sowing, half of the plants in each species were subjected to dry treatment reducing the submerging depth to 5 cm from the bottom, and the remaining half was kept submerged 25 cm from the bottom (wet treatment). Then, in the dry treatment, available water existed deep soil layers. At the onset of heading (*S. italica*; 33 days after the start of treatment (DAT)), *S. glauca*; 39 DAT, *P. miliaceum*; 25 DAT, *P. sumatrense*; 48 DAT in wet treatment and 55 DAT in dry treatment), half of the plants in the dry treatment were subjected to the wet treatment (DW) and half of the plants in the wet treatment were subjected to dry treatment (WD). The remaining half of the plants were kept in the same treatment (WW and DD). In all treatments, soil samples were taken at heading and harvest from each 10cm incremental layer to a depth of 70 cm. Soil moisture was measured gravimetrically after oven-drying at 110°C to a constant weight.

#### 2. Dry matter production and grain yield

Plant was sampled a day before imposing treatment, at heading and at harvest. Leaf area and leaf number were measured before leaf blade, leaf sheath and stem samples were exposed to 110°C for 30 minutes, followed by 65°C for 48 hours. Then they were weighed. Roots were sampled at 10 cm intervals to a depth of 70 cm. The root samples were washed to remove sand and dried for the measurement of dry weight. Plant growth rate (PGR), net assimilation rate (NAR) and mean leaf area (MLA) were estimated by the following equations:

\[
PGR (g \text{ day}^{-1}) = \frac{W_{2} - W_{1}}{T_{2} - T_{1}} \tag{1}
\]

\[
NAR (g \text{ m}^{2} \text{ day}^{-1}) = PGR \times \frac{\log LA_{2} - \log LA_{1}}{LA_{2} - LA_{1}} \times 10^{4} \tag{2}
\]

\[
MLA (cm^{2}) = \frac{LA_{2} - LA_{1}}{\log LA_{2} - \log LA_{1}} \tag{3}
\]

Where, \( W_{1} \) and \( W_{2} \) are the dry weight of whole plant one day before treatment (\( T_{1} \)) and the day heading was started (\( T_{2} \)), respectively; \( LA_{1} \) and \( LA_{2} \) are the total leaf area per plant at \( T_{1} \) and \( T_{2} \), respectively.

\[
LA_{T} / RDW \text{ was calculated as the ratio of } LA_{T} (\text{total leaf area per plant at heading}) \text{ to } RDW (\text{root dry weight per plant at heading}).
\]

Plants in three replicate tubes of each treatment were harvested at maturity for grain yield. Yield components, i.e., number of panicles per plant, number of grains per panicle and grain weight were determined on the harvested plants. Harvest index was calculated as the ratio of seed dry weight to total plant dry weight.

Drought susceptibility index (DSI) was calculated as follows (Fisher and Maurer, 1978):

\[
DSI = \frac{(1-GY_{h}/GY_{w})}{(1-GY_{rdw}/GY_{vmd})} \tag{4}
\]

Where, \( GY_{h} \) is the grain yield of millet crop in dry
3. **Water potential and osmotic potential of leaves at heading**

At 20 days after the water stress treatment, the water potential of the second fully expanded leaves on three plants per treatment was measured in pressure chamber at midday, and the leaves were put into sealed vinyl bag containing a small amount of distilled water, and then subjected to 10°C. After four hours at 10°C, the turgid leaves were wrapped with an aluminum foil, and submerged in liquid nitrogen. Frozen leaves were retained in a freezer at −80°C until they were used for measuring osmotic potential with a thermocouple psychrometer (Decagon Devices Inc., Tru Psi model SC10X). Osmotic adjustment (OA) of leaves was calculated as the difference in osmotic potential between control and stress treatment (Pantuwan et al., 2002b).

4. **Statistical analysis**

Data were analyzed using two-way analysis of variance (ANOVA) and treatment means were compared using the Tukey-Kramer multiple range test. A regression analysis was also performed to explore the relationship between grain yield and each yield component, total plant dry weight and root dry weight.

**Results**

1. **Soil water content at heading**

In the wet treatment, water content at the 0–10 cm depth was lower than the lent capillary point (3.6%), but available water was present at the 10–70 cm depths in all millet types (Fig. 1). In the dry treatment, water content decreased to around the permanent wilting point (1.3%) at the 0–20 cm depth in all millets, and to around the lent capillary point at the 20–30 cm depth in *S. italica*, *S. glauca*, and *P. miliaceum*. Water stress treatment reduced soil water content at depths ranging from 10 to 40 cm in all millets and there was no interspecific difference. There was no significant difference in soil water content between wet and dry treatments at 40–70 cm depths with the millet. Sandy soil was used in this experiment because its water retention character was already known (Inoue and Nomura, 1983) and the water content of sandy soil decreased rapidly when the stress treatment was imposed.
2. Soil water content at harvest

In the wet treatment, the water content at all depths was higher than lent capillary point (3.6%) as shown in Fig. 2. Water content in the dry treatment decreased to around the permanent wilting point (1.3%) at the depth of 0 to 30 cm in *Setaria* *italica*, *S. glauca* and *P. sumatrense* and at the depth of 0 to 20 cm in *P. miliaceum*. Water content in the dry treatment decreased to around lent capillary point at 20-30 cm depth in *P. miliaceum*. Water stress significantly reduced soil water content at depths ranging from 0 to 50 cm in *S. glauca* and *S. italica*, 0 to 40 cm in *P. sumatrense*, and 0 to 30 cm in *P. miliaceum*. There was no significant difference in soil water content between wet and dry treatments at 50–70 cm depth in any millet.

3. Plant growth and leaf water potential at heading

The shortest period (25 days) to heading from onset of the stress treatment occurred in *P. miliaceum* while the longest period (48 days) was in *P. sumatrense* (Table 1). Water stress affected the duration to heading in *P. sumatrense*. The stress decreased the leaf area of all millets and root dry weight except for *S. italica*. The ratio of leaf area to root dry weight decreased with water stress in *Setaria* species but increased in *Panicum* species. Water stress decreased plant growth rate (PGR) and mean leaf area (MLA) rather than the net assimilation rate (NAR) in all millets. The PGR of the plant of water stress treatment varied in the order *S. glauca* > *S. italica* > *P. sumatrense* > *P. miliaceum*.

Water potential of leaf was decreased by the water stress treatment in all millets (Table 2). Osmotic potential at full turgor was decreased by the treatment except *S. italica*. Osmotic adjustment (OA) of the leaf was 0.05 MPa in *S. italica*, 0.15 MPa in *S. glauca*, 0.10 MPa in *P. miliaceum* and 0.17 MPa in *P. sumatrense*.

4. Root growth at heading

The root depth of all millets was not changed by the water stress (Fig. 3). The root dry weight density significantly increased at the depth of 40 to 50 cm in *S. italica*, and 40 to 60 cm in *S. glauca* and *P. sumatrense*. Water stress decreased the root dry weight density at the depth of 20 to 30 cm in *S. italica*, 0 to 40 cm in *S. glauca*, 0 to 30 cm in *P. miliaceum* and 0 to 20 cm in *P. sumatrense*.

5. Grain yield and yield components

The drought susceptibility index (DSI) of *Setaria* species was significantly smaller than that of *Panicum* species and *S. italica* was the most drought tolerant of the four millets (Table 3). The grain yield of *S. italica* and *S. glauca* decreased to 90 and 70% of the control (wet treatment) under water stress; and that of *P. miliaceum* and *P. sumatrense* decreased to 36 and 20% (Table 3). The water stress treatment imposed before heading, decreased the grain yield of *P. sumatrense*, *S. glauca* and *S. italica* decreased more severely than that after heading. Water stress reduced the panicle number in all millets except *S. italica* and had no effect on grain weight. Water stress also reduced the grain number per panicle in *S. italica* and *P. miliaceum* but increased it in *S. glauca* and had no effect on that of *P. sumatrense*. Water stress decreased the total dry weight of all millets and had no effects on the harvest index of *S. italica*, *S. glauca* and *P. miliaceum* but decreased it in *P. sumatrense*. There were highly significant correlations between panicle number and grain yield in the millets except for *S. italica* (Fig. 4). There was also a highly significant correlation

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### Table 1. Influence of water stress on growth parameters and osmotic adjustment (OA) in leaves of four millets at the heading stage.

| Crop          | Treatment | Days to heading | PGR (g day<sup>-1</sup>) | NAR (mg m<sup>-2</sup> m<sup>3</sup> day<sup>-1</sup>) | MLA (m<sup>2</sup>) | LA (cm<sup>2</sup> plant<sup>-1</sup>) | RDW (g plant<sup>-1</sup>) | LA/RDW<sup>(2)</sup> |
|---------------|-----------|-----------------|---------------------------|-----------------------------------------------|-------------------|------------------------------|-------------------|-------------------|
| *S. italica*  | W         | 33              | 0.71                      | 23.7                                          | 300               | 1086                         | 4                 | 277               |
|               | D         | 33              | 0.44**                    | 20.4*                                         | 218**             | 701**                        | 3.7<sup>NS</sup>**| 191<sup>**</sup> |
| *S. glauca*   | W         | 39              | 1.31                      | 14                                            | 937               | 4083                         | 5.9               | 692               |
|               | D         | 39              | 0.62**                    | 14.9<sup>NS</sup>                            | 418**             | 1415**                       | 2.9<sup>**</sup>   | 480<sup>**</sup> |
| *P. miliaceum*| W         | 25              | 0.73                      | 21.5                                          | 340               | 1023                         | 3.6               | 309               |
|               | D         | 25              | 0.26**                    | 13.8<sup>**</sup>                            | 185**             | 457**                        | 1.0<sup>**</sup>   | 482<sup>**</sup> |
| *P. sumatrense*| W        | 48              | 0.68                      | 12.9                                          | 524               | 2179                         | 4.7               | 502               |
|               | D         | 55              | 0.34**                    | 10.9<sup>**</sup>                            | 312**             | 1195**                       | 2.2<sup>**</sup>   | 570<sup>**</sup> |

ANOVA

| Crop          | ** | ** | ** | ** | ** | ** | ** |
|---------------|----|----|----|----|----|----|----|
| Treatment     | ** | ** | ** | ** | ** | ** | ** |
| Crop × Treatment | * | ** | ** | ** | ** | ** | ** |

W=Wet treatment, D=Water stress treatment. PGR=Plant growth rate, NAR=Net assimilation rate, LA=leaf area, MLA=Mean leaf area. ** and * indicate that W and D are significantly different at p=1% and 5%, NS indicates not significant. 1) Days to heading from initiation of the treatment.
Table 2. Effects of water stress treatment on leaf water potential ($\Psi_L$), leaf osmotic potential ($\pi_L$) at full turgor, and leaf osmotic adjustment (OA) at 15 days after the onset of stress treatment started.

|        | $\Psi_L$ (MPa) | $\pi_L$ (MPa) | OA (MPa) |
|--------|----------------|---------------|----------|
| S.italica |               |               |          |
| W      | −1.07          | −1.51         | 0.05     |
| D      | −1.22**        | −1.56 NS      |          |
| S.glauca |               |               |          |
| W      | −0.72          | −1.26         | 0.15     |
| D      | −1.15**        | −1.41*        |          |
| P.miliaceum |             |               |          |
| W      | −0.92          | −1.24         | 0.10     |
| D      | −1.32**        | −1.34*        |          |
| P.sumatrense |           |               |          |
| W      | −0.8           | −1.21         | 0.17     |
| D      | −1.47**        | −1.38*        |          |

ANOVA

Crop ** ** ** NS **
Treatment ** ** NS
Interaction ** NS

W=Wet treatment, D=Water stress treatment. ** indicate significant differences at $p=1\%$ and NS indicates not significant.

Fig. 3. Influence of water stress on root growth of four millets at the onset of heading.
W=Wet treatment, D=Water stress treatment. ** and * indicate significant differences at $p=1\%$ and 5\%, respectively. NS indicates not significant.

Table 3. Influence of water stress on grain yield and yield components of four millets.

|        | DSI$^1$ | Days$^2$ | Grain yield (g plant$^{-1}$) | Panicle number (plant$^{-1}$) | Grain number per panicle (panicle$^{-1}$) | Grain weight (mg) | Total dry weight (g plant$^{-1}$) | Harvest index |
|--------|---------|----------|-----------------------------|-----------------------------|--------------------------------------------|-------------------|-----------------------------------|--------------|
| S.italica | WW     | 76       | 17.7 a                      | 1 a                         | 8761 a                                     | 2.2 a             | 55.7 a                            | 0.32 a        |
|         | WD     | 76       | 17.1 a                      | 1 a                         | 8016 a                                     | 2.3 a             | 51.7 a                            | 0.33 a        |
|         | DW     | 76       | 14.3 b                      | 1 a                         | 6479 b                                     | 2.2 a             | 43.8 b                            | 0.31 a        |
|         | DD     | 76       | 14.1 b                      | 1 a                         | 6228 b                                     | 2.3 a             | 42.3 b                            | 0.33 a        |
| S.glauca | WW     | 93       | 18.3 a                      | 87 a                        | 118 b                                      | 2.1 a             | 89.0 a                            | 0.22 a        |
|         | WD     | 95       | 15.5 ab                     | 74 a                        | 113 b                                      | 2.2 a             | 79.7 a                            | 0.19 a        |
|         | DW     | 85       | 13.2 b                      | 41 b                        | 162 a                                      | 2.2 a             | 58.5 b                            | 0.22 a        |
|         | DD     | 89       | 12.8 b                      | 40 b                        | 156 a                                      | 2.2 a             | 67.1 b                            | 0.20 a        |
| P.miliaceum | WW    | 61       | 15.3 a                      | 4 a                         | 1004 a                                     | 4.2 a             | 34.9 a                            | 0.44 a        |
|         | WD     | 61       | 10.0 b                      | 3 ab                        | 1025 a                                     | 4.2 a             | 24.6 b                            | 0.41 a        |
|         | DW     | 61       | 10.7 b                      | 3 a                         | 835 b                                      | 4.2 a             | 28.3 ab                           | 0.38 a        |
|         | DD     | 81       | 5.5 c                       | 1 c                         | 841 b                                      | 4.3 a             | 12.4 c                           | 0.44 a        |
| P.sumatrense | WW  | 95       | 25.7 a                      | 61 a                        | 167 a                                      | 2.8 a             | 96.4 a                            | 0.27 a        |
|         | WD     | 90       | 9.6 b                       | 20 b                        | 186 a                                      | 2.6 a             | 55.8 b                            | 0.17 b        |
|         | DW     | 87       | 5.1 c                       | 13 b                        | 166 a                                      | 2.6 a             | 25.4 c                            | 0.20 b        |
|         | DD     | 87       | 5.0 c                       | 14 b                        | 153 a                                      | 2.6 a             | 24.9 c                            | 0.20 b        |

ANOVA

Crop ** ** ** NS **
Treatment ** ** NS
Crop×Treatment ** ** NS

W=Wet treatment, DD=Water stress treatment from the 25 days after sowing till harvest, WD=Water stress treatment from heading till harvest, DW=Water stress treatment from the 25 days after sowing till heading. $^1$ Drought susceptibility index. $^2$ Days to harvesting from onset of water stress. Means with the same letter are not significantly different according to Tukey-Kramer multiple range test (5\%). ** indicate significant differences at $p=1\%$ and NS indicates not significant.
between grain number per panicle and grain yield in *S. italica*. In all millets, there was a significant correlation between total dry weight and grain yield and in *P. sumatrense*, there was a significant correlation between harvest index and grain yield.

6. Root growth at harvest

The plant root must develop to maintain plant growth under water deficit. The root dry weight (RDW) density under water stress increased significantly at the depth of 40 to 60 cm in *S. italica* and *S. glauca* and 40 to 50 cm in *P. miliaceum* (Fig. 5); it decreased significantly at the depth of 20 to 30 cm in *S. italica*, 10 to 30 cm in *S. glauca*, 0 to 40 cm in *P. miliaceum* and 0 to 30 cm in *P. sumatrense*. In Setaria species, the RDW density at the depth of 0 to 10 cm was maintained but that of Panicum species decreased under water stress. When the water stress was imposed before heading, the RDW density at the depth of 50 to 60 cm increased in *S. italica*, but decreased at depths of 10 to 40 cm in *S. glauca*, 10 to 30 cm in *P. miliaceum* and 0 to 20 cm in *P. sumatrense*. There were highly significant correlations between RDW and total plant dry weight in *S. glauca*, *P. miliaceum* and *P. sumatrense* but not in *S. italica* (Fig. 6).

Discussion

1. Soil water content

In the field, soil water often decreases near the soil surface, but that in deeper soil is available for the plant. In this experiment, water stress condition was created to determine if millet can develop a deeper root system to utilize adequate water in PVC tubes similar to those reported by Liu and Li (2005). Soil water content largely reduced at 10 −40 cm depths but not in deeper soil layers in all millets and no interspecific differences were observed at heading (Fig. 1). Plants in the wet treatment could take up water adequately from all depths in which water content was higher than the lent capillary point (Inoue and Nomura, 1983). Plants under water stress could take up water from soil depths deeper than 20 cm in which water content exceeded the lent capillary point. At harvest, there are interspecific differences at depths of 30 −50 cm (Fig. 2). However, plants under water stress could uptake water from soil depths deeper than 30 cm.

2. Grain yield

Grain yield under water stress may depend on both yield potential (grain yield without water stress) and susceptibility
to water stress (Fisher and Maurer, 1978). The latter was defined as drought susceptibility index (DSI) by Fisher and Maurer (1978) for comparisons between drought levels and experiments. The DSI has been widely used to classify sensitive and resistant genotypes and appeared to be a suitable selection index for distinguishing resistant cultivars because it was inversely correlated with grain yield under stress (Fernandez, 1992; Sio-Se Mardeh et al., 2006). We considered that yield potential did not contribute to the interspecific differences in drought tolerance among the four millets in our experiment due to absence of a significant correlation between grain yield in the wet and dry treatments. The value of DSI in this experiment, as calculated by the yield of the wet and dry treatments, was much lower in *Setaria* species than *Panicum* species (Table 3). This suggests that *Setaria* species were more drought tolerant than *Panicum* species in spite of a closer relationship between *Setaria* and *Panicum* among seven small millets shown by genomic analysis (Lakshmi et al., 2002).

In earlier investigations cereals were grouped into three categories depending on whether the cereals showed (1) a maximum response and/or the only response to soil moisture conditions at specific growth stages, (2) a response to soil moisture at all stages of growth, (3) no response to soil moisture conditions at any stage; most previous reports came into category (1) (Salter et al., 1967). When water stress was imposed before heading, the grain yield of all millets decreased (Table 3). In *Panicum* species, water stress after heading also decreased grain yield. This means that *Panicum* species are also susceptible to water stress after heading. In our experiment, results of statistical analyses of grain yield showed that *Setaria* species fell into category (1) and *Panicum* species fell into category (2), respectively. It was previously reported that drought stress during heading markedly affected the grain yield of common millet (Pullman, 1909). Mahalakshmi et al. (1985, 1993) reported that productivity was limited by water stress during flowering and early grain filling in pearl millet because of decreased availability of photosynthate for translocation. Salter et al. (1967) suggested that millets were most sensitive to soil moisture conditions during the latter part of shoot development, heading and flowering. The growing period of *P. miliaceum* was the shortest among the four millets; thus, we suggest that *P. miliaceum* is as
susceptible to water stress after heading as before heading. For rice, many reports showed that water deficit imposed during the reproductive period reduced grain yield markedly (Cruz and O’Toole, 1984; Lilley and Fukai, 1994; Pantuwan et al., 2002a). However, Liu et al. (2006) showed that water deficit for six days from 7 and 0 days before heading most affected grain yield of rice by decreasing spikelet fertility.

Araus et al. (2008) showed that the number of grains and the individual grain weight were the main yield components in cereals. Our results showed that grain number per panicle and/or panicle number per plant determines grain yield under water stress (Table 3 and Fig. 4). Karyudi and Fletcher (2003) also reported a significant correlation between grain number and grain yield among varieties of *S. italica* under water stress. Our data also showed a significant correlation between total dry weight and grain yield (Fig. 4). This result suggests that maintenance of plant growth was very important when water stress was imposed before heading. Karyudi and Fletcher (2003) showed a significant correlation between root dry weight and total dry weight except *S. italica* (Fig. 6). These results suggest that the balance between transpiration and water uptake was better improved in *Setaria* species than in *Panicum* species, and root development may be an important characteristic for maintaining grain yield by keeping whole plant growth under water stress conditions with the available water in deeper soil layers.

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