Development and Distribution of Root System in Two Grain Sorghum Cultivars Originated from Sudan under Drought Stress

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Abstract: The difference in rooting pattern between two grain sorghum cultivars differing in drought tolerance was investigated under drought stress. The cultivars, Gadambalia (drought-tolerant) and Tabat (drought-susceptible), were grown in bottomless wooden or acrylic root boxes to examine root parameters. Gadambalia consistently exhibited higher dry matter production and leaf water potential than Tabat under drought stress in both root boxes. In the experiment with wooden root boxes, under a drought condition, Gadambalia extracted more water from deep soil layers (1.1-1.5 m), which was estimated from the reduction in soil water content, than Tabat. This was because Gadambalia had a significantly higher root length density in these soil layers. The high root length density was due to enhanced lateral root development in Gadambalia. In the other experiment with acrylic root boxes, though total root length in the upper soil layer (0-0.5 m) was declined by limited irrigation in both cultivars, the reduction in Gadambalia was moderate compared with that in Tabat owing to the maintenance of fine root growth. Unlike Tabat, Gadambalia had an ability to produce the nodal roots from higher internodes even under drought, which resulted in the high nodal root length of Gadambalia. The growth angle of nodal roots was significantly correlated with root diameter, and the nodal roots from the higher internodes had large diameters and penetrated into the soil more vertically. These results indicate that the responses of roots (i.e., branching and/or growth of lateral root, and nodal root emergence from higher internodes) to soil dryness could be associated with the drought tolerance of Gadambalia.

Key words: Branching of root, Drought stress, Drought tolerance, Growth angle of nodal root, Plagiogravitropism, Root diameter, Root length density, Sorghum bicolor (L.) Moench.

Water deficiency is a serious limitation to crop production in large areas of the world. Sorghum [Sorghum bicolor (L.) Moench] is one of the most important crops in arid and semi-arid regions where precipitation is low and highly variable. For sorghum production in these areas, the cultivars are expected to be tolerant to less rainfall and/or limited irrigation. We previously studied dry matter production and shoot water relations in response to water shortage in sorghum cultivars from Sudan (Tsuji et al., 2003) to understand eco-physiological strategies for drought adaptation of the African sorghum. Under soil drying conditions, a local cultivar with drought tolerance (Gadambalia) could maintain higher leaf water potential and photosynthetic rate than a drought-susceptible cultivar (Tabat) improved for irrigated cropping. These differences were likely influenced by the ability to extract water under soil drying condition, i.e., the contribution of root development especially in the deep soil profile. However, little is known about the contribution of root system to drought tolerance in sorghum cultivars.

Root distribution of monocotyledonous plants is the result of growth of different types of roots (Klepper, 1991). Depth and expansion of a root system are primarily determined by the trajectory of the axile roots consisting of seminal and nodal roots. Furthermore, rooting depth of the axile roots is determined by the growth direction and the length of the roots (Araki et al., 2000). In a field experiment, Nakamoto et al. (1991) observed that cultivars of maize and foxtail millet, whose nodal roots orientated downward, exhibited high root length density in deep soil layers. A positive correlation was reported between “Root Depth Index” and growth angle of wheat seminal roots (Oyanagi et al., 1993a), which
are the deepest axile roots in the wheat root system (Morita et al., 1993; Araki and Iijima, 2001). Growth direction of axile roots in cereals is determined by plagiogravitropism (Oyanagi et al., 1993b). The intensity of the plagiogravitropism in axile roots is affected by genotypes (Nakamoto, 1991; Oyanagi et al., 1993a; Araki and Iijima, 2001), environmental factors such as soil temperature (Tardieu and Pellerin, 1991) and soil moisture (Nakamoto, 1993; Oyanagi et al., 1995), and internode positions from which axile roots emerged (Nakamoto et al., 1991; Araki et al., 2000). The growth direction of axile roots, which is determined by genotype-dependent plagiogravitropism and influenced by environmental factors, can be said to determine the shape of the root system.

Root distribution in soil is also determined by the extent of branching and elongation of lateral roots. Lateral roots compose a great proportion of root length in cereal crops (Yamauchi et al., 1987a). In water-limited environments, growth of the lateral roots is important for crops to acquire more water from a dry soil. Water extraction from given depths was closely related to root length density (Fukai and Cooper, 1995). The growth of the lateral roots is highly influenced by soil moisture (Kono et al., 1987; Pardales and Kono, 1990). Bañoc et al. (2000a) indicated that branching ability of the root would be involved in the genetic differences in adaptation to fluctuating soil moisture (dry-submerged cycle) in rice cultivars.

The objective of this study was to investigate the developmental patterns of the root systems of two sorghum cultivars differing in drought tolerance under drought stress. We compared the root distribution profiles in the soil and their modification by soil drying. As the factors determining the developmental pattern of roots, growth angle, length, initiation of nodal roots, and the extent of branching of lateral roots were also examined, and how the developmental responses of roots to soil dryness contribute to drought tolerance of the sorghum cultivars was discussed.

Materials and Methods

Plant materials and experiment site

Two grain-sorghum cultivars, Gadambalia (drought tolerant) and Tabat (drought susceptible), were used in the present study. Seeds of both cultivars were provided by the Agricultural Research Corporation (ARC), Sudan. Gadambalia is a local drought-resistant cultivar, and Tabat is an improved cultivar released for irrigated cultivation (Salih et al., 1999; Tsuji et al., 2003). Root distribution in the soil profile and rooting pattern of the axile and lateral roots were separately examined in a plastic greenhouse, under two contrasting soil water regimes (wet and dry), at the Arid Land Research Center, Tottori University, Japan. The study plot (110 m²) was covered with a transparent plastic vinyl sheet that permitted transmission of more than 95% of incident solar radiation. The soil at the experimental site was sandy with about 98% sand to a depth of about 5.0 m. The two sorghum cultivars and two water regimes were arranged in a completely randomized design with three replications in the following two experiments.

**Experiment 1. Soil water content and root distribution in the soil profile**

The two sorghum cultivars were grown in bottomless wooden root boxes (0.3 m wide, 0.9 m long, 1.8 m high) made of veneer plywood boards (12 mm thick). The root boxes were filled with air-dried sandy soil at a bulk density of 1.5 Mg m⁻³. A compound fertilizer containing major elements (N: P₂O₅: K₂O = 0.13: 0.13: 0.16 g g⁻¹) was applied to the root boxes at the rate of 15 g per root box as top dressing. A compound trace element fertilizer mainly containing MgO: MnO: B₂O₃: = 0.14: 0.003: 0.003 g g⁻¹ and calcium hydroxide were also applied to each root box at rates of 10 g and 25 g, respectively, to supplement the fertility and to adjust the pH (7.6) of the acidic sandy soil. The root boxes were buried in soil by 1.7 m deep to fix them and prevent any increase in soil temperature caused by solar radiation. An observation pit was dug along the sidewall (0.3 m wide, 1.8 m high) of the root box. Ten seeds of sorghum per root box were sown in the central part of the root boxes, and seedlings were thinned to two plants per root box four wk after sowing. Irrigation water was adequately applied until the start of the soil water treatments. Fifty-two days after sowing, the last irrigation of root boxes to 0.35 m was made. Thereafter, daily irrigation was applied only to the wet treatment, while irrigation in the dry treatment was completely withheld until the end of the experiment at 145 d after sowing.

At the flowering stage, 55 d after the start of water treatments, water potentials of flag leaves were measured with a pressure chamber (Model 1000, PMS Instrument Co.) between 1100 and 1400. At early maturity stage, four holes (28 mm diameter) were made at depths of 0.3, 0.7, 1.1 and 1.5 m on the sidewall, facing the observation pit beside the root box, to measure soil water content using a profile probe (Type PR1/4, Delta-T Devices). After access tubes were horizontally inserted into each hole, output values were measured at four positions in the tube. The average output values (V) were converted to volumetric water content (VWC) according to a calibration formula, VWC = 1.4053V-0.1486 (r² = 0.995). After measurement of VWC, larger holes (0.15 m diameter) were perforated at the same position for collecting roots. A metallic cylinder (0.15 m in diameter, 0.38 m length) was inserted into the soil to sample a soil core with roots. After collection of the soil core, a soil column of 20 mm adjacent to the
wall of the root box was cut to remove roots bristling along the wall. The soil samples were carefully washed with showering tap water on a fine meshed sieve (less than 0.5 mm), and the collected roots were preserved in FAA solution (Formaldehyde: Acetic acid: 70% ethanol = 1: 1: 18). The root lengths were measured with a root length scanner (Root Length Scanner, Commonwealth Aircraft Co. Ltd.) to calculate the root length density (RLD). After measurement, the roots were dried in an oven at 80°C for 3 d, and weighed. Specific root length (a ratio of root length to root dry weight, SRL) was calculated from the root length and dry weight. SRL is an indicator of root morphology which shows the thickness of roots and/or extent of branching (Eissenstat, 1992). Dry weights of excised shoots were also weighed after dried in the oven at 80°C.

**Experiment 2. Rooting pattern of nodal and lateral roots**

The sorghum plants were grown in bottomless acrylic root boxes (0.5 m wide, 0.5 m long, 0.5 m high), which were placed on the sandy soil. The root boxes were covered with aluminum foil to prevent the rise in soil temperature caused by solar radiation. Four steel-wire meshes (4×4 mm) fixed by steel frames were vertically inserted at intervals of 0.15 m to observe the growth angle of nodal roots (Fig. 1). The steel meshes separated the rooting zone into three large compartments. Three plants at intervals of 0.1 m were grown between the inner two steel meshes (Fig. 1). The soil and fertilizers applied were the same as those in Experiment 1 with wooden root boxes. We applied 1.0 L of water to each root box from the top every day. The plants were subjected to two different irrigation treatments from 25 d after sowing. The wet treatment received 1.0 L water every day, while the dry treatment received 0.5 L water every two days.

At the late vegetative stage on 25 d after the start of water treatments, water potentials of the highest fully expanded leaves were measured with a pressure chamber (Model 1000, PMS Instrument Co.) between 1000 and 1400. At the flowering stage, 52 d after the start of water treatments, the acrylic boards were removed to observe elongation direction and initiation of the nodal roots. At this time, Tabat in the dry treatment was still in the vegetative stage. The whole root system was carefully washed with running tap water. The position of the plant base (coordinate A) and the crossing position of the nodal roots on the steel meshes (coordinate B) were recorded with three-dimensional coordinates (Fig. 1). One corner of the root box was determined as the origin O (0, 0, 0), and then coordinate A and B were shown by \((a_x, a_y, a_z)\) and \((b_x, b_y, b_z)\), respectively. Growth angle of each nodal root \(\theta\) was calculated by the following formula:

\[
\theta = \tan^{-1}\left[\frac{|a_y-b_y|}{\sqrt{(a_x-b_x)^2+(a_y-b_y)^2+(a_z-b_z)^2}}\right] \left(0^\circ \leq \theta \leq 90^\circ\right)
\]
where, $\theta$ represents the angle between soil surface and the line joining with the base of plant and the root-crossing points on the mesh, so the greater $\theta$ indicates that the nodal roots elongated vertically. Mean growth angle of nodal roots ($\theta_m$) was calculated for each replicated plant.

After the determination of $\theta$, internodes from which nodal roots emerged were traced. The number of nodal roots in each internode was also counted. The diameter of nodal roots at 5 mm from the base was simultaneously measured with a digital vernier caliper. The data above were limited to those from the nodal roots, i.e., no data were obtained for the seminal roots. In the root systems preserved in FAA solution, nodal and lateral roots were classified and their lengths were measured with a scale and a root length scanner (Root Length Scanner, Commonwealth Aircraft Co. Ltd.), respectively. Branching index (BI; Morita and Collins, 1990) was calculated as:

$$BI = \frac{\text{Lateral root length}}{\text{Nodal root length}}$$

BI indicates branching ability of parental roots and/or growth of lateral roots. After drying the roots in the oven at 80°C to obtain the dry weight, SRL was calculated. Dry weights of excised shoots were also weighed after drying in the oven at 80°C.

### Results

1. **Leaf water potential and shoot dry weight**

Water potential of the leaves ($\Psi_L$) was lowered by limited water application more severely in the plants grown in the acrylic root boxes than in those grown in the wooden root-boxes (Table 1). In the wooden root-box experiment, $\Psi_L$ was hardly affected by the limited irrigation in Gadambalia, but significantly dropped to -1.34 MPa in Tabat. In the plants grown in the acrylic root boxes, the $\Psi_L$ of Tabat dropped to below -2.9 MPa by drought, but that of Gadambalia only to -2.2 MPa.

A similar trend was observed in dry matter production (Table 1). In wet conditions, shoot dry weight (SDW) of Tabat was consistently higher than that of Gadambalia in both the wooden and acrylic root-box experiments. However, the SDW of Tabat in

![Image of graph showing VWC and soil depth](image-url)
the dry treatment was significantly low compared with that in the wet treatment. In Gadambalia, the SDW in the dry treatment was hardly affected by the drought in the wooden root-box experiment, and was slightly lower than that in the wet treatment in the acrylic root-box experiment.

2. Water uptake and root distribution in the soil profile
In the wet treatment, the soils in the wooden root boxes with the two cultivars planted on them showed similar volumetric water content (VWC) at each soil depth (Fig. 2). Soil below 0.7 m in the dry treatment was significantly drier in the boxes with Gadambalia than those with Tabat. In the wet treatment, both cultivars exhibited a similar root length density (RLD) across soil depths (Fig. 3). However, the response to drought was markedly different between the cultivars. In the dry treatment, Tabat had a slightly higher RLD than in the wet treatment, though this increase was not significant at the 5% level. Although the RLD of Gadambalia in the wet treatment decreased with increasing depth, that in the dry treatment increased with increasing depth, especially in the deeper (1.1-1.5 m) soil layers (P<0.05). The specific root length (SRL) of Tabat was not affected by drought stress, but that of Gadambalia tended to increase in the dry treatment at 0.7-1.5 m depths, indicating that fine roots in these layers increased in response to the drought stress (Fig. 3).

3. Root length and branching
Detailed analysis on the length of the nodal and lateral roots was carried out for the roots in the
experiment with the acrylic root boxes. In the wet condition, Tabat developed the longest roots and showed the highest branching index (BI) and SRL (Table 2), indicating a higher branching ability than Gadambalia in non-stressed conditions. However, these parameters in Tabat were the lowest in the drought stress treatment. Although the total root length was reduced by drought in both cultivars, the reduction in Gadambalia was only 44.1%, while it was 76.3% in Tabat. Response of nodal and lateral roots to the drought stress also differed with the genotype. By dry treatment, the lengths of nodal and lateral roots were decreased by 38.7 and 44.3%, respectively, in Gadambalia, and 55.5 and 76.9%, respectively, in Tabat. The BI and SRL of Gadambalia were lower than those of Tabat in the wet treatment. These parameters were not affected by the drought stress in Gadambalia, but decreased by the drought stress in Tabat.

4. Growth angle and initiation of nodal roots

The growth angles of nodal roots ($\theta$) determined at the inner and outer meshes were highly correlated with each other ($r_N^{0.895}$ at $P<0.001$). Therefore, only the angles determined at the inner meshes are presented in this paper.

In the whole root system, there were close relationships between $\theta$ and basal diameter of the nodal roots in both cultivars and treatments (Fig. 4). In the wet treatment, there was no genotypic difference in the mean growth angle of nodal roots ($\theta_n$) and the slope of the regression line, i.e., increment of $\theta$ per unit root diameter (Figs. 4, 5). A relatively high $\theta$ was observed in Tabat grown in the wet soil since the plants had roots with large diameters. The slope of the regression lines of $\theta$ against the basal root diameter was not affected by the drought treatment in Gadambalia (Fig. 4). In Tabat, the slope was slightly increased by the drought treatment, but $\theta_n$ was significantly reduced due to the emergence of fewer nodal roots with large diameters (Figs. 4, 5).

Table 3 shows the $\theta$ of the roots emerged from each
The θ is represented by degree of deflection from the soil surface, that is, the bigger the growth angle, the deeper the nodal roots elongate vertically. Dashes mean no emergence of nodal roots. Data are means of three replications ± standard errors.

The θ consistently increased as the rooting internodes were acropetally advanced irrespective of cultivars and treatments. The diameter of the nodal roots at higher internodes was also larger. The θ of roots emerged from the same internode was not different so much between Gadambalia and Tabat irrespective of treatments. Gadambalia produced roots at the 6th and 7th internodes even in the dry treatment as in the wet treatment (Table 4). In contrast, emergence of the roots from the higher internodes (6-8th) was inhibited by dry treatment in Tabat. This explains why the θ of Tabat in the dry treatment was reduced by drought stress.

**Discussion**

Tabat is a cultivar adapted to irrigation, which exhibited higher performance in dry matter production than Gadambalia on a well-irrigated soil (Table 1, Tsuji et al., 2003). In the dry condition, however, a reverse was the case. In Tabat, the SDW and Ψᵣ were significantly reduced by drought stress even in the wooden root-box experiment, in which plants were exposed to moderate drought stress. In Gadambalia, the drought stress hardly influenced the SDW and Ψᵣ in the wooden root-box experiment, but affected them in the acrylic root-box experiment. In addition, depletion of soil water in the root boxes with Gadambalia planted on it was greater than that in the root boxes with Tabat under the water-limited condition (Fig. 2). These results indicated that Gadambalia extracted more water, especially from deep soil, under drought stress. Salih et al. (1999) reported that Gadambalia had higher efficiency in extracting soil water from 0-0.9 m depth than Tabat although Gadambalia had a lower RLD. The present study indicated that Gadambalia extracted more water than Tabat from deeper soil layers (Fig. 2). Gadambalia grown in a root box had an extended RLD in 1.1-1.5 m depth in response to drought, but Tabat did not (Fig. 3). The increased SRL of Gadambalia in the soil deeper than 0.7 m indicated a vigorous development of fine roots under the dry condition (Fig. 3). The increased RLD (Fig. 3) would adaptively enhance water uptake from deeper soil layers, and allow better water relations in the shoot. This character might contribute to the drought tolerance of Gadambalia. Grain sorghum genotypes with drought tolerance from Australia also had a higher RLD in deep soil layers below 1.0 m than susceptible genotypes under drought stress conditions (Wright and Smith, 1983; Ludlow et al., 1990; Santamaría et al., 1990). These reports, together with ours, indicate that adaptive responses of the root development to soil dryness would be an important trait for drought tolerance in grain sorghum.

Lateral roots occupy a great proportion in the total length of the root system (Yamauchi et al., 1987b), and are responsible for a large portion of water extracted by the whole root system (Varney et al., 1993). The responses of roots to drought stress differed between

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**Table 3.** Growth angle of nodal roots (θ) at each internode in two sorghum cultivars under wet and dry treatments.

<table>
<thead>
<tr>
<th>Cultivar</th>
<th>Treatment</th>
<th>Internode</th>
<th>1st</th>
<th>2nd</th>
<th>3rd</th>
<th>4th</th>
<th>5th</th>
<th>6th</th>
<th>7th</th>
<th>8th</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gadambalia</td>
<td>Wet</td>
<td>29.6±2.9</td>
<td>25.2±2.7</td>
<td>34.4±3.5</td>
<td>40.7±0.7</td>
<td>44.0±1.9</td>
<td>50.2±2.3</td>
<td>55.6±2.7</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td></td>
<td>Dry</td>
<td>26.1±2.9</td>
<td>30.4±4.7</td>
<td>29.0±1.2</td>
<td>34.8±3.2</td>
<td>47.0±1.4</td>
<td>50.5±0.7</td>
<td>55.3±0.0</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Tabat</td>
<td>Wet</td>
<td>25.4±2.6</td>
<td>24.3±2.9</td>
<td>29.6±0.3</td>
<td>36.0±1.1</td>
<td>46.5±5.0</td>
<td>58.6±7.0</td>
<td>64.6±0.1</td>
<td>67.7±0.0</td>
<td>–</td>
</tr>
<tr>
<td></td>
<td>Dry</td>
<td>13.0±0.4</td>
<td>22.5±0.5</td>
<td>28.7±2.4</td>
<td>41.6±4.3</td>
<td>49.6±4.7</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
</tbody>
</table>

**Table 4.** Number of nodal roots in total and at each internode of two sorghum cultivars under wet and dry treatments.

<table>
<thead>
<tr>
<th>Cultivar</th>
<th>Treatment</th>
<th>Internode</th>
<th>Number of nodal roots</th>
<th>1st</th>
<th>2nd</th>
<th>3rd</th>
<th>4th</th>
<th>5th</th>
<th>6th</th>
<th>7th</th>
<th>8th</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gadambalia</td>
<td>Wet</td>
<td>3.3±0.4</td>
<td>3.1±0.1</td>
<td>3.1±0.4</td>
<td>3.1±0.1</td>
<td>3.8±0.1</td>
<td>4.0±0.2</td>
<td>2.0±0.7</td>
<td>–</td>
<td>22.7±1.2</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Dry</td>
<td>3.0±0.2</td>
<td>2.4±0.7</td>
<td>3.1±0.2</td>
<td>3.4±0.3</td>
<td>3.8±0.3</td>
<td>3.7±0.4</td>
<td>1.9±1.0</td>
<td>–</td>
<td>21.3±0.2</td>
<td></td>
</tr>
<tr>
<td>Tabat</td>
<td>Wet</td>
<td>2.1±0.3</td>
<td>2.8±0.5</td>
<td>3.6±0.4</td>
<td>3.1±0.1</td>
<td>3.6±0.3</td>
<td>3.4±0.4</td>
<td>1.7±1.1</td>
<td>0.6±0.5</td>
<td>20.8±0.6</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Dry</td>
<td>2.8±0.5</td>
<td>2.9±0.4</td>
<td>3.3±0.4</td>
<td>3.3±0.2</td>
<td>1.0±0.5</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>13.3±0.9</td>
<td></td>
</tr>
</tbody>
</table>

Dashes mean no emergence of nodal roots. Data are means of three replications ± standard errors.
the sorghum cultivars used in this study even in the shallow soil layer. The smaller decrease in Total root length (TRL) under the drought condition in Gadambalia could be attributed to retention of a high BI and SRL on the nodal roots (Table 2). On the contrary, the significant reduction of TRL in the drought-stressed Tabat was attributed to the lower BI and SRL indicating that growth and initiation of the lateral roots were suppressed by drought stress. A drought-tolerant cultivar of upland rice also exhibited an extensive increase in the number of high-order lateral roots produced by first-order lateral roots under fluctuating soil moisture (Bañoc et al., 2000a). Morita et al. (1997) reported that moderate soil drying inhibited the elongation of primary seminal roots in wheat, but accelerated the compensatory branching of lateral roots. These changes in root growth appeared to be adaptive for water acquisition after rewatering (Morita et al., 1997). The crops including sorghum may be required to obtain the ability to generate and elongate the lateral roots under lowered soil water potential to keep BI higher to achieve drought tolerance. Otherwise, water extraction would be depressed by lack of roots resulting in a poor water status in the shoot and low productivity.

The decrease of nodal root length also accounted for the decrease of TRL in the dry treatment (Table 2). The reduction of the nodal root length was moderate in Gadambalia compared with that in Tabat. The inhibition of nodal roots elongation under drought stress has also been observed in sorghum (Pardales and Kono, 1990), sweet potato (Pardales et al., 2000) and rice (Bañoc et al., 2000b). The greater decrease of nodal root length in Tabat would be partly due to the reduction of the number of nodal roots (Table 4). Interestingly, the emergence of nodal roots from higher internodes was suppressed by drought stress in Tabat (Table 4), but was hardly affected in Gadambalia. Initiation and/or differentiation of primordia are sometimes delayed or suppressed by environmental stresses (Nemoto et al., 1995). So far, knowledge on nodal root emergence under soil drying is limited. Although a number of studies have been made on physiological processes involved in the differentiation of lateral roots, for example, the function of growth regulators like hormonal substance, turgor maintenance by osmotic adjustment, and a role of carbon allocation (e.g. Wightman et al., 1980; Westgate and Boyer, 1985; Bañoc et al., 2000a), it is still unknown what determines differentiation of nodal roots in water-limited conditions.

In cereals such as maize, foxtail millet and wheat, growth angle of nodal and seminal roots characterized the root distribution profiles (Nakamoto et al., 1991; Oyanagi et al., 1993a, 1993b; Araki and Iijima, 2001). In the cultivars used in this study, there was a close positive correlation between θ and basal diameter of nodal roots irrespective of cultivars and treatments (Fig. 4). Similar correlations were also observed in other cereals such as lowland and upland rice, maize, and foxtail millet (Yamazaki et al., 1981; Yamazaki and Kaeriyama, 1982; Nakamoto et al., 1991; Araki et al., 2002). In sorghum cultivars, the growth angles of nodal roots are likely to be established by common morpho-physical processes proposed by Abe and Morita (1994) that the growth direction of axile roots may be primarily limited by their diameter. The nodal roots emerging from higher internodes had large diameters and elongated downward irrespective of cultivars and watering treatments (Table 3). Even in the dry treatment, the nodal roots emerged from the 6-7th internodes with the highest θ in Gadambalia, but not in Tabat. Stable emergence of the nodal roots at higher internodes in Gadambalia accounted for the higher θm under drought stress (Fig. 5) and would be partly responsible for the high RLD in deep soil layers. The hydrotropism induced by a water gradient in the medium influenced the growth angle of nodal roots in maize (Leopold and LaFavre, 1989; Nakamoto, 1993) and wheat (Oyanagi et al., 1992). However, this tropism might have little effect on the growth direction of nodal roots in sorghum since the θ of each nodal root was similar between the watering treatments in either cultivar (Table 3).

Water acquisition from deeper soil layers might be determined not only by the root length or root surface area but also by the physiological function of the roots, e.g. hydraulic conductivity (Sperry et al., 2002). Salih et al. (1999) reported that Gadambalia took up more water from deep soil layers despite its lower RLD than Tabat. Furthermore, Gadambalia, unlike Tabat, was not affected by drought stress in cross sectional area and capacity of late metaxylem vessels, which implied high hydraulic conductive potential of the nodal roots of Gadambalia. Functional aspects of roots may also be involved in the high ability to extract water from deep soil layers, and hence, the drought tolerance of Gadambalia. Further research to clarify the function of roots in water extraction by the sorghum cultivars is in progress.

Conclusion

The two sorghum cultivars with contrasting drought tolerance differed in the responses of their root systems to soil drying. The drought tolerance of Gadambalia is derived from deep rooting attribute and an ability to produce thick nodal roots elongating downward from higher internodes, as well as enhanced lateral root branching in deep soil layers under drought condition. In general, thick nodal roots persist longer and produce more and larger branch roots, thereby increasing root length density (Nguyen et al., 1997). Therefore, information on such nodal root emergence would facilitate breeding programs
and management practices for improving drought tolerance in sorghum.

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*In Japanese with English summary