Root system characteristics under different water regimes in three cereal species

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Abstract: Water stress such as drought and waterlogging is considered to be a major limiting factor in crop production. Roots play important roles in crop adaptation to water stress. This study aimed to characterize the vertical root distribution patterns and analyze the root-shoot relationships of different cereal species with different water requirements in response to different soil moisture conditions. Sorghum, maize, and rice were grown under 5% w/w soil moisture content (SMC5), 20% w/w soil moisture content (SMC20) and in waterlogged soil (WL) for 35 days using root box pinboard method. For sorghum and maize, the optimal soil water condition was SMC20 which produced the greatest shoot and root growth, while rice had greatest shoot and root growth under WL. Sorghum significantly increased root to shoot ratio in both water stress conditions, suggesting that sorghum prioritizes carbon partitioning of assimilates towards the roots. Although whole root dry weight and total root length were reduced by water stress, vertical distribution of root traits varied with soil water conditions and promoted root response was observed in specific soil layer. A highly positive relationship between root and shoot traits was observed in rice, suggesting that root and shoot trait responses are coupled with changing soil water conditions. Further studies are needed to confirm root architectural changes focusing on different root component traits as well as other root traits related to root architectural structure.

Keywords: root box, root distribution, soil depth, water stress

Abbreviations: DAS, days after sowing; RDW, root dry weight; RL, root length; RSA, root system architecture; SDW, shoot dry weight; SMC, soil moisture content; SRL, specific root length; WU, water use

Introduction

Plant growth and productivity are limited by various abiotic stresses. Water stress such as drought and waterlogging are considered to be a major limiting factor in crop production. In recent years, the impact of climate change on the availability of water resources for crop production has become more serious, and the development of crops with enhanced adaptation to such water stress is required (Pegoraro et al. 2019).

Roots, as the interface between the plant and the soil, play a vital role in crop adaptation to water stress (Suralta et al. 2018). Root system architecture (RSA) is an important factor determining how efficiently plants can access below-ground resources. In general, deep rooting accesses water from the deeper soil layers and contributes to a high yield under drought stress conditions in rice (Uga et al. 2013), maize (Ali et al. 2016), wheat (Fang et al. 2017), and sorghum (Tsuji et al. 2005; Mace et al. 2012). On the other hand, a shallow root system which retains a relatively high oxygen concentration...
at the soil surface, has a higher waterlogging tolerance than the deeper root systems of wheat (Oyanagi et al. 2004, Haque et al. 2012) and barley (Shiono et al. 2019). Thus, plants change RSA in response to soil water conditions and understanding root characteristics is necessary for improving plant adaptations to water stress.

However, isolation of roots from soil causes impairment and disturbance to its structure. To evaluate the RSA, the root box pin-board method (Kono et al. 1987, Kano-Nakata et al. 2012) was adapted in this study. This method was applied to the three species of cereals: sorghum (Sorghum bicolor L. Moench.), maize (Zea mays L.), and rice (Oryza sativa L.), which are important staple food/feed crops and have different water requirements. Sorghum and maize are cultivated in upland conditions, but maize requires more water than sorghum (Hasan et al. 2017). While drought tolerance in sorghum and maize have been relatively well studied (Zegada-Lizarazu et al. 2012, Schittenhelm and Schroetter. 2014), the information on the root response to waterlogged soils in these crops is sparse, particularly in sorghum (Pardales et al. 1991). Singh et al. (2010) showed that the root systems of maize and sorghum differed in morphology and architectural development; sorghum produces a single seminal root and coleoptile node roots in the 4–5 leaf stage, whereas maize produces 3–7 seminal roots and coleoptile node roots at the second leaf stage. Rice grows in a wide range of ecosystems (Khush et al. 1997), and a lowland rice cultivar that has been grown under waterlogging was used.

Because water requirements of crop depend on species, both optimal and stressed soil water conditions were set. It was hypothesized that optimum shoot and root growth for sorghum and maize would be in between drought and waterlogging, while those of rice would increase as soil water increased. The objectives of this study are to characterize the root architectural changes focusing on vertical distribution patterns in response to different soil water conditions (drought to waterlogging) of different cereal species (sorghum, maize, and rice), and to analyze the root-shoot relationships under changing soil water condition.

**Materials and Methods**

**Plant materials and growth conditions**

Sorghum ‘GS401’ (grain type forage sorghum, Snow Brand Seed Co., Ltd., Japan), maize ‘SH3815’ (forage maize, Snow Brand Seed Co., Ltd., Japan), and rice ‘Nipponbare’ (japonica rice cultivar) were used in this study. Seeds were soaked in water with 5% sodium hypochlorite for 10 min and rinsed with tap water. Then seeds were kept in an incubator at 30 °C for 48 hours prior to sowing.

The experiment was conducted in a greenhouse at Nagoya University, Nagoya, Japan (136°56′6″ E, 35°9′5″ N). The maximum and minimum temperatures during the experimental period (as recorded by the Japan Meteorological Agency for Nagoya, 136°57′9″ E, 35°10′0″ N), was 36.7°C and 18.0°C, respectively. During the daytime, the actual temperature inside the greenhouse was projected to be 5 to 10°C higher than the city atmosphere from the data taken in October (data not shown).

The root box pin-board method (Kono et al. 1987, Kano-Nakata et al. 2012) was used for crop management. For the preparation of the root box, silicon sealant was applied around the wall of polyvinyl chloride (PVC) root box (L × W × H = 25 cm × 2 cm × 40 cm) and root box was bound with six clips to prevent water leakage. On 20th August 2018, one pre-germinated seed of each crop was sown in a root box filled with 2.5 kg of air-dried, sandy loam soil pre-mixed with 0.5 g of chemical fertilizer per box (N:P:K = 14:14:14, Itochu Co. Tokyo, Japan). The seedlings were first grown under 10% w/w soil moisture content (SMC) for 7 d. On the eighth day after sowing (DAS), plants were grown under 5% w/w of SMC (SMC5), 20% w/w of SMC (SMC20), and continuously waterlogged soil (WL) until harvesting. SMC5 for drought treatment was kept at the level of 15–16% of field capacity (FC). SMC20, which is 61–63% of FC was considered as optimal water condition for sorghum and maize but mild drought for rice. In WL, the water level was maintained 1–3 cm above the soil surface in the root box until the end of the experiment. Each root box was weighed daily or every other day, and water was added to maintain the target SMC. The evapotranspiration was calculated by measuring weight loss of the root boxes. The plant transpiration was estimated as the difference in water loss between root boxes, with and without plants (blank), and water use was calculated as the accumulated plant transpiration from 8 DAS up to 35 DAS.

**Sampling and root analysis**

Shoots were collected at 35 DAS and oven-dried at 70°C for 2 d to record the dry weight. Root boxes were soaked in the water pool overnight after shoot sampling. Roots were collected using a pin-board, following the method of Kano-Nakata et al. (2012). Prior to the taking of digitized photographs of the whole root system, root samples were sandwiched
with plastic sheets and stained with 0.25% Coomassie Brilliant Blue R aqueous solution for 48 hours. Then the stained root samples were rinsed with tap water and placed in a light box. Root samples were subsequently preserved in AA solution (acetic acid: 70% ethanol = 5:95).

Preserved root samples were cut at 0–12 cm (upper layer), 12–24 cm (middle layer) and >24 cm (lower layer) from the soil surface to evaluate the root distribution patterns. Roots from each soil layer were scanned at adequate resolution (600 dpi) using an EPSON scanner (EPSON Expression 11000XL, EPSON). The scanned images were analyzed for root length using WinRHIZO 2016 software (Regent Instrument Inc., Saint-Foy, Canada). Root samples were oven-dried at 70ºC for 2 d and dry weight was measured. The root to shoot ratio was determined as the ratio of the root dry weight to the shoot dry weight. Specific root length was calculated as the root length divided by the root dry weight.

### Statistical analysis

A randomized complete block design was applied with four replications for each treatment. Multiple comparisons were performed using a two-way analysis of variance (ANOVA) followed by Tukey’s honestly significant difference (HSD) test using R software (v. 3.3.1).

The correlation across the traits was presented as Pearson’s correlation coefficients with the pairwise deletion method. Then color map was performed to visualize the correlations using JMP 15 (SAS Institute Inc., Cary, NC, USA).

### Results

The effect of species (S), water treatment (W) and the S × W interaction were significant in almost all of the traits, except on the effect of S on total root length (TRL) which was not significant (Table 1). Sorghum and maize showed the greatest shoot dry weight (SDW), TRL, and root dry weight (RDW) in SMC20, and significant reductions in shoot and root growth were observed in SMC5 and WL for both species. However, the reduction in dry matter based on SMC20 was larger in WL for sorghum (81.9% for SDW, 67.2% for RDW) and in SMC5 for maize (93.4% for SDW, 92.9% for RDW), respectively. The response of TRL differed from RDW; decreased TRL was larger in SMC5 than in WL for both species. Shoot and root growth of rice was significantly higher in WL, followed by SMC20 and SMC5. Root to shoot ratio (R/S ratio) of sorghum increased to approximately 110% and 80% in SMC5 and WL compared to SMC20, respectively. However, there was no significant difference in R/S ratio among the water treatments for maize and rice.

By the observation of intact entire root system, RSA changed with different water treatment for all the species (Fig. 1). Sorghum and maize showed the greatest root system development with deep roots under SMC20 in the three soil moisture conditions. In addition, sorghum had greater root growth than maize and rice in SMC5. On the other hand, root system development of rice was apparently inhibited when soil moisture decreased.

### Table 1. Mean value of shoot dry weight (SDW), root dry weight (RDW), root to shoot ratio (R/S ratio), and total root length (TRL) per plant grown under three different water treatments for sorghum, maize and rice

| Species | Water treatment | SDW (mg) | RDW (mg) | R/S ratio (%) | TRL (cm) |
|---------|----------------|----------|----------|---------------|----------|
| Sorghum | SMC5           | 612.5 ± 134.5 b | 224.0 ± 42.5 b | 37.7 ± 2.7 a | 1773.5 ± 450.4 c |
|         | SMC20          | 3023.2 ± 91.8 a | 509.9 ± 16.0 a | 16.9 ± 0.5 b | 6201.6 ± 520.1 a |
|         | WL             | 547.2 ± 23.3 b | 167.0 ± 12.6 b | 30.6 ± 2.4 a | 3761.8 ± 170.3 b |
| Maize   | SMC5           | 410.3 ± 162.9 b | 75.8 ± 24.4 b | 21.7 ± 3.8 a | 776.3 ± 243.0 b |
|         | SMC20          | 6180.4 ± 1477.3 a | 1073.6 ± 324.5 a | 16.0 ± 1.9 a | 7559.9 ± 1831.9 a |
|         | WL             | 1105.1 ± 113.5 b | 213.3 ± 9.9 b | 19.7 ± 1.4 a | 3103.4 ± 215.7 b |
| Rice    | SMC5           | 109.3 ± 16.2 c | 9.2 ± 1.4 b | 8.7 ± 1.3 b | 247.6 ± 33.8 c |
|         | SMC20          | 424.3 ± 13.0 b | 45.4 ± 7.0 b | 10.6 ± 1.3 ab | 2522.4 ± 286.3 b |
|         | WL             | 657.2 ± 95.9 a | 93.9 ± 15.3 a | 14.2 ± 0.3 a | 5681.0 ± 698.3 a |

ANOVA

|       | Species (S) | *** | *** | *** | ns |
|-------|-------------|-----|-----|-----|----|
|       | Water treatments (W) | *** | *** | *** | *** |
|       | S×W         | *** | *** | *** | *** |

Values represent means ± SE (n = 4). Values labeled using different letters differ significantly across treatments within each species (P < 0.05, Tukey’s HSD test). *** and ns indicate significant at P < 0.001 and no significance, respectively. SMC5, 5% w/w of soil moisture content; SMC20, 20% w/w of soil moisture content; WL, waterlogged soil.
specific root length (SRL) at different soil depths varied: 0–12 cm (upper layer), 12–24 cm (middle layer) and >24 cm (lower layer) from the soil surface as a vertical profile of the root system (Fig. 2). RL and RDW varied with soil depth of sorghum and were highest in the upper soil layer, followed by the middle and lower layers in SMC5 and WL. A greater root distribution in sorghum was observed within the lower soil layer in SMC20, over SMC5 and WL. The vertical profile of RL and RDW in maize was similar to that of sorghum, but RDW of maize was larger than that of sorghum in SMC20. Rice differed in the distribution of RL and RDW from the other two species; roots were distributed

Fig. 1. Root system profiles of sorghum (a, d, and g), maize (b, e, and h), and rice (c, f, and i) grown under 5% w/w of soil moisture content (SMC5; a-c), 20% w/w of soil moisture content (SMC20; d-f) and waterlogged soil (WL; g-i) at 35 days after sowing. Root systems were sampled using the root box pin-board method (Kano-Nakata et al. 2012). Plant with average growth size was selected for photo documentation.
mostly in the upper soil layer, followed by the middle and lower layers under any soil water condition, but the difference was not observed in RL between the upper and middle soil layers. Sorghum and maize had a much smaller SRL than that of rice, which increased the SRL in WL above 12 cm of soil depth. In contrast, rice showed a proliferation of SRL below 12 cm in WL soils as well as in SMC20.

A color map representation was used to show the Pearson’s correlation values among the traits (Fig. 3). High positive correlation values were found in rice followed by maize and sorghum ($P < 0.05$). RDW and TRL showed significantly positive correlation with SDW in all species. In addition, WU were correlated to SDW in maize and rice but not in sorghum. Among the 11 root traits examined in this study, 10 traits and 8 traits were significantly positively correlated to WU in rice and maize respectively, but only 2 traits were significantly correlated to WU in sorghum. R/S ratio was negatively correlated with SDW in sorghum and maize, however, it was significant only in sorghum. In contrast, there was a significant positive correlation between R/S ratio and SDW in rice.

**Discussion**

The most optimal soil water condition for sorghum and maize was at SMC20 to maximize both shoot and root growth, while rice exhibited the greatest shoot and root growth in WL soil. Sorghum showed smaller biomass reduction in root growth compared to maize under water stress conditions (SMC5 and WL) (Table 1). Schittenhelm and Schroeter (2014) reported that increasing drought stress reduced the aboveground and root dry weight of maize more severely than that of sorghum. High drought adaption of sorghum over maize could be because
Fig. 3. The traits correlation color map across water treatments for sorghum, maize and rice. The color plotted in the heat map grid indicates the strength of a particular correlation between two traits. Significant correlations (-0.58 ≤ r ≥ 0.58, n = 12) are colored in red for positive and or blue for negative and gray for no correlation, as represented in the color key. Self-self correlations are described as the cell with diagonal line. Similar variables were grouped into the same cluster. SDW, shoot dry weight; RDW, root dry weight; RL, root length; SRL, specific root length; WU, water use.
sorghum penetrates the soil faster, more intensively, and capture the water from deep soil layer (Tsuji et al. 2005, Schittenhelm and Schroetter 2014). Our study results agreed with this by greater RDW and RL at >24 cm in sorghum than in maize, but we could not confirm whether the deep roots contributed to water absorption from deep soil layer in this study. For maize, effect of water stress tended to be greater in SMC5 than in WL but there is no significant difference in shoot and root growth (Table 1). However, in a previous study which evaluated maize root response to both shortage and excess of soil water for two weeks, the decrease in root number and length in plants grown under waterlogging was greater than under drought (Grzesiak et al. 2014). Our study used sandy loam soil where mechanical impedance is small for root growth while Grzesiak et al. (2014) used the wax layer/high bulk density soil as compacted soil which restricted root growth. In contrast, rice response was similar to our previous studies using root box, wherein it is well studied that SMC20 with sandy loam soil considers to be mild drought condition (reviewed by Suralta et al. 2018). Thus, the root response is likely to differ depending on the environmental conditions, methodologies, and the different characteristics of each experimental setup (Wade et al. 2015).

Sorghum, in the current study, significantly increased the R/S ratio in both stress conditions (SMC5 and WL) (Table 1). The increase in R/S ratio observed in sorghum was a result of a greater reduction in SDW rather than an increase in RDW and then resulted in negative correlation between R/S ration and SDW (Table 1 and Fig. 3). Xu et al. (2015) found that the greater proportion of dry matter and soluble sugar to roots is responsible for the increase in R/S under drought stress in rice. Our result also suggests that sorghum prioritizes carbon partitioning of assimilates towards the roots under water stress conditions. Among root types, lateral roots mainly constitute the whole root system, and there are two types of lateral roots; L-type and S-type (Yamauchi et al. 1996). For lateral roots, especially L-type lateral roots, which is generally thick in diameter and long with the ability to branch into high order (Yamauchi et al. 1996), were regulated through the involvement of less stem starch accumulation via increased root sugars; glucose and sucrose in rice (Lucob-Agustin et al. 2020). More works are needed to confirm the root characteristics by different type of roots.

Although whole root dry weight and total root length was significantly reduced by water stress, vertical distribution of root varied with soil water conditions and promoted root response was observed in specific soil layer (Table 1 and Fig. 2). For example, sorghum and maize increased/maintained its RL at 0–12 cm upper soil layer in WL where the RDW likely decreased as compared to SMC20, resulting in increased SRL in upper soil layer and then higher TRL in WL than in SMC20 (Table 1 and Fig. 2). Plants distributed its roots to the deep soil layer under drought and had more roots in shallow soil in WL soils, possibly as an adaptive mechanism to facilitate water and nutrient uptake under drought (Tsuji et al. 2005; Uga et al. 2013; Fang et al. 2017) and also oxygen supply with excess water (Oyanagi et al. 2004, Haque et al. 2012, Shiono et al. 2019). Such vertical distributions of root traits may be associated with root anatomical changes along root axis (Kadam et al. 2015).

It has been reported that root trait responses to water stress are more heterogeneous than shoot trait responses (Kano-Nakata et al. 2019, Lozano et al. 2020). From the results of the correlation heatmap, different interactions among traits were observed clearly between rice, sorghum and maize indicating that root-shoot relationships are different among these species (Fig. 3). Lozano et al (2020) also reported that root trait responses were variable and differed among plant species. A highly positive relationship between root and shoot traits was observed in rice (Fig. 3), suggesting that root and shoot responses are coupled with changing soil water conditions. In addition, high number of root traits showed significantly positive correlation to WU indicating that roots contributed functionally to the plant water uptake.

Although the current study demonstrated root distribution using the root box pin-board method, the RSA is mainly determined by root growth angle and root length (Abe and Morita 1994, Araki et al. 2002). Together with other phenotypic root traits (including root growth angle and root elongation), further studies are needed to investigate root characteristics under different soil water conditions. A greater understanding of the change in RSA in major crops will facilitate the establishment of ideotype of root system for more efficient use of resources and thus contribute to the improvement for sustainable production and management in the agroecosystem.

In conclusion, we have demonstrated that in sorghum and maize, the optimal soil water condition was SMC20 which produced the greatest shoot and root growth, while rice had greatest shoot and root growth under WL. Increased R/S ratio in sorghum under water stress conditions was observed suggesting that sorghum prioritizes carbon partitioning of assimilates towards the roots. Regarding the root shoot interaction, root and shoot
trait responses are coupled with changing soil water conditions in rice which mostly exhibited high positive relationship between root and shoot traits.

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