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Plasticity in root system architecture of rice genotypes exhibited under different soil water distributions in soil profile

Mana Kano-Nakata^{a,b}, Tomomichi Nakamura^a, Shiro Mitsuya^a and Akira Yamauchi^a

^aGraduate School of Bioagricultural Sciences, Nagoya University, Nagoya, Japan; ^bInstitute for Advanced Research, Nagoya University, Nagoya, Japan

ABSTRACT

The root system architecture (RSA) has been reported to be determined by several root traits such as branching, elongation, and growth angle. This study aimed to evaluate the genotypic variation of plasticity in RSA in response to different soil water distributions in a soil profile. IR64 (shallow root system), YTH183 (adapted to rainfed lowland conditions due to high plasticity in root elongation), and Kinandang Patong (KP – deep root system) were grown in PVC root boxes for 34 days under continuously waterlogged conditions and with soil moisture fluctuations (SMF). For SMF, watering was done from the top of the root box (TI-SMF) or from the bottom of the root box (BI-SMF). A water gradient was observed more clearly in BI-SMF than in TI-SMF, while mean soil moisture content in the root box was kept at around 23% (v/v) after first irrigation in both SMF treatments. RSA changed drastically with SMF in all cultivars, all of which tended to shift root distribution to deeper soil layers in response to SMF. Such changes in RSA resulted from different degrees of plasticity exhibited mainly in nodal root and L-type lateral root development. YTH183 showed a greater ability to change its root growth angle and thus its root distribution in the deeper soil layer compared to IR64 and KP under SMF, indicating that YTH183 could help to improve RSA in cultivars adapted to SMF.

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KEYWORDS

Rainfed; rice; root growth angle; soil moisture fluctuation

Introduction


Soil water is rarely constant but changeable as a result of rainfall, watering and water uptake by plants. Understanding root development in response to soil moisture heterogeneity is important for maintaining plant growth under water-stressed conditions, which is a major limiting factor for plant growth. Root system architecture (RSA) is spatially affected by soil water distribution. The position of water supply in soil profile may also affect the soil water distribution, and thus RSA and plant growth (Kono et al., 1987a). Generally, water is supplied from the soil surface by rainfall and irrigation. In the case of a rice ecosystem that is distributed on a toposequence such as a slope hill, water is supplied from the subsoil through groundwater as well as from the topsoil (Boling et al., 2008).

In this aspect, we conducted studies on the effects of soil moisture on rice plant growth using experimental sloping beds, which, as an artificial toposequence with a ground water table, successfully mimicked the soil moisture gradient along the toposequence (Kameoka, Suralta, Mitsuya & Yamauchi, 2015; Menge et al., 2016). Using this experimental system, plasticity in lateral root

development, in addition to the vertical root distribution along the soil profile has been observed to improve the shoot dry matter production under progressive drought conditions (Kameoka et al., 2015; Menge et al., 2016). However, in these studies, it was difficult to exactly evaluate the nature of RSA because this method does not allow to keep the RSA of sampled root systems as they are in soil. In this aspect, we have been using the root box-pinboard method (Kano-Nakata, Suralta, Niones & Yamauchi, 2012; Kono, Yamauchi, Nonoyama, Tatsumi & Kawamura, 1987b) to evaluate the exact nature of RSA. The RSA, i.e. the spatial distribution of roots in a soil profile, is mainly determined by root growth angle and root length (Abe & Morita, 1994; Araki, Morita, Tatsumi & Iijima, 2002). Therefore, in this study, we focused on root growth angle, root elongation, and root branching for evaluation of RSA.

To evaluate the RSA, we focused on three rice cultivars; IR64 (*indica*), YTH183, and Kinandang Patong (KP) (*tropical japonica*), which have different RSAs. IR64 is a lowland cultivar and has a shallow root system, whereas KP is an upland cultivar that is reported to be deep-rooting because it has narrow rooting angles (Uga et al., 2018; Uga, Kitomi, Ishikawa & Yano, 2015; Uga

CONTACT Mana Kano-Nakata  mnakata@agr.nagoya-u.ac.jp

 Supplemental data for this article can be accessed [here](#).

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et al., 2013). YTH183 is an introgression line developed by backcrossing a New Plant Type (NPT) accession with IR64 as the recurrent parent (Fujita et al., 2009); it showed high plasticity in root elongation in response to re-watering after drought (Kano-Nakata et al., 2013), and also deep rooting under aerobic conditions (Kato et al., 2011).

On the basis of these findings, we hypothesized that different soil moisture gradients in a soil profile may modify the RSA as a result of varied expression of plasticity of nodal and lateral roots, even the amount of water supplied was the same. Then, we experimentally created different moisture gradients by watering from the top and from the bottom of the root box. We additionally hypothesized that IR64 and KP may always show shallow and deep root systems, respectively, i.e. the root growth angle may not be affected by the distribution of water, while YTH183 may show the highest plasticity of RSA in response to the soil moisture gradient, and then maintain its shoot growth.

The objectives of this study were therefore to evaluate the genotypic variation in the plasticity of RSA in response to the distribution of soil water, and to quantify their contribution to shoot growth.

Materials and methods

Plant materials

Three cultivars of rice, IR64, YTH183, and Kinandang Patong (KP) were used in this study. Seeds were soaked in water with the fungicide benomyl (Benlate; Sumitomo Chemical Garden Products Inc., Tokyo, Japan, 0.5% w/v) and germinated at 28°C for 3 days.

Experimental design and treatments

The experiment was conducted in a vinyl house at Nagoya University, Nagoya, Japan (136°56'6"E, 35°9'5" N) using a root box system (Kano-Nakata et al., 2012; Kono et al., 1987b). Three pre-germinated seeds of each cultivar were sown in a PVC root box (L × W × H = 25 cm × 2 cm × 40 cm) filled with 2.5 kg of air-dried sandy loam soil (Figure S1a) on 18 September 2015. The seedlings were first grown under 20% (w/w) soil moisture contents (SMC) and then the seedlings were thinned to one seedling per box at 5 days after sowing (DAS). From 7 DAS, the plants were exposed to two soil moisture conditions: continuously waterlogged (CWL, control) and soil moisture fluctuations (SMF). In CWL, the root box was submerged in the water until end of the experiment. In SMF, water deficit was applied by withholding irrigation

until 20 DAS. At 20 and 27 DAS, 150 mL of water was supplied from the top of the soil surface (top irrigation; TI-SMF) or from the bottom of the root box (bottom irrigation; BI-SMF) for each root box. For BI-SMF, watering was done by using a syringe inserted at the bottom of the root box (Figure S1b). Thus, three water treatments were set up in this study.

During the experimental period, the temperature was recorded using a thermometer (T&D Thermo Recorder TR-72Ui, T&D Corporation, Japan). The maximum and minimum temperatures were 38.1 and 15.2°C, respectively.

Measurement

SMC were measured using Time Domain Reflectometry (TDR; Tektronix Inc., Wilsonville, OR, USA) based on the previous works (Kameoka et al., 2015; Nguyen et al., 2018; Suralta et al., 2018a). Two stainless steel rods (15 cm in length and 3 cm apart) were equally inserted into the side wall of the root box at 6.5 cm (upper), 19.5 cm (middle) and 32.5 cm (lower) from the top of the soil surface, allowing 3 cm protruding above the soil surface (Figure S1a). TDR probes were attached to these nails to obtain SMC readings at 8, 14, 20, 23, 25, 27, 28, 31, and 33 DAS.

At 34 DAS, plants were harvested. Before harvesting, plant height and number of tillers were recorded. Shoot samples were oven-dried at 70°C for three days and the dry weight was measured. Roots were collected using a pinboard following the methods of Kano-Nakata et al. (2012). Root samples were washed well and stained in 0.25% Coomassie Brilliant Blue R aqueous solution for 48 hrs. The stained root samples were rinsed with tap water and placed in a light box to be photographed to get the digitized images. Regarding to root growth angle, root corn angle was measured with the method of Bettembourg et al. (2017) with slight modifications. The angle of the root cone, which was made by two most external left and right nodal roots, to the vertical axis (soil surface) was measured in degrees using angle tool in ImageJ (Version 1.42q, NIH, USA) on digitized images of the root system.

Root samples were cut at 0–13 cm (upper layer), 13–26 cm (middle layer), and 26–39 cm (lower layer) from the soil surface and preserved in 50% ethanol solution for further measurements. The number of nodal roots of each plant was manually counted. Roots from each soil layer were scanned at 600 dpi (EPSON Expression 10000XL, Epson, Long Beach, CA, USA) and scanned images were analyzed using WinRhizo v. 2007d (Régent Instruments, Québec, QC, Canada) with the pixel threshold value at 175. Root were classified according to their diameter: <0.1 mm, 0.1–0.2 mm and >0.2 mm. Roots with a diameter less than 0.2 mm were considered as lateral

roots (Sandhu et al., 2016) and the total nodal root length (NRL) was estimated as the difference between the total root length (TRL) and the total lateral root length (LRL). For LRL, diameter classes of less <0.1 mm and 0.1–0.2 mm were considered as S-type (short, non-branching) and L-type (thick, long and branching), respectively (Yamauchi, Kono & Tatsumi, 1987).

Statistical analysis

The experiment was arranged in a split-plot design using a Randomized Complete Block Design with four replications. Two-way analysis of variance (ANOVA) was conducted to determine the individual and interaction effects of cultivar (IR64, YTH183, KP) and water treatment (CWL, TI-SMF, BI-SMF). Tukey's honest significant difference (HSD) test was conducted to compare the mean value at the 5% probability level in R v. 3.2.2 (<https://cran.r-project.org>). The coefficient of variation (CV) was calculated as follows: $100 \times (\text{standard deviation}/\text{mean}) (\%)$.

Results

Soil moisture distribution

Under the SMF conditions, during withholding irrigation (from 8 to 14 DAS), SMC in the upper soil layer was depleted probably due to water absorption from roots. Mean SMC in the root box were kept at around 23% (v/v) after 20 DAS (first irrigation) in both SMF treatments. A water gradient was observed more clearly in BI-SMF than in TI-SMF (Figure 1). SMC was high in the lower soil layer and low in the upper soil layer in BI-SMF conditions. Although the lower soil layer displayed the highest SMC, SMC in the middle and upper soil layer were similar under TI-SMF conditions.

Shoot growth

Table 1 shows shoot growth at harvest for the three cultivars grown under different water treatment conditions. The effects of cultivar and treatment were

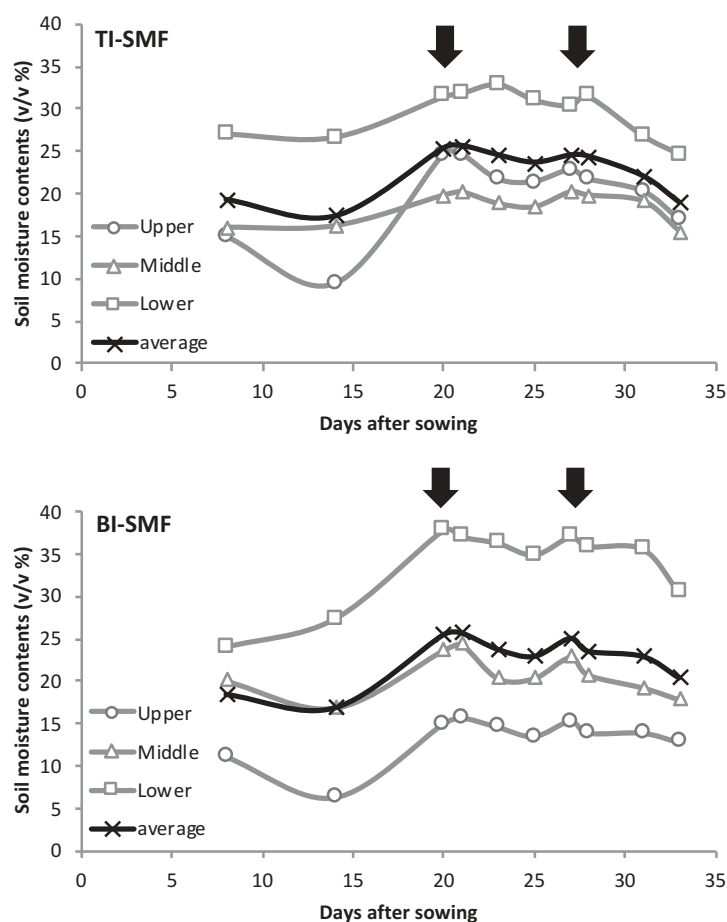


Figure 1. Soil moisture dynamics at levels of 6.5 cm (upper), 19.5 cm (middle), and 32.5 cm (lower) from the top of the root box and its average. Values shown are means of readings from two root boxes. Arrowheads indicate the times of watering. (Top) TI-SMF; (bottom) BI-SMF.

Table 1. Shoot traits of IR64, YTH183, and KP grown under CWL, TI-SMF, and BI-SMF conditions at 34 DAS. Values are means of four replicates.

| Cultivar | Treatment | Plant height (cm) | | | Tillers | | | Shoot dry weight (g) | | |
|---------------|-----------|-------------------|----|---------|---------|----|---------|----------------------|----|---------|
| IR64 | CWL | 42.6 | a | SMF/CWL | 4.0 | b | SMF/CWL | 0.53 | a | SMF/CWL |
| | TI-SMF | 37.4 | b | 0.9 | 6.5 | a | 1.6 | 0.65 | a | 1.2 |
| | BI-SMF | 32.6 | c | 0.8 | 4.0 | b | 1.0 | 0.59 | a | 1.1 |
| | Mean | 37.5 | B | | 4.8 | B | | 0.59 | B | |
| | CV | 12.2 | | | 32.5 | | | 13.2 | | |
| YTH183 | CWL | 46.1 | a | SMF/CWL | 4.8 | b | SMF/CWL | 0.76 | a | SMF/CWL |
| | TI-SMF | 41.5 | b | 0.9 | 7.0 | a | 1.5 | 0.93 | a | 1.2 |
| | BI-SMF | 35.5 | c | 0.8 | 6.5 | a | 1.4 | 0.88 | a | 1.2 |
| | Mean | 41.1 | B | | 6.1 | A | | 0.86 | A | |
| | CV | 11.1 | | | 18.3 | | | 12.7 | | |
| KP | CWL | 58.2 | a | SMF/CWL | 2.5 | a | SMF/CWL | 0.68 | a | SMF/CWL |
| | TI-SMF | 54.0 | a | 0.9 | 3.0 | a | 1.2 | 0.83 | a | 1.2 |
| | BI-SMF | 46.0 | b | 0.8 | 3.0 | a | 1.2 | 0.71 | a | 1.0 |
| | Mean | 52.8 | A | | 2.8 | C | | 0.74 | B | |
| | CV | 11.0 | | | 13.2 | | | 13.3 | | |
| ANOVA | | | | | | | | | | |
| Cultivar (C) | | | ** | | | ** | | | ** | |
| Treatment (T) | | | ** | | | ** | | | ** | |
| CxT | | | ns | | | * | | | ns | |

Values labeled using different letters differ significantly across treatments within each variety ($p < 0.05$, Tukey's HSD test). *, ** and ns indicate significance at $p < 0.05$, $p < 0.01$, and no significance, respectively.

significant for all traits and the interaction of cultivar and treatment was significant for tiller production. Shoot dry weight (SDW) is highest in TI-SMF, followed by BI-SMF and CWL for all three cultivars. Although plant height and tiller production were influenced by treatments, there was no significant difference in SDW across the treatments for all the cultivars. The mean SDW was greatest in YTH183, followed by KP and IR64.

Root system architecture (RSA)

RSA changed drastically with SMF for all the cultivars as shown by the root system profile (Figure 2). The root distribution shifted to the deeper soil layer and lateral root development was more observed in SMF than in CWL.

To evaluate the RSA, different component root traits were measured at harvest for the three cultivars grown under different water treatments (Table 2). Overall, the effect of cultivar was significant for all the traits, and significant effect of treatment was observed except for LRL and S-type LRL. The interaction of cultivar and treatment was significant for nodal root production, root cone angle, NRL and L-type LRL.

Within each cultivar, nodal root production was not affected by TI-SMF, while it was significantly reduced by BI-SMF for the three cultivars. Similarly, root cone angle was not affected by TI-SMF, while it was significantly reduced by BI-SMF (i.e. root growth became more vertical) for IR64 and YTH183. KP tended to reduce the angle but not significantly because the original angle in CWL was already significantly smaller than the other two cultivars. TRL was not affected by the water

treatments except KP whose TRL was increased by BI-SMF, which was resulted from increased length of nodal roots. NRL was significantly increased by the two water treatments for YTH183 and KP while it was not affected for IR64. In contrast, LRL was not affected by the treatments for any of the cultivars. Comparing the two types of lateral roots, S-type LRL was not affected while L-type LRL was significantly increased by TI-SMF for IR64 and by BI-SMF for YTH183.

Root length by soil depth, as significant trait for the vertical profile of RSA, was significantly different between CWL and SMF in the 0–13-cm soil layer (IR64 and KP), in the 13–39 cm soil layer (IR64 and YTH183), and in the 26–39-cm soil layer (IR64, YTH183, and KP) (Figure 3). The root profile of IR64 was similar to that of YTH183, which showed the largest root length at 0–13 cm depth, but YTH183 had longer roots than IR64 at 13–26 cm and 26–39 cm under SMF. On the other hand, KP had smaller root length than IR64 and YTH183 at 0–13 cm depth.

The relationship between root development and shoot dry matter

The TRL was positively and significantly correlated with SDW for all cultivars, and so were NRL and L-type LRL (Table 3). YTH183 showed positive and significant correlation coefficients for all the root traits as shown in Table 3. However, number of nodal roots was neither significantly correlated with SDW, nor with the root cone angle for the three cultivars (data not shown).

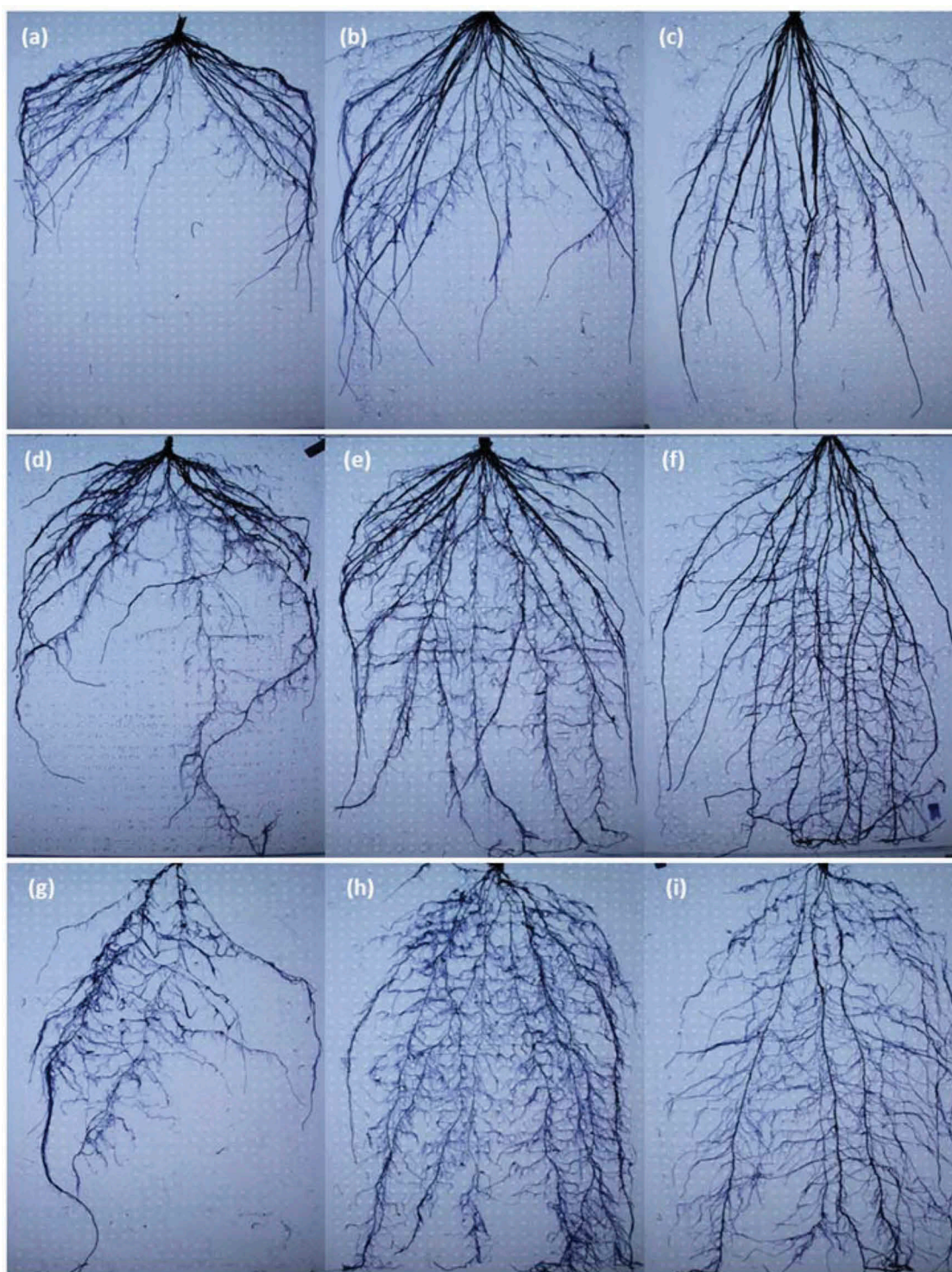


Figure 2. Root system profiles of IR64 (a, d, and g), YTH183 (b, e, and h) and KP (c, f, and i) grown under CWL (a–c), TI-SMF (d–f) and BI-SMF (g–i) conditions at 34 DAS. Root systems were sampled by the root box–pinboard method.

Discussion

Variation in shoot and root traits across water treatments

Although the effect of treatments on SDW and TRL was not significant or negligible for each cultivar, root traits

had relatively high variations with CV ranging from 13.8 to 59.2, as compared with shoot traits (11.0–32.5) (Tables 1, 2). Kono et al. (1987a) attempted to differentiate traits of the RSA of soybean, which did not change from those that changed in response to different soil moisture conditions. Likewise, in this study, we

Table 2. Root traits of IR64, YTH183, and KP grown under CWL, TI-SMF, and BI-SMF conditions at 34 DAS. Values are means of four replicates.

| Cultivar | Treatment | Nodal roots | | Root cone angle | | Total root length (cm) | | Nodal root length (cm) | | Lateral root length (cm) | | S-type lateral root length (cm) | | L-type lateral root length (cm) | |
|---------------|-----------|-------------|---------|-----------------|---------|------------------------|---------|------------------------|---------|--------------------------|---------|---------------------------------|---------|---------------------------------|---------|
| | | SMF/CWL | SMF/CWL | SMF/CWL | SMF/CWL | SMF/CWL | SMF/CWL | SMF/CWL | SMF/CWL | SMF/CWL | SMF/CWL | SMF/CWL | SMF/CWL | SMF/CWL | SMF/CWL |
| IR64 | CWL | 45.5 | a | 135.2 | a | 7601.8 | a | 1331.2 | a | 6270.6 | a | 5831.0 | a | 439.6 | b |
| | TI-SMF | 39.0 | a | 129.6 | a | 8474.7 | a | 2131.4 | a | 1.6 | 6343.4 | a | 5677.8 | a | 1.5 |
| | BI-SMF | 6.0 | b | 91.0 | b | 7248.7 | a | 1704.5 | a | 1.3 | 5544.2 | a | 4965.1 | a | 0.9 |
| | Mean | 30.2 | AB | 118.6 | A | 7775.1 | B | 1722.4 | B | 6052.7 | B | 5491.3 | B | 561.4 | B |
| | CV | 59.2 | | 18.1 | | 16.8 | | 28.3 | | 15.6 | | 15.9 | | 23.9 | |
| YTH183 | CWL | 48.8 | a | 109.1 | a | 9258.0 | a | 1647.6 | b | 7610.4 | a | 7064.0 | a | 546.4 | b |
| | TI-SMF | 48.8 | a | 128.5 | a | 12,543.7 | a | 3631.4 | a | 2.2 | 8912.2 | a | 8028.4 | a | 1.1 |
| | BI-SMF | 15.0 | b | 77.5 | b | 12,152.0 | a | 3387.6 | a | 2.1 | 8764.4 | a | 7710.4 | a | 1.1 |
| | Mean | 37.5 | A | 105.1 | A | 11,317.9 | A | 2888.9 | A | 8429.0 | A | 7600.9 | A | 828.1 | A |
| | CV | 48.7 | | 21.7 | | 22.0 | | 33.6 | | 21.0 | | 20.5 | | 33.6 | |
| KP | CWL | 22.8 | a | 77.8 | a | 6663.1 | b | 1465.5 | b | 5197.6 | a | 4690.2 | a | 507.3 | a |
| | TI-SMF | 20.5 | a | 75.8 | a | 8446.8 | ab | 2808.2 | a | 1.9 | 5638.6 | a | 5044.9 | a | 1.1 |
| | BI-SMF | 12.0 | b | 60.6 | a | 9142.2 | a | 2893.3 | a | 2.0 | 6248.9 | a | 5657.5 | a | 1.2 |
| | Mean | 18.4 | B | 71.4 | B | 8084.0 | B | 2389.0 | AB | 5695.0 | B | 5130.9 | B | 564.1 | B |
| | CV | 29.3 | | 17.2 | | 18.4 | | 31.8 | | 16.0 | | 16.4 | | 13.8 | |
| ANOVA | | | | | | | | | | | | | | | |
| Cultivar (C) | ** | ** | ** | ** | ** | ** | ** | ** | ** | ** | ** | ** | ** | ** | ** |
| Treatment (T) | ** | ** | ** | ** | ** | ** | ** | ** | ** | ** | ** | ** | ** | ** | ** |
| CxT | ** | ** | ** | ** | ns | ns | * | ns | ns | ns | ns | ns | ns | * | * |

Values labeled using different letters differ significantly across treatments within each variety ($p < 0.05$, Tukey's HSD test). *, **, and ns indicate significance at $p < 0.05$, $p < 0.01$, and no significance, respectively.

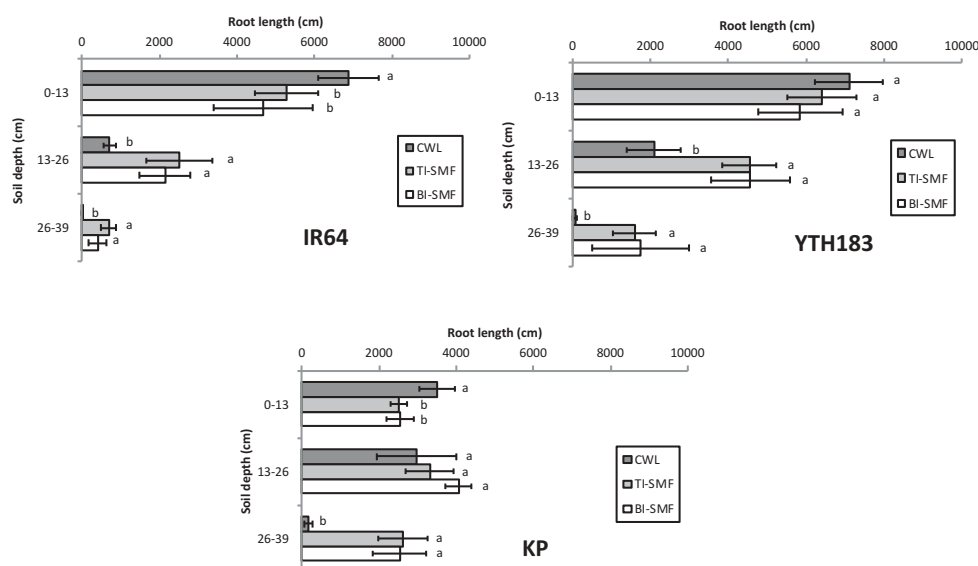


Figure 3. Profile of root length of IR64, YTH183, and KP grown under CWL, TI-SMF, and BI-SMF conditions at 34 DAS. Values are means \pm S.D. of four replicates. Values labeled using different letters differ significantly across treatments within each variety ($p < 0.05$, Tukey's HSD test).

Table 3. Coefficients of correlation between root traits and shoot dry weight in IR64, YTH183, and KP.

| | IR64 | YTH183 | KP |
|-------|---------|--------|---------|
| TRL | 0.69* | 0.81** | 0.67* |
| NRL | 0.72** | 0.67* | 0.74** |
| LRL | 0.59* | 0.73** | 0.54 ns |
| S-LRL | 0.53 ns | 0.70* | 0.51 ns |
| L-LRL | 0.69* | 0.70* | 0.74* |

*, ** and ns indicate significance at $p < 0.05$, $p < 0.01$, and no significance, respectively.

found out that NRL was more plastic (CV 28.3–33.6) than LRL (CV 15.6–21.0) in the three cultivars (Table 2). Among lateral roots, L-type (CV 23.9–33.6) was more plastic than S-type (CV 15.9–20.5) in IR64 and YTH183 (Table 2). In addition, the number of nodal roots showed the highest CV (29.3–59.2) due to the large reduction under BI-SMF for the three cultivars. This was caused by the lower SMC in the upper soil layer under BI-SMF than under TI-SMF as a result of irrigation from the soil surface being suspended. Thus, BI-SMF seemed to result in more severe stress than TI-SMF.

Genotypic variations in plasticity of RSA

As we mentioned above, this study examined the root growth angle (root corn angle), root elongation, and root branching to evaluate the RSA. All of the three cultivars exhibited plasticity in RSA but expressed in different ways and degrees. IR64 changed its RSA by shifting root distribution to deeper soil layers (Table 2, Figure 2). This cultivar significantly reduced its root cone angle under BI-SMF, while the other traits remained unaffected. As

a result, root length in the upper soil layer reduced while those in middle and lower layers increased. YTH183 similarly shifted roots to deeper soil layers but in different manner (Table 2, Figure 2). It tended to widen the root cone angle in TI-SMF but significantly reduced it in response to BI-SMF, which resulted in maintained root length in upper soil layer (Figure 3). This cultivar increased NRL as well as L-type LRL in both water treatments, which resulted in significantly increased root length in middle and lower soil layers (Figure 3). In contrast, root cone angle of KP did not differ significantly across treatments (Table 2 and Figure 2). This result and the narrow root angle even in CWL indicate that KP is deep rooting in nature (Uga et al., 2018, 2015, 2013), but did not show apparent root plasticity in this trait. It showed a tendency of increased NRL while LRL did not respond to any of the water treatments. As a result, KP showed an apparent plasticity in RSA and shifted roots to deeper layer more sharply in response to SMF with significantly decreased root length in upper layer while drastically increased in the lower layer (Figure 3).

Dro1-NIL, which was developed from a cross between IR64 and KP, showed a higher yield than IR64 under upland conditions with drought stress (Uga et al., 2013) as well as on irrigated lowland fields (Arai-Sanoh et al., 2014). However, we demonstrated that IR64 had the ability to change its root cone angle and become deep rooting like *Dro1-NIL* when it was growing under limited water availability, as shown in Figure 2. Furthermore, YTH183 showed high plasticity of the root cone angle, i.e. YTH183 can change its root

cone angle to both wide and narrow according to the position of the water supply (Table 2 and Figure 2). Plasticity of the root system development in response to SMF has been studied in terms of root elongation and branching in rice (Kano-Nakata et al., 2013; Nguyen et al., 2018; Niones, Inukai, Suralta & Yamauchi, 2015; Owusu-Nketia et al., 2018; Suralta, Inukai & Yamauchi, 2010; Suralta et al., 2018b, 2018a). Our study noted that plasticity of root growth angle was also exhibited under different soil water distribution in SMF, while most of the studies are focused on natural phenotypic variability of root growth angle (Bettembourg et al., 2017; Kato, Abe, Kamoshita & Yamagishi, 2006; Uga et al., 2015).

The root box–pinboard method is advantageous for analyzing the intact root system using two-dimensional (2D) images. For analyzing RSA, three-dimensional (3D) image is ideal because it is difficult to obtain the exact root growth angle with 2D image; many roots overlap on the 2D image, resulting in an underestimation of the root length (Uga et al., 2018). Further analysis combined with 3D images will be beneficial for understanding both the root phenotype and its function (Morris et al., 2017).

Key root traits and their contribution to shoot growth

The positive correlations between root traits and SDW suggest that under SMF the TRL, NRL, and L-type LRL are important root traits in any of the cultivars in this study (Table 3). For LRL, L-type contributed more to shoot dry matter production and this result supports the findings of Toyofuku, Matsunami and Ogawa (2015), as they demonstrated the importance of L-type lateral roots for the plant adaptation to osmotic stress in rice. We showed that although root development was promoted, there was no significant increase in SDW under SMF (Table 1). Such results well agree with those of Sandhu et al. (2016) who observed that root architectural plasticity was related to yield stability in variable growing environments.

Among the three cultivars tested in this study, YTH183 showed the highest SDW regardless of water treatments (Table 1). YTH183 had a higher ability to change its RSA, which resulted from higher ability to change root growth angle, and to promote nodal root elongation and lateral root branching compared to IR64 and KP under SMF (Table 2). Since we did not measure the different component root traits by soil depth, further study is needed to understand the RSA by different soil profile. YTH183 was reported as promising genetic material for the enhancement of yield potential (Ishimaru et al., 2017). Furthermore, QTL for efficient root elongation under a wide range of nitrogen

concentrations were identified from YTH183 (designated as YP5) (Obara et al., 2014). Together with the research findings in this study, this would help to develop rice that is adapted to SMF in upland and rainfed lowland conditions.

Disclosure statement

No potential conflict of interest was reported by the authors.

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