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Matching the Expression of Root Plasticity with Soil Moisture Availability Maximizes Production of Rice Plants Grown in an Experimental Sloping Bed having Soil Moisture Gradients

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Abstract: Soil moisture distributions in rainfed lowland rice environments are largely determined by the position in the toposequence. In this study, we developed an experimental sloping bed that can simulate the soil hydrological conditions in sloping rainfed lowland rice environments to examine if the expression of promoted root system development in relation to soil moisture availability along the soil profile may maximize water uptake and dry matter production under drought. The gradient of available water along both the surface soil layer and the vertical soil profile was successfully created by manipulating ground water levels in the experimental sloping bed indicating the practical effectiveness of this experimental system. Then, two contrasting genotypes, IRAT109 (upland rice adapted *japonica*) and KDML105 (lowland adapted *indica*) were grown for plasticity evaluation. Dry matter production was maintained even at a higher position in the toposequence in IRAT109, but decreased in KDML105. Such maintenance of dry matter production in IRAT109 was attributed to its greater ability to increase root length density in a deeper soil layer, where more soil moisture is available. In contrast, KDML105 maintained root length density in the upper soil layer, and could not utilize the soil moisture available in the deeper soil layer. These results imply that the genotype that expressed root plasticity with root system developing in the soil portion where more soil moisture was available showed greater dry matter production than the genotype that showed root plasticity in the soil layer where soil moisture was less available.

Key words: Deep root, Drought, Root plasticity, Toposequence, Water deficit.

The global rice production area covers over 100 million ha, 89% of which is in Asia. Forty-five percent of this rice area, is rainfed, 25% of which is never flooded and thus classified as upland (Serraj et al., 2009). The rainfed rice-growing areas are commonly located in a sloping terrain and thus, a large proportion of the variations in water-stress is determined by the position in the toposequence (Fukai and Ouk, 2012). In a lower position, there may be continuous standing free water that is connected to underground water. However, in a higher position, the underground water level may be well below the soil surface and there may be no standing water or only perched water above the hardpan (Fukai and Ouk, 2012). The paddies in the upper toposequence are often classified as drought-

prone environments (Jongdee et al., 2006). Roots play a critical role in plant growth in a water-limited environment, and to enhance the drought resistance, access to available water in soil by the roots should be maximized in each ecosystem.

The ability of roots to respond to changing soil moisture content known as plasticity is important for the growth of rice plants under fluctuating soil moisture conditions (O'Toole and Bland, 1987; Bañoc et al., 2000). We have been conducting a series of studies on root plasticity, and specifically showed that the plasticity in root system development exhibited by promoted lateral root development and new nodal root production plays a key role in maintaining plant growth under fluctuating soil

Received 18 November 2014. Accepted 31 December 2014. Corresponding Author: A. Yamauchi (ayama@agr.nagoya-u.ac.jp, fax +81-52-789-4022). **Abbreviations:** LRL, lateral root length; NRL, nodal root length; NRN, nodal root number; RLD, root length density; SDW, shoot dry weight; SMC, soil moisture contents; SRL, specific root length; TRL, total root length. This research was funded by the Grant-in-Aid for Scientific Research (No.26292012) from the Japan Society for the Promotion of Science, and partially supported by the Japan Science and Technology Agency (JST) / Japan International Cooperation Agency (JICA), the Science and Technology Research Partnership for Sustainable Development (SATREPS).

moisture levels in shallow soil layer such as above the hardpan (Bañoc et al., 2000; Suralta et al., 2010; Niones et al., 2012). This plasticity in root system development is functionally effective and efficient for the enhancement of water uptake especially under mild water deficit conditions (Kano-Nakata et al., 2011). On the other hand, it has been well established that deep rooting avoids drought-induced stress by extracting available water from the deep soil layers (Azhiri-Sigari et al., 2000; Kato et al., 2007; Gowda et al., 2011). A typical example of advantageous effects of deep rooting were recently reported by Uga et al. (2011), who mapped a quantitative trait locus (QTL) for deep rooting, DEEPER ROOTING 1 (DRO1) that enables rice plants to produce more grains under drought-induced stress without yield penalty. They further showed the mechanism by which this QTL only alters root growth angle and does not decrease either shoot or root biomass (Uga et al., 2013). However, little attention has been paid to the mechanism in most of the studies whether the deep rooting is a constitutive trait or the consequence of root plastic responses to changing soil environments. Therefore, by examining the root system development along the depth in the soil profile with increase in the position in the toposequence, we may be able to evaluate the plasticity in deep rooting.

As for water availability, by using the Agricultural Production Systems Simulator (APSIM) crop simulation model (Keating and Carberry, 2003) that simulates soil water extraction by crop plants, Peake et al. (2013) showed that the extraction of soil water is limited to soil layers into which roots have penetrated. The concept clearly shows that soil moisture availability should be determined not by either moisture content or root distribution alone but by a combination of both moisture distribution and root distribution in the soil profile. Previous studies have shown differences in spatial distribution of water among fields located at different positions in the toposequence (Homma et al., 2004; Tsubo et al., 2007; Inthavong et al., 2011) but its relationship with root distribution along soil profile and growth performance is still unclear. For maximizing water availability to plants during drought, roots should be distributed where the soil moisture is distributed at a certain portion along the soil profile depending on the hydrology brought about by environmental changes such as toposequence. In this case, root distribution should mean not simply the existence of a root, but a certain amount of effective root length density that ensures effective water uptake.

For better understanding of the yield performance at various toposequence positions, both the evaluation of hydrology in the target environmental conditions and genotypic characteristics of the root distribution in response to the soil moisture availability are necessary. We hypothesized that in order for root plasticity to function

for water uptake to increase potential drought resistance and to maintain dry matter production, root plasticity should be expressed in the soil portion where the more soil moisture is available. To test the above hypothesis, we need an appropriate experimental system that simulates the change in soil hydrological conditions in sloping rainfed lowland rice fields. Thus, we developed and calibrated an experimental sloping bed that can create a gradient of available water both along the soil surface and along the vertical soil profile by manipulating the ground water level in the sloping bed. Then, we also used contrasting genotypes in terms of root plasticity expression in response to drought stress; KDML105 (lowland type), which has known root plasticity expression at the shallow soil layer (Bañoc et al., 2000; Kano-Nakata et al., 2013) and IRAT109 (upland type), which has known deep root development under drought stressed upland conditions (Kato et al., 2006, 2007). We expect that under an increasing toposequence where moisture availability shifts from shallow to deeper soil layers, the shoot dry matter production of KDML105 may be reduced while that of IRAT109 is maintained. However, it is still unclear whether the deep rooting characteristic of IRAT109 is a constitutive trait or a consequence of expression of plasticity including allocation pattern of dry matter from shoots to roots. Furthermore, the ability of KDML105 to express deep root development under drought with the increase in soil height is also unclear. Thus, we intentionally excluded the hardpan in the experimental set up to allow the expression of its deep root development trait in response to the lowering of available soil moisture to deeper soil layers. The objectives of this study were to examine the expression pattern of root plasticity in relation to the position of available soil moisture along the soil profile with increasing depths under a calibrated experimental sloping bed, to determine the effects on dry matter productions, and to evaluate the practical applicability of using experimental sloping bed for soil moisture manipulation to simulate the change in soil hydrological conditions in sloping rainfed lowland rice fields.

Materials and Methods

The experiments were conducted at the experimental farm of Nagoya University, Nagoya, Japan (lat. 35°6'42"N, long. 137°4'57"E).

1. Experiment 1. Design and manipulation of soil moisture content in the experimental sloping bed

Experiment 1 was conducted from July to November 2010. The experimental sloping bed was constructed in a watertight pool with impermeable plastic sheet under a rain-out shelter (Fig. 1). Removable metallic bars and frames were used to hold and support the soils and they neither root development nor water movement was

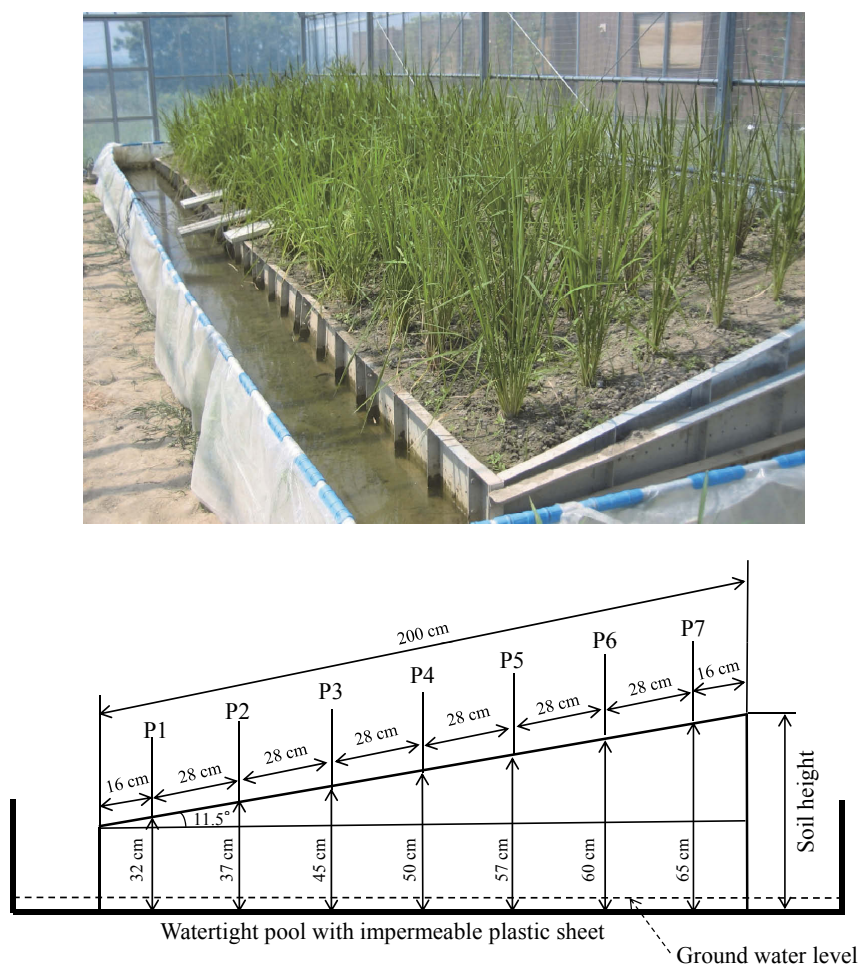


Fig. 1. Diagram of the simulated sloping bed. The sloping bed was established in a watertight pool with impermeable plastic sheet. Each genotype was planted in a row of 2 m in length with a spacing of 50 cm between rows and 28 cm between hills, which were randomized. P1 – P7 indicates a plant grown on the soil height of 32, 37, 45, 50, 57, 60 and 65 cm from the bottom, respectively.

interrupted. The length, maximum and minimum soil height of the experimental sloping bed were 200, 30 and 80 cm, respectively. The soil used was sandy loam (72.3% sand, 20.9% silt, 6.8% clay; pH 5.5) with field capacity at 27.7% w/w (gravimetric).

The soil moisture contents at soil surface (0 – 12 cm) were measured using the time domain reflectometry probe (TDR; Tektronix Inc., Wilsonville, OR, USA). Two stainless steel rods (15 cm in length) were inserted into the soil at a depth of 12 cm allowing a 3 cm protruding above the soil surface where TDR probes were attached to obtain soil moisture content readings (Fujita et al., 2011). The two steel rods, which were 3 cm apart from each other, were placed in the middle of two plants in each row.

The value provided by TDR (x) was converted into soil water content (% w/w) (y) from an equation calibrated in 2013 according to the gravimetric methods.

$$y = 0.5023x + 0.6245 \quad (n = 40, r = 0.81, P < 0.001) \quad (1)$$

Soil puddling was not done and thus there was no soil

hardpan created in this study.

In experiment 1, we used three genotypes that were reported to be resistant to drought. Dular (upland rice *Aus*), has drought resistance associated with deep root growth (Henry et al., 2010). Rexmont (lowland rice *japonica*) that is one of the rice diversity research set of germplasm (RDRS) (Kojima et al., 2005) shows drought resistance associated with root plasticity under mild drought stress conditions (Inoue, 2009). CSSL50 that is one of the chromosome segment substitution lines (CSSL) derived from a cross between Nipponbare and Kasalath, shows drought resistance due to its great ability to express root plasticity under mild drought conditions in the field (Kano et al., 2011). Seeds of Rexmont and CSSL50 were provided by the Rice Genome Research Center (RGRS), National Institute of Agrobiological Sciences (NIAS), Japan.

The seeds from each genotype were soaked in water and incubated in a seed germinator at 28°C for 48 hrs prior to

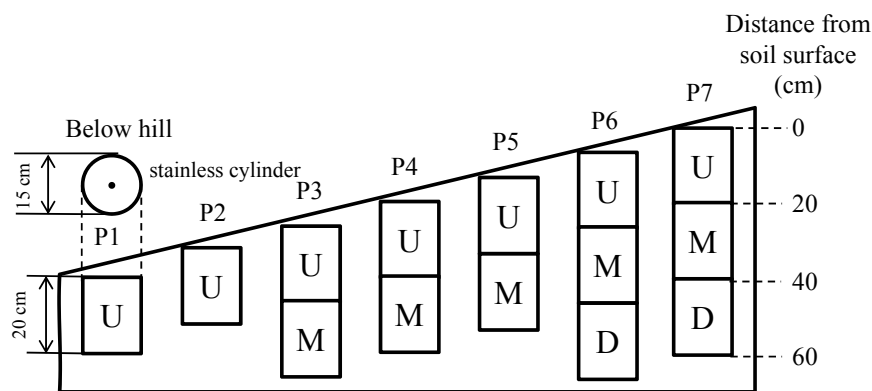


Fig. 2. Schematic diagram showing positions of root sample collection using stainless cylinder of 15 cm in diameter in Experiment 2. P1 – P7 indicates a plant grown on the soil height of 32, 37, 45, 50, 57, 60 and 65 cm from the bottom, respectively. U: Upper soil layer (0 – 20 cm), M: Middle soil layer (20 – 40 cm), D: Deeper soil layer (40 – 60 cm).

sowing. Pre-germinated seeds from each genotype were sown in nursery boxes at 3 seeds per hole. The seedlings in each hole were later thinned to one seedling at 3 days after sowing. The seedlings were raised under well-watered conditions for 48 days prior to transplanting. Each genotype was transplanted in a row with a length of 2.0 m. One seedling with an intact root system was transplanted per hill on the experimental sloping bed on July 26, 2010. Plant spacing was 50 cm between rows and 28 cm between hills. Each row contained 7 plants of a genotype that were exposed to different soil heights with increase in position in the toposequence. Thus, 7 plants of each genotype in each row were grown on the soil height of 32, 37, 45, 50, 57, 60 and 65 cm from the bottom (Fig. 1). Chemical fertilizer (N, P, K = 14.0, 14.0, 14.0%) was side applied up to 3.0 cm soil depth for each plant right after transplanting at a rate of 50 g m^{-2} , and no more topdressing was applied. The soil bed was kept well-watered by using sprinkler irrigation for 14 days after transplanting (DAT) for plant establishment. Thereafter, the drought stress was imposed by withholding the sprinkler irrigation and decreasing the ground water level down to 15 cm depth (Fig. 1). We first kept the ground water levels at 15 cm from the bottom until maximum tillering stage, then lowered it from 15 cm to 5 cm at 39 DAT and then kept at 5 cm until sampling (126 DAT). To determine the relationship between the ground water level (water table height from the bottom) and the intensity of drought stress in the soil surface along the increasing position in the toposequence, we measured the soil moisture content at soil surface (0 – 12 cm) by using TDR at 39 and 46 DAT with the corresponding ground water level at 15 and 5 cm, respectively.

SPAD (an indirect estimate of chlorophyll content) was measured on the flag leaf of all genotypes between 10–11 AM on August 31 ($n = 3$ for each soil height). At 126 DAT, the shoots of all genotypes were cut at the base and oven-dried at 70°C for 3 days to record the shoot dry weight.

2. Experiment 2. Root and shoot growth responses to the increase in position in the toposequence using the calibrated experimental sloping bed

Experiment 2 was conducted from June to September in 2011 using a previously constructed and calibrated experimental sloping bed as described in Experiment 1. The ground water level used in this experiment was 5 cm from the bottom.

(1) Genotypes used and crop management

We selected and used two contrasting rice genotypes based on their pattern of root plasticity expression in response to drought stress. These genotypes were IRAT109 (upland-adapted *japonica*) and KDML105 (lowland-adapted *indica*). In our previous study, KDML105 (lowland type) showed greater root plasticity especially at the shallow soil depths (Bañoc et al., 2000; Kano-Nakata et al., 2013) while IRAT109 (upland type) showed faster root elongation rate (Bañoc et al., 2000) and greater deep root ratio (ratio of deep root length below 30 cm depth to total root length) (Kato et al., 2006, 2007). The seed sowing, seedling management and transplanting were done in a similar manner to those in Experiment 1. Transplanting to the experimental sloping bed was done on June 13, 2011 using 25-day-old seedlings. The experiment was laid out following a completely randomized design with 3 replications. The assignment of genotypes in each row was randomized. Chemical fertilizer (N, P, K = 14.0, 14.0, 14.0%) was applied at the base of each plant right after transplanting at a rate of 50 g m^{-2} , and topdressings were applied on July 29 (46 DAT) at a rate of $30 \text{ g m}^{-2} \text{ plant}^{-1}$. The soil bed was kept well-watered by using sprinkler irrigation for 2 weeks after transplanting for plant establishment. Thereafter, the drought stress was imposed by withholding the sprinkler irrigation to decrease the water level down to 5 cm depth. Ground water level in the experimental sloping bed (Fig. 1) was kept at 5 cm until 105 DAT, when the experiment

was terminated.

At 105 DAT, the plants were harvested. Shoots were cut at the base and oven-dried at 70°C for 3 days before recording the shoot dry weight.

(2) Root sampling and measurements

Root sampling was done immediately after harvesting the shoot samples. Soil samples with roots were acquired by using a stainless cylinder 15 cm in diameter (Kang et al., 1994) (Fig. 2). The soil containing roots were separated based on depth increments at 20 cm intervals such as 0 – 20 (upper soil layer), 20 – 40 (middle soil layer) and 40 – 60 (deeper soil layer) cm below the soil surface (Fig. 2).

The extracted roots were carefully washed with water in a 1.5 mm mesh screen and fixed in a solution (acetic acid, 50% ethanol; 5: 95 parts by volume) for further measurements. For total root length measurements, each root sample was rinsed with water and spread on a transparent sheet with minimal overlap. The digitized images were taken using a scanner with a resolution of 300 dpi and an output format of 256 grey scales. The total root length was determined using a macro program developed by Kimura et al. (1999), and Kimura and Yamasaki (2001) on the NIH image software version 1.60 (public domain released by the National Institute of Health, USA). The root length density was calculated as the root length per unit volume of soil from which roots were extracted. The nodal root number and nodal root length in the upper soil layer (0 – 20 cm) for each plant were manually measured. The lateral root length in the upper soil layer (0 – 20 cm) for each plant was calculated as the difference between total root length and total nodal root length. Branching index in the upper soil layer (0 – 20 cm) for each plant was calculated as lateral root length divided by nodal root length (Morita and Collins, 1990).

After scanning, root samples were oven dried at 70°C for 3 days prior to the recording of the root dry weight. The specific root length was calculated as the ratio between total root length and root dry weight from each soil layer. The upper root dry weight ratio was calculated as the ratio of the root dry weight in the upper soil layer to the total root dry weight. The deep root length ratio of the uppermost position on the toposequence (P7, Fig. 1) was calculated as the ratio of the root length in the deeper soil layer to the total root length. The deep root weight ratio of P7 was calculated as the ratio of the root length in the deeper soil layer to the total root length.

3. Statistical analysis

In Experiment 1, the statistical significance between the soil moisture content was determined by Student's paired *t*-test. The relationships between soil heights and root traits in Experiment 2 were determined using correlation analysis. In Experiment 2, the statistical significance

Table 1. Soil moisture contents at surface soil layer (0 – 12 cm) at different soil heights from the bottom (32, 37, 45, 50, 57, 61 and 65 cm) measured by using a time domain reflectometry probe (TDR; Tektronix Inc., Wilsonville, OR, USA) at 39 and 46 DAT with the corresponding ground water level at 15.0 and 5.0 cm, respectively in Experiment 1. * and ** indicates significance at $P < 0.05$ and $P < 0.01$ confidence interval for mean difference compared by paired *t*-test.

Soil height (cm)	Ground water level (cm)		Differences
	15.0	5.0	
32	25.0	18.4	6.6 *
37	23.2	16.5	6.7 *
45	18.8	13.2	5.7 *
50	16.3	12.0	4.3 *
57	14.4	11.3	3.1 *
60	13.4	10.6	2.7 **
65	11.7	9.3	2.4 **

* and ** indicates significance at $P < 0.05$ and $P < 0.01$ confidence interval for mean difference compared by paired *t*-test.

between the two mean values of root traits in deeper soil layer was determined by Student's *t*-test.

Results

1. Experiment 1. Soil moisture dynamics in the soil surface with different water table depths in the experimental sloping bed

The soil moisture content in the surface soil layer (0 – 12 cm) gradually decreased with the increase in soil height (Table 1). When the ground water level was lowered from 15 to 5 cm, the intensity of drought stress significantly increased with the increase in soil height along the toposequence (Table 1). In Experiment 2 conducted in 2011, we measured the soil moisture content in the surface soil layer (0 – 12 cm) four times (29 DAT, 44 DAT, 65 DAT and 75 DAT), but observed no significant differences in soil moisture content among measurements (data not shown). These observations in Experiment 2 suggest that the soil moisture content in the experimental sloping bed remained stable throughout the growth stage with a constant ground water level.

The shoot dry weight regardless of genotype used was not progressively reduced with the decrease in soil moisture brought about by the increase in soil height in the toposequence when the ground water level was set at 15 cm depth (Fig. 3). Thus, in Experiment 2, the ground water level in the experimental sloping bed was lowered and set to 5 cm depth. The resulting soil moisture content (% w/w) in the surface soil layer ranged from 22 at the lowest to about 10% at the highest position of the toposequence.

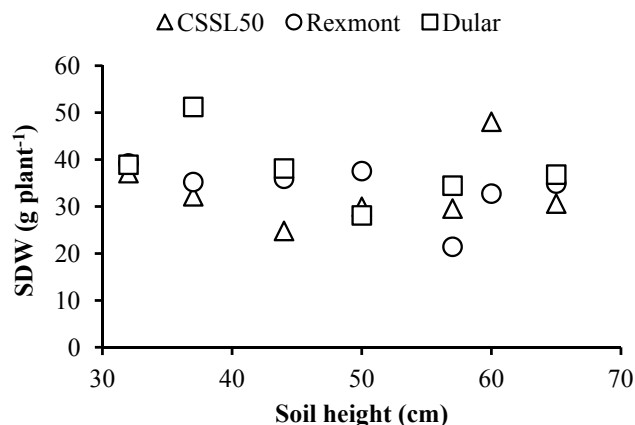


Fig. 3. Shoot dry weight (SDW) across genotypes at different soil heights at 126 days after transplanting in Experiment 1 (Δ CSSL50, \circ Rexmont and \square Dular).

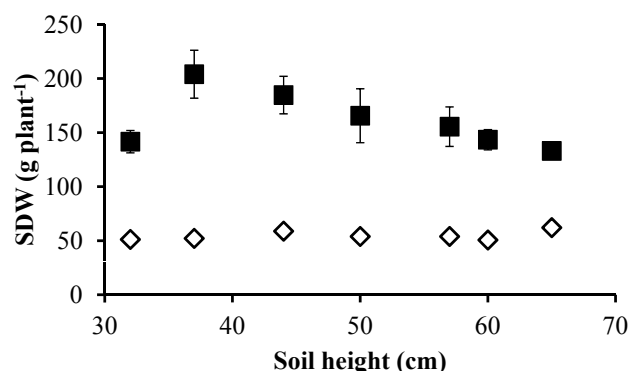


Fig. 4. Shoot dry weight (SDW) at different soil height from the bottom (32, 37, 45, 50, 57, 60 and 65 cm) for rice genotypes (\diamond IRAT109 and \blacksquare KDML105) determined at the maturity stage in Experiment 2. Bars indicates standard errors ($n = 3$).

2. Experiment 2. Shoot growth and root development under increasing soil height in the experimental sloping bed

The shoot dry weight of KDML105 initially increased with the increase in the position in the toposequence from the lowest (32 cm soil height) to the next position in the toposequence at a (37 cm). Thereafter, the shoot dry weight gradually decreased with a further increase in the position in the toposequence (Fig. 4). In contrast, the shoot dry weight of IRAT109 was maintained despite the increase in the position in the toposequence.

The root length density dynamics along soil depths corresponding to the increase in the position in the toposequence generally varied with the genotype (Fig. 5). KDML105 generally showed a decrease in root length density in the upper soil layer with an initial increase in the position in the toposequence. However, as the position in the toposequence further increased, the root length density of KDML105 in the upper soil layer significantly increased back to the same level of that in the lowest position. In contrast, IRAT109 showed significant reduction in root length density in the upper soil layer with the increase in the position in the toposequence.

The root length density in the middle soil layer did not significantly vary with the position in the toposequence, but the values were generally lower than those in the upper soil layer in both genotypes (Fig. 5). The root length density in the deeper soil layer was comparable with that in the middle soil layer, but generally larger than those in the middle soil layer especially in IRAT109. In KDML105, the root length density in the deeper soil layer was significantly lower than that in the upper soil layer, and comparable to that of the middle soil layer.

The root dry weight in the upper soil layer was significantly decreased with the increase in the position in the toposequence and the trend was similar for both

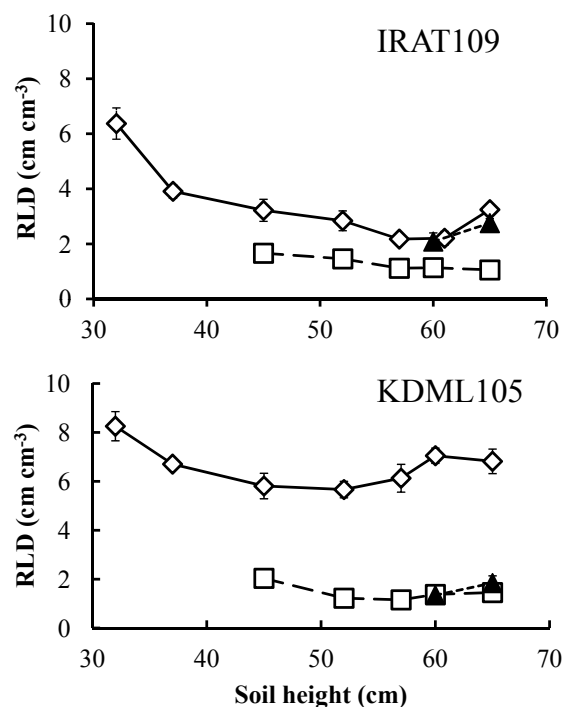


Fig. 5. Root length density (RLD) at different soil layers (\diamond , 0 – 20; \square , 20 – 40; \blacktriangle , 40 – 60 cm from the surface) at different soil heights (32, 37, 45, 50, 57, 60 and 65 cm) in rice genotypes IRAT109 and KDML105 in Experiment 2. Bars indicate standard errors ($n = 3$).

genotypes (Fig. 6a). The specific root length in the upper soil layer significantly increased with the increase in the position in the toposequence in KDML105 only (Fig. 6b). On the other hand, nodal root number (Fig. 6c) in the upper soil layer significantly decreased with the increase in the position in the toposequence in both genotypes. The root branching index in the upper soil layer significantly increased with the increase in the position in the toposequence in KDML105 whereas it was not affected in

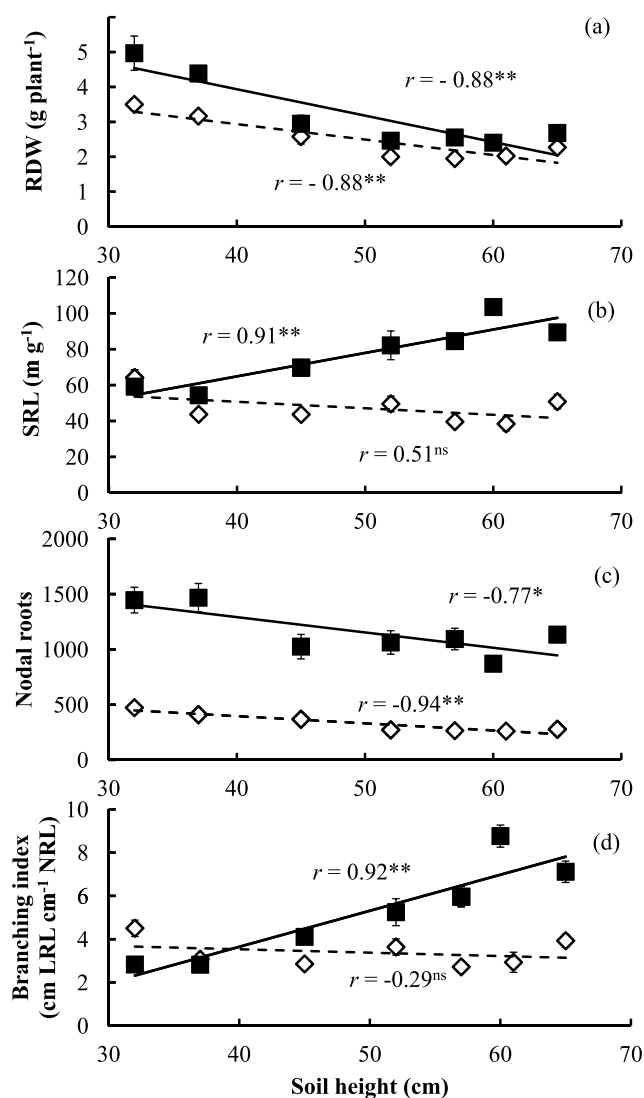


Fig. 6. Root dry weight (RDW) (a), Specific root length (SRL) (b), Nodal root number (c) and Branching index (d) in the upper soil layer (0 – 20 cm depth from soil surface) at different soil heights (32, 37, 45, 50, 57, 60 and 65 cm) (◇ IRAT109 and ■ KDML105) in Experiment 2. Bars indicate standard errors ($n = 3$). * and ** indicates significance at $P < 0.05$ and $P < 0.01$ respectively.

IRAT109 (Fig. 6d).

IRAT109 showed significantly larger deep root length ratio (Fig. 7a) and deep root weight ratio (Fig. 7b) than KDML105. Furthermore, both genotypes showed similar specific root length in the deeper soil layer (Fig. 7c).

Discussion

1. Soil moisture content with an experimental sloping bed (Experiment 1)

The decrease in soil moisture content and the corresponding increase in drought intensity in the surface soil layer were successfully generated by the experimental sloping bed (Table 1). The intensity of soil moisture levels

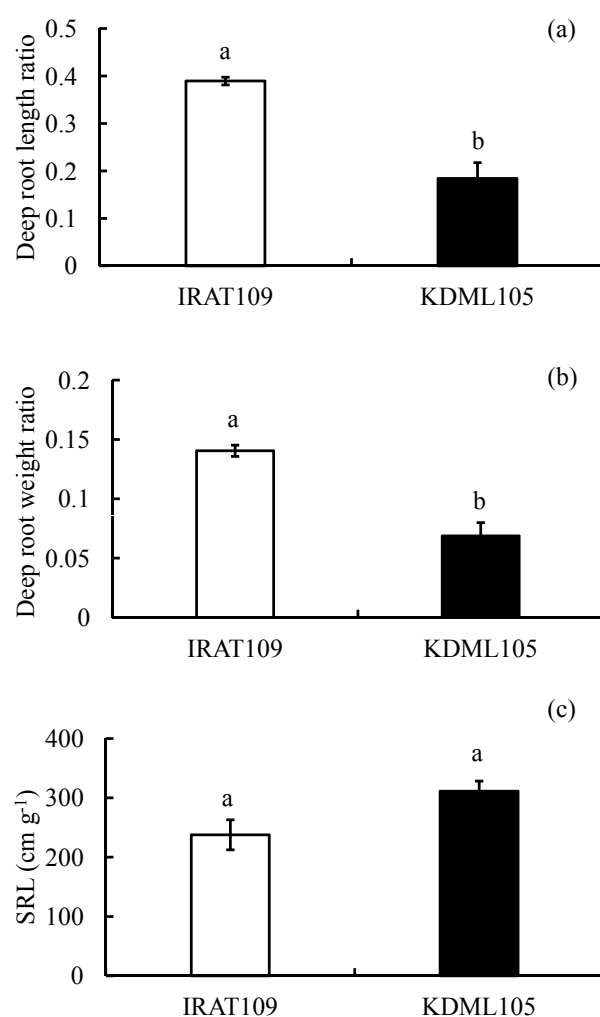


Fig. 7. Deep root length ratio (a), deep root weight ratio (b) and specific root length (SRL) (c) of P7 plant in deeper soil layer (40 – 60 cm depth) in Experiment 2. Deep root length ratio was calculated as the ratio of the root length in the deeper soil layer to total root length (TRL). SRL was calculated as the ratio of TRL to RDW in the deeper soil layer. The deep root weight ratio was calculated as the ratio of the root weight in the deeper soil layer to total root weight. Bars indicate standard errors ($n = 3$). Values followed by the same letter in a column within each treatment are not significantly different at the 5% level by Student's *t*-test.

along the toposequence could also be manipulated by adjusting the height of the ground water level (Table 1). Furthermore, the distribution of soil moisture availability shifted from shallow to the deeper soil layer by the increase in the height of the position in the toposequence especially when the ground water depth was set to 5 cm (Table 1) without significant difference in SPAD values of the plants grown at different soil heights (data not shown). These results show that the experimental sloping bed we developed is practically applicable for simulating the changes in soil hydrological conditions in sloping rainfed lowland rice fields, and for determining the effects of

matching the expression pattern of root plasticity with the position of available soil moisture for dry matter production along the soil profile while soil nutritional effects were scarcely involved in the observed plant response.

2. Expression of root plasticity in relation to soil moisture availability (Experiment 2)

Both genotypes used in this study expressed their root plasticity in response to the drought, but there were significant genotypic differences. In KDML105, the plasticity in root system development was expressed as maintained root length density in the upper soil layer, while the plasticity in IRAT109 was expressed through the allocation of more dry matter to the roots in deeper soil layer, resulting in increased root length density. The production of greater root lengths in the deeper soil layer in IRAT109 as reflected in its greater root length density (Fig. 5) and deep root length ratio (Fig. 7a) than in KDML105 was attributed mainly to more allocation of dry matter to roots in the deeper soil layer (Fig. 7b) rather than to the efficiency in lateral root production as evidenced by the fact that specific root length was similar in these genotypes (Fig. 7c). Also, the amount of root dry matter in the upper soil layer was reduced (Fig. 6a) in favor of more distribution of dry matter for the root system development in the deeper soil layer (Fig. 7b) in IRAT109. Consequently, the greater plasticity in root development in the deeper soil layer in IRAT109 was effectively expressed due to distribution of more dry matter in a deeper soil layer in response to the increase in soil moisture deficit brought about by the increase in the position in the toposequence.

The greater root length density in the deeper soil layer in IRAT109 (Fig. 5) contributed to its higher efficiency for water uptake when grown at the highest position in the toposequence, because it could take advantage of the available soil moisture deep down below the soil surface (Kato et al., 2007). Thus, the maintenance of dry matter production even at the high position in the toposequence in IRAT109 (Fig. 4) was suggested to be attributed to its ability to plastically promote root branching in the deeper soil layer (Fig. 5), which was in accordance with the soil moisture available at that soil layer.

In contrast, KDML105 reduced shoot dry weight with the increase in the toposequence (soil height in Fig. 4) because it expressed its root plasticity in the upper soil layer in the form of promoted lateral root development (Figs. 5 and 6d), which however was not in accordance with the soil moisture that was more available in the deeper soil layer. These results clearly show that KDML105 is a shallow-rooted genotype because even in the absence of hardpan and under the condition where the water was more available in the deeper soil layer, it still did not

express deep root system development. This genotype exhibited its root plasticity through promoted lateral root development exclusively in the upper soil layer only.

In addition, the fact that the largest shoot dry weight in KDML105 was not found in the plant grown at the lowest height (32 cm) but found at 37 cm (Fig. 4) suggests that the optimal soil water condition for KDML105 may be slightly drier than the wettest condition in this experiment. The similar growth responses were also reported for the high-yielding cultivars whose shoot biomass at maturity in aerobic culture was greater than in flooded culture (Katsura et al., 2010).

3. Plasticity in root branching in a shallow soil layer and rooting in the deep soil layer

KDML105 has widely been cultivated in rainfed lowland rice areas of Northeastern Thailand (Jongdee et al., 2006; Kanjoo et al., 2012). The rainfed lowlands are characterized by the presence of a hardpan, which impedes deep root development, and the soil moisture fluctuations between aerobic and anaerobic conditions in the upper soil layer above the hardpan, and therefore, root distributions are commonly shallow and most of available water tends to be limited to the shallow soil layer (Clark et al., 2002; Samson et al., 2002; Kato et al., 2013). The root plasticity in terms of greater root branching ability in the upper soil layer has an important role in the efficient capture of water in recovering process after rewetting and relieved from the drought period (Kondo et al., 2003; Kano-Nakata et al., 2013). Thus KDML105 may show better adaptation in rainfed lowland condition compared with IRAT109 because of its greater branching ability in the upper soil layer. In fact, KDML 105 consistently showed better root growth adaptation than any other genotypes tested to fluctuating soil moisture conditions in this study (Fig. 6d) as well as in our previous studies (Bañoc et al., 2000; Kano-Nakata et al. 2013) although the experiments were conducted under controlled conditions.

In contrast, under fluctuating soil moisture conditions, IRAT109 may not be able to effectively collect soil moisture that is often available at the shallow soil surface because its plasticity is expressed in chasing lowering ground water levels. In this study, however, soil moisture was maintained and more available in the deeper soil layer. In such a case, IRAT109 exhibited better performance than KDML105 because it was able to match its root plasticity to soil moisture, which is more available in the deeper soil layer. This pattern of root plasticity exhibited by IRAT109 may be one of the possible reasons why some rice genotypes maintained their yield potential even when planted at higher toposequential positions with limited soil moisture supply in the upper soil layer (Tsubo et al., 2006; Boling et al., 2008).

4. Effectiveness of the experimental sloping bed

Using the experimental sloping bed, the corresponding reduction rate of shoot dry weight exhibited by KDML105 (Fig. 4) with the increase in the position in the toposequence was 20% (Fig. 4), which was similar to those reported in actual rainfed rice areas in Asian monsoon regions (Homma et al., 2003; Samson et al., 2004; Boling et al., 2008). Our results showed smaller reduction in shoot dry matter production against the increase in position in the toposequence than in the study using a similar sloping experimental setup but with more severe drought stress (Fujii, 1993), and showed significant genotypic differences in the vertical root system distribution against the increase in the position in the toposequence (Fig. 5).

Furthermore, it is interesting to note that at relatively high soil moisture content in the surface soil layer brought about by higher ground water level (15 cm depth), the shoot dry weight was not affected by the increase in soil height in the toposequence regardless of the genotypes used (Fig. 3). However, when the soil moisture was decreased by lowering the ground water level to 5 cm depth, significant genotypic differences in the dry matter production were observed. KDML105 showed a decrease in shoot dry weight while that of IRAT109 was not affected by the increase in the position in the toposequence (Fig. 4). In addition, the SPAD values of the two genotypes grown at different heights did not significantly differ as stated earlier. These facts suggest that the genotypic differences in response of shoot dry matter production to the increasing toposequence were mainly affected by the intensity of drought stress imposed. The increase in soil volume brought about by the increase in soil height could affect the root and shoot growth and development, which is a subject for further study

Conclusion

In this study, the experimental sloping bed we developed successfully created the soil moisture gradient along the shallow soil surface and within the soil profile. The distribution of the soil moisture content shifted to the deeper soil layer as a consequence of the increase in the position in the toposequence, which was more evident when the ground water level was lower than when it was higher. These results demonstrate practical applicability of the experimental sloping bed in simulating the changes in soil hydrological conditions in sloping rainfed lowland rice fields. Using this experimental sloping bed, we showed different responses in root plasticity to drought along the increasing position in the toposequence. In KDML105, the expression of root plasticity was in the form of maintained root length density in the upper soil layer due to the maintenance of lateral root development, while in IRAT109, the plasticity was in the form of allocation of more dry matter to the deeper soil layer to increase root

length density. In spite of the root plasticity expressed in the upper soil layer in KDML105, shoot dry weight was decreased as the position in the toposequence increased, suggesting that the maintenance of dry matter production in IRAT109 was attributed to its plasticity in the ability to promote deep rooting that was consistent with the soil moisture available in the deeper soil layer. This study implies that in order for rice plants to increase potential drought resistance and maintain dry matter production, the root plasticity should be expressed in soil portions where the soil moisture is more available.

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