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Developmental Plasticity of Rice Root System Grown under Mild Drought Stress Condition with Shallow Soil Depth; Comparison between Nodal and Lateral roots

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ABSTRACT:

The plasticity in root system development (RSD) is a key trait for the adaptation of rice to mild drought. However, the enhanced RSD due to the plasticity may not be always a sole function of promoted lateral root (LR) production, but also of the integrated responses of nodal root (NR) development. In this study, we aimed to evaluate the effects of mild drought intensities on the development of the NR and LR, and their contribution to the entire RSD. We used six genotypes including KDML105 (*indica*, lowland adapted), a high lateral rooting ability genotype. The plants were grown up to heading or maturity stage for two years under soil with limited soil depth (20 cm) assuming the presence of the hardpan and at different moisture gradients generated by the line source sprinkler system. The effects of drought intensities generally differed between the development of NR and LR. In both years, all genotypes showed highest LR development under mild drought stress intensities. However, in some genotypes including KDML105, NR development was maintained in a limited soil moisture range only, which was narrower and wetter than that in which LR plasticity was expressed. Furthermore, the entire RSD was maintained only when both the NR and LR were simultaneously promoted or maintained. These results suggest that the NR have less plasticity than the LR in response to drought and the contribution of the plasticity in LR development to the entire RSD is dependent on both the soil moisture and nodal rooting ability.

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Deep rooting; drought tolerance; hardpan; rainfed lowland; root water uptake

It is estimated that about one third of world rice area is rainfed lowlands and mostly prone to drought (Maclean, Dawe, Hardy, & Hettel, 2002). Water deficit is one of the major constraints to rice production in rainfed lowlands.

Several studies have demonstrated that increased root length density at depth is associated with greater water extraction from deeper soil layers (Bernier et al., 2009; Henry, Gowda, Torres, McNally, & Serraj, 2011; Lilley & Fukai, 1994; Wade, Fukai, Samson, Ali, & Mazid, 1999). However, roots are commonly distributed in shallow soil layers in rainfed lowland rice fields, presumably brought about by the presence of a hardpan that impedes deep rooting (Clark, Cope, Whalley, Barraclough, & Wade, 2002; Samson, Hasan, & Wade, 2002). Peake, Huth, Kelly, and Bell (2013) showed that the extraction of soil water is limited to soil layers into which roots penetrated. So, in rainfed lowlands with the presence of hardpan, root system development (RSD) above the hardpan is important for the water absorption by the plants (Kano-Nakata et al., 2013). We have conducted a series of studies on phenotypic plasticity in RSD expressed in response to heterogeneous soil environment. The plasticity is defined as an ability of a

genotype to alter its phenotypic expression in response to the environment (O'Toole & Bland, 1987). The phenotypic plasticity in RSD can be expressed in the enhanced aerenchyma formation associated with lateral root (LR) development under fluctuating soil moisture conditions (Suralta, Inukai, & Yamauchi, 2008; Suralta, Inukai, & Yamauchi, 2010; Niones, Suralta, Inukai, & Yamauchi, 2012), and the QTLs which control such phenotypic plasticity were detected on chromosome 12 (Niones, Inukai, Suralta, & Yamauchi, 2015). Moreover, the expression of phenotypic plasticity in RSD triggered by mild drought stress can be enhanced with higher nitrogen application, which contributed to the maintenance of dry matter production (Tran et al., 2014; Tran et al., 2015). We specifically showed that the phenotypic plasticity in LR development under heterogeneous soil environment with limited soil depth is a key trait that effectively contributed to plant dry matter production through increased total root length (TRL) and thus water uptake, especially under mild drought stress (Kano, Inukai, Kitano, & Yamauchi, 2011; Kano-Nakata, Inukai, Wade, Siopongco, & Yamauchi, 2011).

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Our previous study also showed that there were mainly two types of root plasticity expression in rice grown under various drought intensities and soil depths but without hardpan so allow expression of deep rooting ability (Kameoka, Suralta, Mitsuya, & Yamauchi, 2015). Specifically, KDML105 (lowland-adapted *indica*) expressed its root plasticity in the form of maintained RSD in the upper soil layer due to the maintenance of LR development, while in IRAT109 (upland type, *indica*), the plasticity was expressed in the form of allocation of more dry matter to the deeper soil layer, which promoted root system development. Therefore, it is of particular interest to examine how the root plasticity of each genotype would be expressed under the lowland soil conditions and with the presence of hardpan.

Among various root traits, the functional significance of root length is often recognized as important trait for plant productivity under stress because it determines the size of contact of root system with the soil. Rice root system consists of different component roots; mainly one seminal root, nodal roots, and their LRs, which differed in origin, age, and morphological and anatomical features (Yamauchi, Fukai, Samson, Ali, & Mazid, 1996). Thus, root system development, which is often expressed in TRL, is determined by the integrated development of different component roots. For instance, Kano-Nakata et al. (2013) showed that the promoted development of entire root system of rice due to plasticity triggered by drought was a result of integrated responses of promoted production of nodal roots from the tillers and its elongation, and promoted LR elongation. Although plasticity in LR development is expressed under mild stress condition (Kano et al., 2011; Kano-Nakata et al., 2011), the response of nodal root to different drought intensities maybe different from that of the LRs.

In this study, we therefore aimed to compare the effects of mild drought intensities on the developmental responses between the nodal and LRs, which may differently contribute to the entire RSD, specifically under lowland rice fields where the hardpan normally exists at about 20 cm deep (Kato et al., 2013). Thus, the soil depth used in this study was set at 20 cm to eliminate the advantageous effects of deep rooting, which may be inhibited by hardpan under lowland soil conditions. For the precise control of drought intensity, we used line source sprinkler (LSS) system (Lanceras, Pantuwan, Jongdee, & Toojinda, 2004; Kano et al., 2011) that can create the smooth gradient from wet to dry soil conditions.

Materials and methods

Plants materials

Six contrasting rice genotypes based on their rooting pattern or drought tolerance were selected and used. These

genotypes were KDML105 (lowland-adapted *indica*), IRAT109 (upland-adapted *japonica*), FR13A (submergence tolerant *aus*), Nipponbare (lowland-adapted *japonica*), Rexmont (lowland-adapted *japonica*), and Swarna (lowland-adapted *indica*). In our previous studies, KDML105 showed greater ability for root plasticity, especially at the shallow soil depths (Bañoc, Yamauchi, Kamoshita, Wade, & Pardales, 2000; Kameoka et al., 2015) while IRAT109 showed faster root elongation rate (Bañoc et al., 2000) and greater deep root ratio (deep root length below 30 cm depth to TRL) (Kato, Abe, Kamoshita, & Yamagishi, 2006; Kato, Kamoshita, & Yamagishi, 2007) under drought soil conditions. FR13A is one of the most outstanding cultivars for submergence tolerance identified by International Rice Research Institute (Mackill, Coffman, & Garrity, 1996). Nipponbare is often used as a drought susceptible genotype and has poor root plasticity under drought (Kano et al., 2011). Rexmont (lowland rice *japonica*) is one of the rice diversity research sets of germplasm (Kojima, Ebana, Fukuoka, Nagamine, & Kawase, 2005), which showed drought resistance associated with root plasticity under mild drought stress (Inoue, 2009). Swarna is an important rainfed lowland rice cultivar grown in millions of hectares in Asia, but is highly susceptible to drought and aerobic soil conditions (Venuprasad et al., 2009).

Field experiment

The field experiments were conducted at the experimental farm of Nagoya University, Nagoya, Japan (lat. 35°6' 42"N, long. 137°4'57"E) during the summer season of 2010 and 2011. The experiments were conducted in the watertight experimental bed with LSS system under a rain-out shelter following the protocol as described by Kano et al. (2011) and Tran et al. (2014). The field was kept watertight with an underlying polyvinyl chloride (PVC) sheet laid at the soil depth of 20 cm below the soil surface assuming the presence of hardpan and a manually operated drainage system. Water mists were supplied from the nozzles on the PVC pipe installed in the center of the soil bed. Therefore, it is possible to create gradients of soil moisture or in other words, different intensities of drought stress (Figure 1). The soil type used was sandy loam (72.3% sand, 20.9% silt, 6.8% clay; pH 5.5) with field capacity at 27.0% w/w (gravimetric).

The seeds from each genotype were soaked in water and incubated in a seed germinator at 28 °C for 48 h prior to sowing. Pre-germinated seeds from each genotype were sown in nursery boxes at three seeds per hole. The seedlings were later thinned to one per hole at three days after sowing. The seedlings were raised under well-watered conditions for 25 days prior to transplanting. Each genotype was transplanted in a row with a length of 1.6 m. One healthy seedling with intact root system was transplanted per hill on the experimental field on 3 June 2010

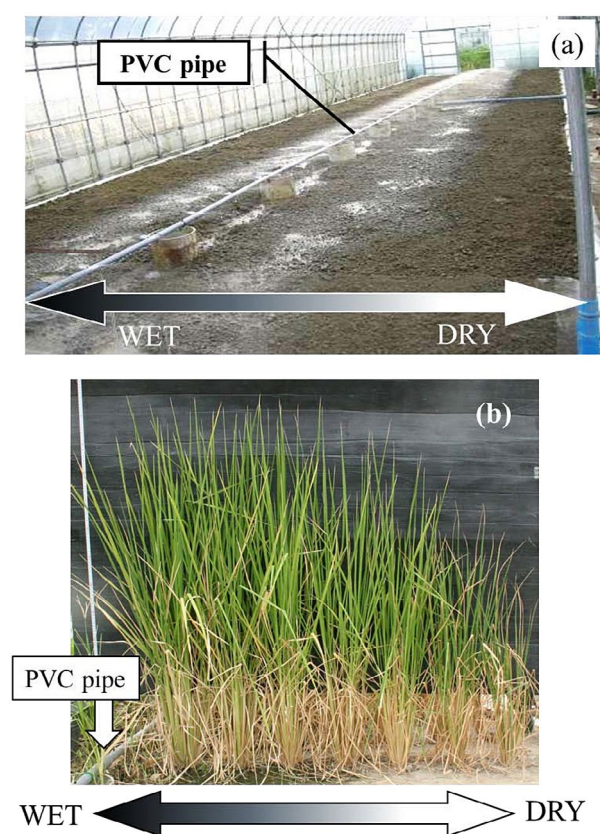


Figure 1. Line source sprinkler system in field experiment. (a) The soil moisture gradient along the distance perpendicular to the sprinkler system was created by the water comes out form the nozzles of the PVC pipe which is set at the center of the field. (b) Seven plants of KDML105 which are planted at 20, 40, 60, 80, 100, 120, and 140 cm from the PVC pipe at 113 DAT in 2010.

and 8 June 2011. Plant spacing was 40 cm between rows and 20 cm between hills such that each row contained 7 plants in 2010 and 8 plants in 2011 of a certain genotype that were exposed to different soil moisture contents (SMCs) as their distance from the LSS increased. Thus, the plants of each genotype in each row were grown at 20, 40, 60, 80, 100, 120, and 140 cm (in 2010) and up to 160 cm (in 2011) from LSS. The experiment was laid out following the randomized complete block design with three replications (1 row = 1 replication) for each genotype. Chemical fertilizer (14.0% N, 1.0% P₂O₅ and 14% K₂O) was applied up to 3.0 cm soil depth for each plant at a rate of 50 g m⁻² right after transplanting. The soil was kept well-watered using sprinkler irrigation for 14 days after transplanting (DAT) for optimum establishment. Thereafter, the drought stress was imposed by adjusting the irrigation pressure of the sprinkler.

Soil moisture measurements

The SMC at five points from the PVC pipe were constantly monitored with soil moisture sensors (EC-5 Decagon, Utah,

USA), so as to adjust the amount of irrigation to maintain the moisture gradient whenever necessary. In 2011, the water pressure from the LSS was adjusted intentionally to higher setting than that in 2010. As a result, the soil moisture condition was wetter in 2011 than that in 2010 as intended. For monitoring the effect of soil moisture intensities on plant growth, the number of tillers of KDML105 at different distances from LSS (0, 20, 40, 60, 80, 100, 120, and 140 cm) was measured at 21, 39, and 104 DAT in 2010 and at 9, 33, and 81 DAT in 2011.

The SMC at the soil depth of 0–12 cm were also measured using the time domain reflectometry probe (TDR; Tektronix Inc., Wilsonville, OR, USA) at 61 DAT in 2010 and at 55 DAT in 2011. Two stainless steel rods (15 cm in length) were inserted into the soil depth of 0–12 cm leaving a 3-cm length protruding above the soil surface, where TDR probes were attached to obtain SMC readings (Fujita, Nakamura, & Kameoka, 2011). The two parallel steel rods, which were 3 cm apart from each other, were inserted in the middle of two plants within each row.

The values provided by TDR (x) were converted into soil water contents (% w/w) (y) from an equation calibrated according to the gravimetric methods.

$$y = .6593x - 1.7033(n = 23, r = .99, p < .001) \quad (1)$$

Shoot sampling and measurement

The shoots were cut at the base on 110 DAT (at maturity for IRAT109, Rexmont and Nipponbare) in 2010 and on 64 DAT for IRAT109, 70 DAT for Rexmont, 76 DAT for Nipponbare and 81 DAT for KDML105, FR13A and Swarna (at heading stage for IRAT109, Rexmont and Nipponbare) in 2011, and then oven-dried at 70 °C for three days prior to recording of the shoot dry weight (SDW). KDML105, FR13A and Swarna did not flower in both 2010 and 2011 due to their photosensitivity.

Root sampling and measurements

Root samplings were done immediately after taking the shoot samples. Soil samples with roots were extracted by using stainless cylinder of 15 cm in diameter (Kang & Morita, 1994) inserted to the soil down to 20 cm depth. 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. The nodal root number (NRN) was manually counted and nodal root length (NRL) was measured manually with ruler. We have been able to quantitatively evaluate the effects of water deficit, soil moisture fluctuation and nitrogen application on the expression of phenotypic plasticity of RSD and detect the genotypic difference with the same monolith method (Kano et al., 2011; Niones et al., 2012;

Tran et al., 2014), and so we conclude that the variance in the root number cut by monolith among genotypes would be negligible for the evaluation of the root response to the soil moisture conditions among genotypes. For TRL 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 gray scales. The TRL was determined using a macro program developed by Kimura, Kikuchi, and Yamasaki (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 lateral root length (LRL) for each plant was calculated as the difference between TRL and total NRL. Branching index (BI) for each plant was calculated as LRL divided by NRL (Morita & Collins, 1990).

Statistical analysis

The analysis of variance (ANOVA) was performed in R ver. 3.1.2 (R Foundation for Statistical Computing, Vienna, Austria). Mean comparisons were determined using Tukey's honestly significant difference at 5% level of significance. A Pearson correlation was used to generate and analyze the association among component root traits.

Results

Trends in moisture gradients at shallow soil depth at different distances from the LSS

The SMC at the soil depth of 0–12 cm gradually decreased with time and increase with distance from the LSS in both years (Figure 2). The SMC at all distances from the LSS on 61 DAT in 2010 were significantly lower than those at 55 DAT in 2011 except at the distances of 20 and 40 cm from the LSS (Figure 3).

Effects of soil moisture gradient on tiller production with strength of water pressure and transmission of time

Figure 4 shows the effects of soil moisture gradients on the number of tillers during different stages of growth. At the onset of drought treatment, the number of tillers was similar among plants regardless of distance from LSS. As the different intensities of drought progressed with time, the number of tillers significantly differed among plants with different distances from LSS and years of experiment. In 2010, the number of tillers of KDML105 at the distances of more than 40 cm from the LSS was lower than those closer to the LSS at 39 and 104 DAT. In 2011, on the other hand, the number of tillers of KDML105 at the distances

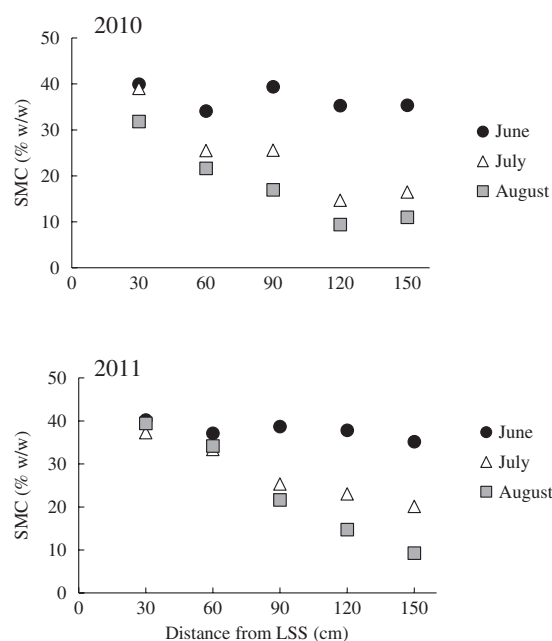


Figure 2. SMC at surface soil layer (0–12 cm) at different distances from line source sprinkler (0, 30, 90, 120, and 150 cm) measured using soil moisture sensors (EC-5 Decagon, Utah, USA). The SMC was measured every hour and then averaged for each month.

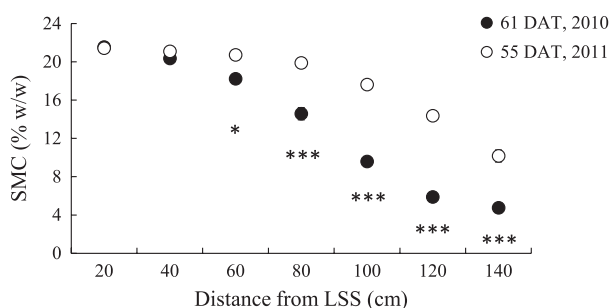


Figure 3. SMC at surface soil layer (0–12 cm) at different distances from line source sprinkler (0, 20, 40, 60, 80, 100, 120, and 140 cm) measured using a time-domain reflectometry probe (TDR; Tektronix Inc., Wilsonville, OR, USA) on 61 DAT, 2010 and on 55 DAT, 2011. * and *** indicate significant difference at $p < .05$ and $p < .001$ between SMC in each year by student's t -test, respectively.

of more than 40 cm was lower than those closer to LSS at 81 DAT but not at 33 DAT (Figure 4).

Shoot dry matter production and root system development

The BI at 40, 60, and 80 cm from the LSS were significantly higher than that at 20 cm from the LSS in 2010, while that at 60 and 80 cm from the LSS were significantly higher than that at 20 cm from the LSS in 2011 (Table 1). Tables 2 and 3 show the SDW, the number of tillers and the different root traits at different distances from the LSS in 2010 or both

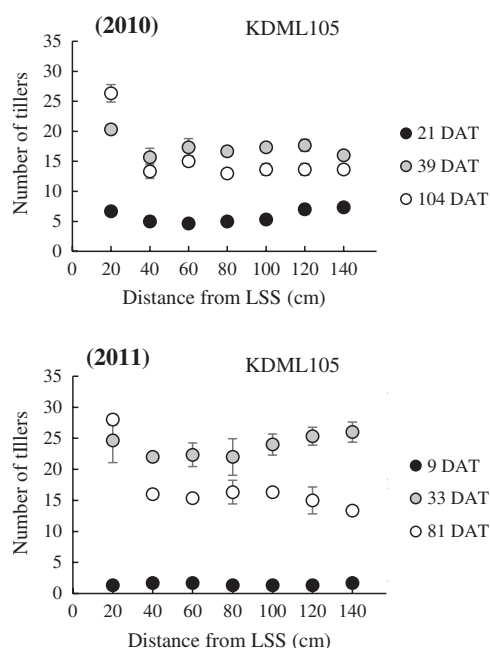


Figure 4. Number of tillers of KDML105 at different distances (0, 20, 40, 60, 80, 100, 120, and 140 cm) from line source sprinkler at 21, 39, 62, and 104 DAT in 2010 and at 9, 55, 81 DAT in 2011.

Table 1. BI at the different distances from LSS.

Distance from LSS (cm)	2010	2011
20	10.7 b	7.9 bc
40	14.5 a	10.3 ab
60	15.5 a	11.8 a
80	16.3 a	11.3 a
100	11.2 b	9.9 ab
120	9.6 b	10.1 ab
140	9.3 b	6.6 c

Note. Values followed by the same letter within each year are not significantly different at $P < .05$ by Tukey's HSD test.

years and the ANOVA on the effects of distances from the LSS and genotype, and their interactions on these traits. There were significant interactions between distances from the LSS and genotype on SDW in both 2010 (Table 2) and 2011 (Table 3). On the other hand, there was significant interaction between the distances from the LSS and genotype on TRL, NRN per tillers, NRL per NRN in 2010 only. There were no significant interactions between distances from the LSS and genotypes on BI in both 2010 and 2011 (Table 2). All the genotypes showed higher BI at the distances of 40, 60, and 80 cm from the LSS compared to that of 20 cm from the LSS in both years (Tables 2 and 3).

It is interesting to note that IRAT109 and Rexmont showed maintained RSD in both years, which was associated with maintained nodal root development and less promoted branching due to less expressed plasticity compared to KDML105 in 2010.

Discussion

Soil moisture control with LSS system

The soil moisture gradient along the distance perpendicular to the sprinkler system was successfully generated by the LSS throughout the experimental period in both years (Figure 2). The drought intensity generated by the LSS was significantly higher in 2010 than in 2011 (Figure 3) due to their differences in the strength of sprinkler water pressure, which also explained why the response in plant growth appeared in earlier in 2010 than in 2011 (Figure 4). These results show that the intensities of moisture gradients in the soil above hardpan can be precisely manipulated with careful adjustment of the irrigation pressure in the LSS system.

Expression in the plasticity of LRs in response to soil moisture availability

All genotypes showed similar trends in the expression of increased branching (LR development) based on BI in response to decreasing soil moisture gradients in both years (Table 1) suggesting that the expression of increased branching in response to the drought may be common regardless of rice genotypes. The expression of increased branching was more evident in the middle distance from LSS than either the closest (wettest soil) or farthest (driest soil) from the sprinkler (Table 1). Using chromosome segment substitution lines derived from Nipponbare and Kasalath crosses, Kano et al. (2011) and Kano-Nakata et al. (2011) showed that the increase in branching was greatest under mild drought as a result of expression of root plasticity. These findings suggest that soil conditions at the distances from the LSS where the greatest increase in branching was observed in this study are defined as mild drought conditions under which root plasticity in branching (LR development) was expressed. Thus, the distances of 40, 60, and 80 cm from the LSS in 2010 (14.6~20.4% w/w SMC on 61 DAT) and the distances of 60 and 80 cm from the LSS in 2011 (19.9~20.7% w/w SMC on 61 DAT) were considered as mild drought conditions in this study.

Effect of drought intensity on nodal root development and its contribution to the entire root system development

The increase in NRN and NRL were less than in BI under mild drought condition relative to those at 20 cm from the LSS in both years (Tables 2 and 3). Especially, NRN under mild drought condition tended to be lower than that at 20 cm from the LSS in both years. Furthermore, the significant genotypic differences in the expression of nodal

Table 2. Shoot dry weight (SDW, g plant⁻¹), Number of tillers (TN plant⁻¹), TRL (TRL, m plant⁻¹), NRN per tiller number (NRN TN⁻¹), NRL per NRN (NRL NRN⁻¹, m), and branching index (BI) among six genotypes at different distances from LSS (20, 40, 60, and 80 cm) on 110 DAT in 2010.

	SDW (g plant ⁻¹) (relative value; %)		TN (plant ⁻¹) (relative value; %)		TRL (m plant ⁻¹) (relative value; %)		NRN (TN ⁻¹) (relative value; %)		NRL(m NRN ⁻¹) (relative value; %)		BI(LRL NRL ⁻¹) (relative value; %)	
2010												
20 cm from LSS												
KDML105	142.7	-100	26	-100	492.8	-100	42	-100	.049	-100	8.2	-100
IRAT109	41.9	-100	11	-100	248.9	-100	18	-100	.109	-100	10.5	-100
FR13A	109.7	-100	28	-100	497.7	-100	28	-100	.06	-100	9.7	-100
Nipponbare	49.1	-100	13	-100	283.9	-100	45	-100	.059	-100	7.2	-100
Rexmont	21.7	-100	7	-100	273.1	-100	31	-100	.078	-100	14.6	-100
Swarna	58.9	-100	22	-100	423.5	-100	22	-100	.06	-100	14.3	-100
40 cm from LSS												
KDML105	78.2	-57	13	-52	516.8	-105	46	-110	.056	-115	14.3	-177
IRAT109	26.4	-71	9	-85	285.7	-114	20	-114	.101	-93	13.8	-137
FR13A	103.1	-94	22	-81	496.2	-100	29	-105	.062	-103	11.6	-120
Nipponbare	38.3	-78	14	-110	332	-117	33	-73	.066	-111	9.5	-132
Rexmont	19.3	-88	7	-99	313.2	-112	29	-95	.082	-105	18.4	-123
Swarna	49.1	-84	18	-85	528.9	-126	22	-102	.063	-106	19.4	-142
60 cm from LSS												
KDML105	75.2	-55	15	-58	410.5	-82	28	-65	.059	-121	15.6	-196
IRAT109	40.1	-107	10	-91	310.8	-125	22	-123	.094	-87	14.2	-141
FR13A	84.5	-77	19	-67	448.4	-90	26	-94	.057	-95	15.1	-156
Nipponbare	38.3	-78	14	-105	316.3	-111	34	-76	.063	-106	9.6	-134
Rexmont	22.1	-101	8	-113	342.6	-126	25	-83	.081	-103	20.4	-140
Swarna	46.7	-80	17	-81	491.3	-117	22	-102	.068	-113	17.8	-132
80 cm from LSS												
KDML105	51.9	-38	13	-50	212	-42	20	-46	.045	-93	16.5	-205
IRAT109	35.6	-93	10	-88	260.3	-105	22	-122	.092	-85	12.2	-124
FR13A	62.6	-57	14	-51	357.1	-72	24	-87	.061	-102	16	-165
Nipponbare	27.9	-57	14	-108	230.6	-81	25	-55	.06	-100	9.5	-132
Rexmont	22.1	-101	7	-100	298.7	-112	24	-80	.075	-96	21.8	-154
Swarna	40.4	-69	19	-89	604.4	-147	18	-84	.076	-127	21.8	-167
Distance	***	*	***	***	ns	***						
Genotype	***	***	***	***	***	***						
D × G	***	**	***	***	*	ns						

Note. D – distance from LSS; G – genotype.
* $P < .05$; ** $P < .01$; *** $P < .001$, respectively.

root development under mild drought conditions were evident in 2010 only, the year in which the moisture gradients were drier than in 2011 (Tables 2 and 3). These results suggest that nodal root development was more susceptible to drought than the LR development, with some evidence of genotypic differences in their magnitude of nodal developmental responses to drought. On the other hand, LR development consistently showed plasticity under mild drought conditions, which contributed in the promoted root system development. These observations can be typically exhibited by KDML105, which drastically reduced its TRL under mild drought stress in 2010 in spite of its greater promotion in LR development (branching). Such reduction in the entire RSD in KDML105 under mild drought was attributed to the greater reduction in its ability to maintain nodal root production from individual tiller. Thus, under mild drought in 2010, the ability to maintain greater RSD under mild drought was a function of the ability to maintain nodal root production and elongation but not LR development (Tables 2 and 3).

Furthermore, the results above also show that nodal root and LR have differing developmental responses to drought conditions. The nodal root development in response to drought is genotype dependent, while that of the LRs is consistent regardless of genotypes as shown in the current study. Furthermore, it is also worth noting that the nodal root development is an important factor that determined the entire RSD, especially when the drought stress was more intensified (Tables 2 and 3).

As stated earlier, we previously reported that IRAT 109 expressed its deep rooting trait by allocating greater amount of dry matter to deeper soil layer under the condition of no hardpan (Kameoka et al., 2015). On the other hand, it showed relative stable growth responses of nodal roots and less plasticity in branching (LR development) under various drought intensities in this study in which roots were confined in the shallow soil layer. In contrast, KDML105 showed very sharp plasticity in LR development regardless of drought intensities, while its nodal root development tended to be inhibited shown in this study. These

Table 3. Shoot dry weight (SDW, g plant⁻¹), Number of tillers (TN plant⁻¹), TRL (TRL, m plant⁻¹), nodal root number per tiller number (NRN TN⁻¹), NRL per NRN (NRL NRN⁻¹, m), and branching index (BI) among six genotypes at different distances from LSS (20, 40, 60, and 80 cm) on 64 DAT for IRAT109, 70 DAT for Rexmont, 76 DAT for Nipponbare and 81 DAT for KDML105, FR13A and Swarna in 2011.

	SDW (g plant ⁻¹) (relative value; %)	TN (plant ⁻¹) (relative value; %)	TRL (m plant ⁻¹) (relative value; %)	NRN (TN ⁻¹) (relative value; %)	NRL(m NRN ⁻¹) (relative value; %)	BI(LRL NRL ⁻¹) (relative value; %)	SDW (g plant ⁻¹) (relative value; %)	TN (plant ⁻¹) (relative value; %)	TRL (m plant ⁻¹) (relative value; %)	NRN (TN ⁻¹) (relative value; %)	NRL(m NRN ⁻¹) (relative value; %)	BI(LRL NRL ⁻¹) (relative value; %)
2011												
20 cm from LSS												
KDML105	124	-100	28	-100	473.6	-100	29	-100	.06	-100	9.3	-100
IRAT109	47.1	-100	14	-100	349.8	-100	26	-100	.1	-100	9.2	-100
FR13A	134.5	-100	27	-100	476.7	-100	36	-100	.07	-100	7.5	-100
Nipponbare	50.2	-100	16	-100	356.5	-100	49	-100	.06	-100	6.7	-100
Rexmont	35.9	-100	11	-100	222.2	-100	28	-100	.1	-100	6.9	-100
Swarna	80	-100	38	-100	390.5	-100	18	-100	.07	-100	7.7	-100
40 cm from LSS												
KDML105	93.5	-77	16	-57	502	-107	39	-134	.06	-112	12	-127
IRAT109	28.8	-67	11	-80	337.8	-101	26	-101	.11	-112	10.4	-113
FR13A	91.6	-72	17	-82	516.4	-108	34	-100	.07	-107	11.3	-159
Nipponbare	39.4	-79	14	-88	348.9	-100	45	-92	.06	-104	8.1	-123
Rexmont	24.1	-69	9	-85	226.6	-103	28	-100	.1	-100	8.6	-126
Swarna	59.2	-75	25	-65	462.6	-118	21	-120	.07	-105	11.6	-150
60 cm from LSS												
KDML105	82.9	-68	15	-55	512.1	-109	30	-104	.07	-119	15.8	-169
IRAT109	32.5	-75	11	-79	365	-106	24	-95	.11	-116	12	-131
FR13A	91.5	-71	17	-80	469.9	-98	29	-86	.07	-105	12.1	-168
Nipponbare	43	-86	16	-99	346.1	-99	36	-75	.07	-114	8.2	-124
Rexmont	32.4	-94	12	-115	271.3	-127	24	-89	.1	-99	9	-132
Swarna	56.7	-71	26	-69	461.6	-118	17	-99	.07	-107	13.6	-177
80 cm from LSS												
KDML105	70.3	-57	16	-58	399.1	-86	25	-84	.08	-136	12.5	-134
IRAT109	32.5	-78	11	-82	311.7	-92	24	-94	.1	-105	11.2	-122
FR13A	66.8	-53	15	-74	402.1	-84	25	-75	.07	-107	14.1	-200
Nipponbare	43.5	-88	17	-103	330.2	-96	35	-71	.06	-111	8	-122
Rexmont	30.7	-89	10	-99	261.7	-118	24	-88	.09	-97	10.5	-159
Swarna	45.2	-57	24	-64	369.3	-96	17	-95	.07	-109	11.4	-148
Distance	***	ns	***	***	**	***						
Geno- type	***	***	***	***	***	***						
D × G	*	ns	ns	ns	ns	ns						

Note. D – distance from LSS; G – genotype.

* $P < .05$; ** $P < .01$; *** $P < .001$.

results suggest that regardless of soil depth and presence of hardpan, the development of both nodal and LR of IRAT 109 are less affected by drought conditions, while KDML105 consistently expresses its plasticity in branching and substantially reduced its nodal root development under drought condition.

Furthermore, Swarna was not as drought tolerant as IRAT109 and Rexmont despite its ability to increase TRL under mild drought (Tables 2 and 3). These findings suggest that the root water uptake ability in Swarna may have severely decreased under drought compared with other genotypes such as IRAT109 and Rexmont. Some studies showed no relationship between TRL and water uptake ability (e.g. Gowda, Henry, Vadez, Shashidhar, & Serraj, 2012; Lilley & Fukai, 1994) and a reduced root hydraulic

conductance in rice under drought condition (Matsuo, Ozawa, & Mochizuki, 2009), which may be associated with some morphological changes in RSD (Henry, Cal, Banato, Torres, & Serraj, 2012). To understand the function and mechanism in water uptake of roots under drought, it may be more meaningful if other indicators such as root hydraulic conductivity in addition to TRL will be used for the studying root water uptake ability.

Conclusion

In this study, the LSS system successfully created the soil moisture gradients along the distance perpendicular to water sprinkler in the two-year study conducted. With the higher intensity of drought in 2010, nodal root

development was greatly inhibited in some genotypes including KDML105, which resulted in the reduction of entire RSD in spite of the expression of promoted LR branching. In contrast, with the lower intensity of drought in 2011, nodal root development was generally maintained in all six genotypes and thus RSD was enhanced or maintained by the expression of increased LR branching. Furthermore, the nodal root development mainly determined the entire RSD, especially under drier conditions even within mild drought conditions. These results indicate that the nodal root development generally expresses less plastic response to drought than LR and that nodal root development is important to enhance the contribution of LR branching to the entire root system development. This study also suggests that the effects of soil moisture on root development may be differed depending on the kind of component root trait. The precise assessments of soil environments such as soil moisture condition in the rice fields are quite important for the better understanding of the mechanism of root system responses to drought stress.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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*In Japanese with English abstract.

**In Japanese.