

Growth of Rice (*Oryza sativa* L.) Cultivars under Upland Conditions with Different Levels of Water Supply

3. Root System Development, Soil Moisture Change and Plant Water Status

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Abstract : A deep root system may be a desirable plant characteristic in upland rice because it improves the plant's water extraction capacity. The objective of the present study was to assess the deep root development of rice cultivars in relation to soil moisture change and plant water status under upland conditions with moderate water deficits in the field and in simple lysimeter experiments. We used one upland cultivar ('Yumeno-hatamochi' [YHM]) and two lowland cultivars ('Lemont' [LMT] and 'Nipponbare' [NPB]) in the field experiment, with no supplemental water from 88 to 106 days after sowing (DAS) and 116 to 145 DAS. In the lysimeter experiment, we used YHM and NPB and imposed two water stress periods during the late vegetative stages (71 to 104 DAS and 88 to 104 DAS). In the lysimeter experiment, a higher deep-root length ratio (proportion of the length of deep roots to the total root length) in YHM was associated with a greater deep-root length than in NPB. The difference in deep root development was associated with change in soil water content at the depths of 45 to 70 cm between the two cultivars under the above conditions. The drought in the field experiment was less intense than in the lysimeter experiment, and we observed greater varietal differences in total aboveground biomass than in root system development; this was associated with the change in soil water content during the initial drought period. LMT, with smaller shoots, tended to save water and maintain higher leaf water potential and lower diffusion resistance as the drought progressed. Our results suggest that deep root development of rice was primarily advantageous for soil water extraction and plant water status under moderate water stress in uplands, but that the advantage of a deep root system was affected by total aboveground biomass, which had strong effects on plant water status under these conditions.

Key words : Deep roots, Lysimeter, Minirhizotron, Rice (*Oryza sativa* L.), Soil water depletion, Upland.

The yield of upland rice often decreases when the water supply declines (Kato et al., 2006b, 2007). Rice plants are unable to utilize soil water in the deeper layers because their root system is shallower than that of other crops (Angus et al., 1983; Fukai and Inthapan, 1988; Inthapan and Fukai, 1988; Kondo et al., 2000). If differences among rice cultivars exist in deep root development, they may affect the cultivar difference in the extraction of soil water and the rice plant's water status under water stress.

Several studies of the pot experiments rigorously estimated the dynamic changes of the soil water content in relation to root growth in rice (Azhiri-Sigari et al., 2000; Kamoshita et al., 2000, 2004). However, it is difficult to perform the field experiments to quantify

soil water profiles in the field, and high degrees of variation are usually expected. Thus, there have been still very few quantitative analyses of plant water use in rice in relation to the characteristics of its root system in the field (Lilley and Fukai, 1994a; Kobata et al., 1996). Moreover, there are no studies on detailed monitoring of the time course of soil water profile and soil moisture change during intermittent drought at the canopy level in the field. In contrast, lysimeters offer an effective way to monitor soil water dynamics at the whole-canopy level in the field (Maruyama et al., 1985; Tolk et al., 1997), and the rhizosphere environment is closer to that in agricultural systems than is the case with a long tube or root box.

The development of a deep root system results from

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Abbreviations : DAIS, days after imposing stress; DAS, days after sowing; MRLD, root length density measured by the minirhizotron method; RLD, root length density; RWD, root weight density; TDM, total aboveground dry matter.

Table 1. Root length density (RLD; cm cm^{-2})^(a) and root weight density (RWD; mg cm^{-2})^(a) at 0-60 cm depth and 30-60 cm depth, and DRL ratio (%) (dividing RLD at 30-60 cm by that at 0-60 cm) in three cultivars (Yumeno-hatamochi [YHM], Lemont [LMT] and Nipponbare [NPB]) on 139 days after sowing in the field experiment. Least significant difference (LSD) at $P=0.05$ (*) is also shown.

	RLD at 0-60 cm	RLD at 30-60 cm	RWD at 0-60 cm	RWD at 30-60 cm	DRL ratio
YHM	59	8.8	3.74	0.56	15
LMT	83	11.3	5.98	1.04	14
NPB	80	7.2	4.54	0.45	9
LSD	<i>n.s.</i>	<i>n.s.</i>	1.53*	0.38*	<i>n.s.</i>

n.s. means difference in the same column was not statistically significant.

(a) The soil cores (50-mm diameter) were taken at a distance of 10 cm from a row.

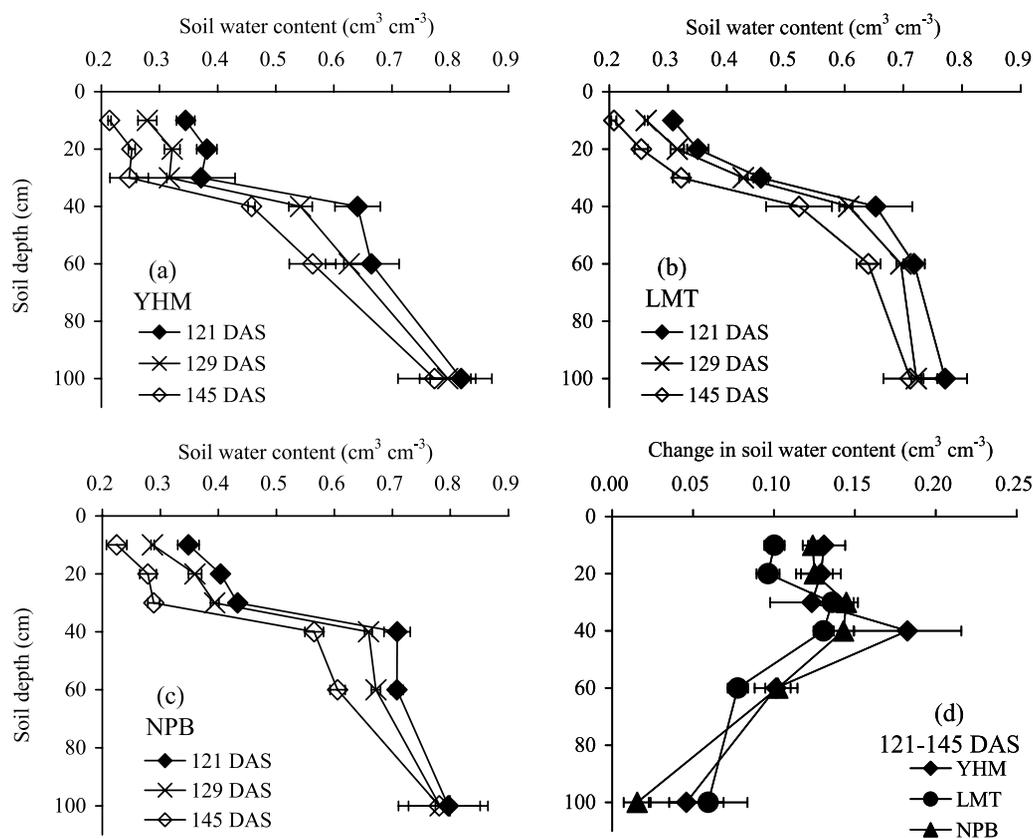


Fig. 1. Profile in soil water content at 121, 129 and 145 days after sowing [DAS] Yumeno-hatamochi [YHM] (a), Lemont [LMT] (b), Nipponbare [NPB] (c), and total amount of change in the content from 121 to 145 DAS (d) in the field experiment. Standard errors were also shown ($n = 3$).

several physio-morphological responses linked to both shoot and root growth (Abe and Morita, 1994; Nemoto et al., 1995; Araki and Iijima, 1998, 2001; Araki et al., 2002), such as the formation and elongation of adventitious roots, root angle, available assimilate and its partitioning between shoot and roots or within the root system, and the formation of lateral roots. Deep root systems are often quantified using different parameters by different researchers. These parameters include maximum rooting depth (Mambani and Lal,

1983; Araki et al., 2000), length or weight of deep roots (Yoshida and Hasegawa, 1982), and root distribution measures such as the deep root ratio (Kondo et al., 2003) and root depth index (Oyanagi et al., 1993). Despite common interest in a deep root system, it is tedious and time-consuming to destructively take root samples. This limits our understanding on the time-related deep root development at the canopy level. In contrast, the use of a minirhizotron method have allowed researchers to nondestructively monitor

Table 2. Leaf water potential (MPa) at pre-dawn (PD; 0400-0600) and mid-day (MD; 1200-1500) for three cultivars (Yameno-hatamochi [YHM], Lemont [LMT] and Nipponbare [NPB]) in the field experiment at 129 and 137 days after sowing (DAS). Least significant difference (LSD) at $P=0.05$ (*) and 0.10 (†) is also shown.

	129 DAS		137 DAS	
	PD	MD	PD	MD
YHM	-0.18	-1.07	-0.16	-1.12
LMT	-0.15	-0.61	-0.13	-0.77
NPB	-0.15	-0.98	-0.16	-0.76
LSD	<i>n.s.</i>	<i>0.37*</i>	<i>0.01*</i>	<i>0.29†</i>

n.s. means difference in the same column was not statistically significant.

the development of a deep root system over time of lowland rice (Beyrouthy et al., 1988), soybean (Hirasawa et al., 1995) and wheat (Asseng et al., 1998). However, there are no studies on the time-related root-system development of upland rice using a minirhizotron method.

For these reasons, in the present study we conducted the experiments using simple lysimeters and field trials to quantify the deep root development of rice and its relationship with change in soil water content and plant water status. We used rice cultivars with contrasting root systems (deep vs. shallow). In the lysimeter experiment, we constructed small, simple lysimeters equipped with soil moisture meters throughout the soil profile to monitor the soil water content at various depths, and combined this with a minirhizotron method to directly monitor root growth at the same time, instead of weighing or floating lysimeters which are costly. We discuss the advantages of a deep root system in rice under moderate water stress under upland conditions by combining the results of the lysimeter, minirhizotron, and field experiments.

Materials and methods

1. Field experiment

We conducted the field experiment at the Field Production Science Center of the University of Tokyo (Nishitokyo, Japan) in 2003. The soil was a volcanic ash soil of the Kanto loam type (Humic Andosol). The topsoil layer (0–35 cm) was a silty loam with bulk density of 0.77 g cm^{-3} , and the subsoil layer (below 35 cm) was a silty clay loam with bulk density of 0.50 g cm^{-3} (Yamagishi et al., 2003). Volumetric soil water content at field capacity (-0.01 MPa) and at wilting point (-1.5 MPa) of topsoil are 0.55 and $0.26 \text{ cm}^3 \text{ cm}^{-3}$, respectively. Volumetric soil water content at field capacity and at wilting point of subsoil are 0.65 and $0.48 \text{ cm}^3 \text{ cm}^{-3}$, respectively. A general description of the

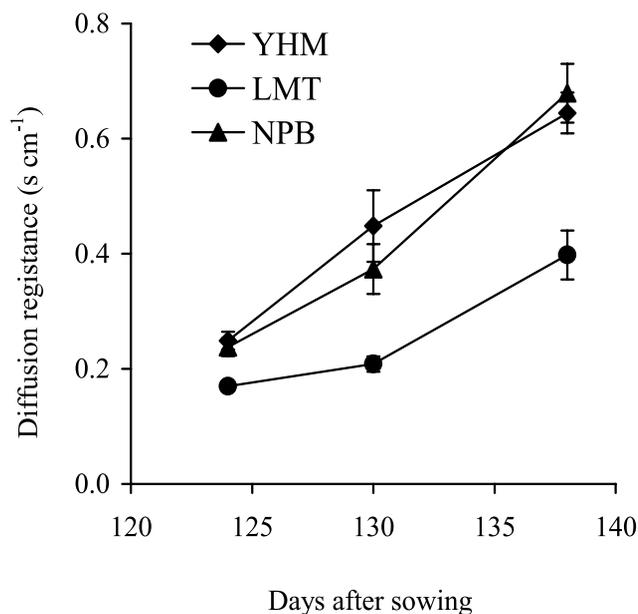


Fig. 2. Time courses of abaxial diffusion resistance in three cultivars (YHM [diamonds], LMT [circle] and NPB [triangle]) in the field experiment. Bars indicate standard error ($n=3$).

experimental design has been provided in a previous paper (Kato et al., 2006a). We used one upland cultivar ('Yumeno-hatamochi', YHM) and two lowland cultivars ('Lemont', LMT, and 'Nipponbare', NPB). YHM, LMT and NPB were sown on 2 May, 25 April and 21 April, respectively, because YHM, LMT matures earlier than NPB and we intended to match the stress period in similar phenological stages among the three cultivars. We calculated days after sowing (DAS) based on the NPB date. The rice was drill-seeded with 0.35 m row spacing, and plants were thinned to 29 hills m^{-2} . In the present paper, we performed our measurements under upland water-deficit conditions in 2003, with rainfall excluded under PVC rain shelter (a permanently installed arch-shaped polyvinyl mulch of 4.5 m height and 5.5 m width) and with irrigation stopped during the period from 88 to 147 DAS (a total of 59 days). However, because unexpected heavy storms flooded the experimental field on 107 and 115 DAS, the actual water deficit was imposed only between 88 and 106 DAS (18 days) and between 116 and 145 DAS (29 days). In addition, many cloudy days with low incident radiation and low temperatures, combined with the flooding, resulted in only moderate levels of drought stress.

We collected root samples at 139 DAS by extracting four soil cores per plot (to a depth of 60 cm , 50 mm in diameter) using a coring tube at a distance of 10 cm from the row of plants (mid position of adjacent hills along the row), as in the previous study (Kato et al., 2006a). We divided the cores into three soil layers: 0 to 15 cm , 15 to 30 cm , and 30 to 60 cm . After washing

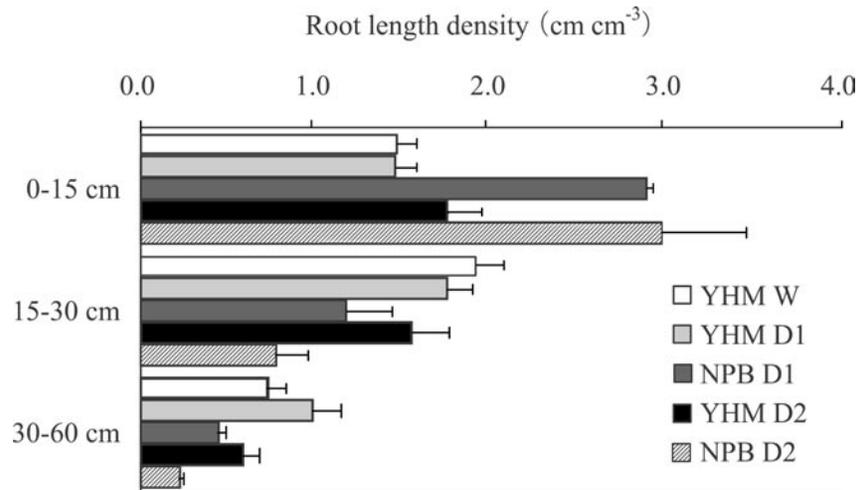


Fig. 3. Profile of root length density measured by core sampling method at 95 days after sowing in Yumeno-hatamochi (YHM) and Nipponbare (NPB) in well-watered (W) and drought plots (D1 and D2). Bars indicate standard error (n = 4).

the samples carefully, we determined root length using a Comair Root Length Scanner (Commonwealth Aircraft, Melbourne, Victoria, Australia), then dried the samples in an oven at 80°C for 3 days and measured root dry weight. The values of these root characteristics are shown by unit area basis (i.e., root length density (RLD); cm cm^{-2} or root weight density (RWD); mg cm^{-2}) for relative comparison among the cultivars, but note that they may not indicate the real values, because the cores were taken at limited positions (10 cm from the row).

We measured the volumetric soil water content in the soil profile (0 to 100 cm) using a profile probe (Profile Probe type PR1, Delta-T Devices, Burwell, UK) based on amplitude-domain reflectometry (Gaskin and Miller, 1996) at 89, 96, 103, 121, 129, and 145 DAS. The profile probe was calibrated in the laboratory for each soil component (topsoil (0–35 cm) and subsoil (below 35 cm)) in advance. We installed one access tube 10 cm from the row of plants in each plot, and took measurements at depths of 10, 20, 30, 40, 60, and 100 cm below the surface.

We measured the leaf water potential of the topmost fully expanded leaf on each of the two or three largest tillers using a pressure chamber (DIK-7002, Daiki Rika Kogyo, Saitama, Japan) during the pre-dawn period (0400 to 0600) and at midday (1200 to 1500) at 129 and 137 DAS. We also measured the diffusion resistance of the abaxial side of the topmost fully expanded leaf of each of the two largest tillers using a steady-state porometer (LI-1600, LI-COR, Lincoln, NE, USA) in the morning (1000 to 1200) on sunny days (124, 130, and 137 DAS). One measurement of midday leaf water potential or leaf diffusion resistance in one cultivar was followed by one of the other two cultivars, in order to minimize the effects of differences in the

sampling time and to make the cultivar comparison valid.

2. Lysimeter experiment

We conducted our lysimeter experiment using five lysimeters under a PVC rain shelter (a permanently installed arch-shaped polyvinyl mulch of 4.5 m height and 5.5 m width). At first, big holes (200 × 200 × 100 cm) was dug, and the lysimeters (200 × 200 × 100 cm) were fully embedded in the soil and covered all four sides and the bottom with a plastic sheet (0.5 mm in thickness). This simple lysimeter can not be weighed, but the inside the lysimeter is separated from the surrounding soil by a plastic sheet. In order to facilitate drainage from the soil, if necessary, we granulated the bottom 25-cm layer, covered by a 5-cm layer of sand. The resulting soil layer above these layers was 70 cm deep, and its bulk density averaged 0.78 g cm^{-3} (with little difference among depths), which was similar to the natural field condition. However, mechanical impedance was much less (i.e. less than 0.2 MPa for all depth) compared with the natural field condition (over 2 MPa in 30–40 cm) (Kato et al., 2007). We installed soil moisture meters with 20-cm-long sensors (EC-1, Decagon Devices, Pullman, USA) at depths of 5, 15, 25, 45, and 65 cm below the surface at a distance of 2.5 cm from the rows of plants in advance. We used five treatments based on two cultivars and three water regimes:

- well-watered (W), YHM cultivar.
- drought during 71–95 DAS (D1; late vegetative stage to panicle initiation), YHM and NPB cultivars.
- drought during 88–104 DAS (D2; around panicle initiation), YHM and NPB cultivars.

YHM and NPB were sown on 2 May and 21

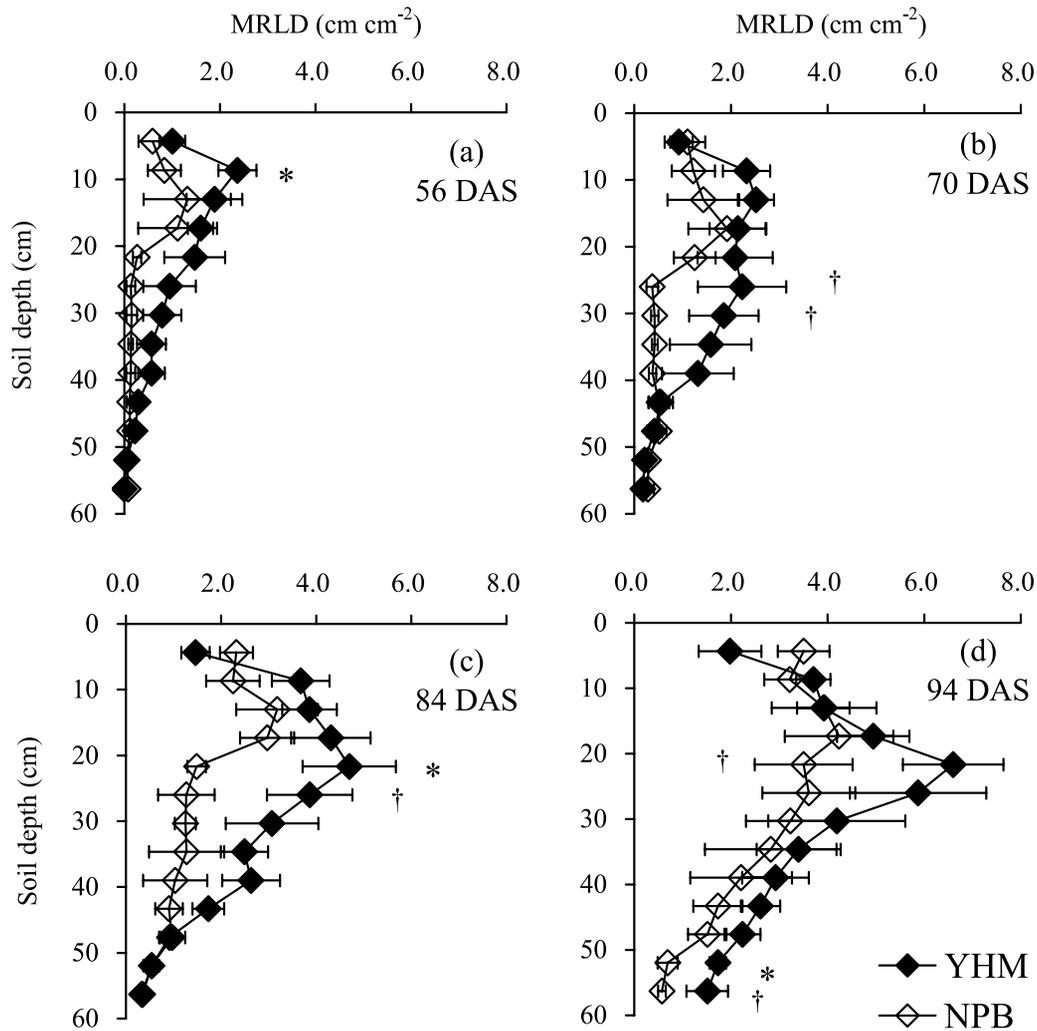


Fig. 4. Profiles of root length density measured by minirhizotron method (MRLD) in Yumehatamochi [YHM; solid symbol] and Nipponbare [NPB; open symbol] in drought plots of D1 at 56 days after sowing [DAS] (a), 70 DAS (b), 84 DAS (c) and 94 DAS (d). Bars indicate standard errors ($n = 4$), and * or † showed significant difference at $P = 5\%$ (*) or 10% (†) between the two cultivars by t-test.

April, respectively, on the same days as in the field experiment, and DAS was again calculated with respect to the planting date for NPB. We sowed three or four seeds in each hill, spaced at 10 cm apart within 25-cm-long rows, and plants were thinned to one plant per hill at 30 to 35 DAS (40 plants m^{-2}). Irrigation (15 mm) was supplied two or three times per week, except during the drought periods in D1 and D2. We applied a mixed fertilizer (High-analysis compound fertilizer A907, Coop Chemical Inc., Tokyo) as a top dressing at the time of sowing, at rate of 60 g m^{-2} (N, P, K = 12.0%, 7.8%, and 13.3%), and 22.9 g m^{-2} of ammonium sulfate (N = 21.2%) as a top dressing at 53 DAS.

We monitored the profile of volumetric soil water content every 6 hours (0000, 0600, 1200 and 1800) by connecting the soil moisture sensors to a datalogger (Em5R, Decagon Devices, Pullman, WA, USA). We estimated that the soil water content at depth of 65

to 70 cm is the same as the values at 65 cm. We also measured the volumetric soil water content in the 10-cm surface layer at five positions between the rows and hills with a portable time-domain reflectometry (HydroSense, Campbell Scientific, Logan, UT, USA) at 71, 81, 91, 98, and 104 DAS to check soil water status at the surface.

We sampled shoots and roots at 95 DAS in all the plots. We harvested the aboveground organs of nine plants from three randomly selected positions in each lysimeter, and determined TDM after drying the sample in an oven at 80°C for at least 3 days. We obtained root samples from four plants at a mid-row position, determined root lengths and weights, and calculated root length density through destructive sampling (RLD) for each soil layer, using the same procedure as in the field experiment. In D1, we monitored root growth to a depth of 60 cm at 56, 70,

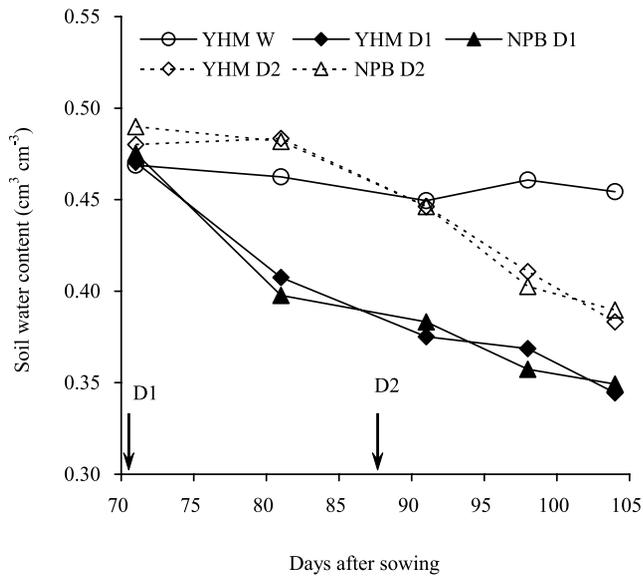


Fig. 5. Changes in soil water content at the surface (0-10 cm) with time (from 71 days after sowing [DAS] to 104 DAS) for Yumeno-hatamochi (YHM) and Nipponbare (NPB) in well-watered plot (W) and drought plots (D1 and D2) in the lysimeter experiment. Arrows indicate the onset of drying period (71 DAS in D1 and 88 DAS in D2).

80, and 94 DAS using a minirhizotron system (Daiki Rika Kogyo Co., Ltd, Saitama, Japan). Two transparent acrylic tubes (122 cm long, 5 cm square) were installed per plot, running parallel to the rows of plants but at an angle of 60 degrees to the soil surface. The portion of the tube that projected above the ground was covered with tinfoil to prevent exposure of the root system to sunlight. Color images of the soil profile (i.e., tube-soil interface) were obtained by resolution of 2000 dpi at 1.25-cm intervals along the acrylic tube with inserting a device equipped with a digital video camera (single 1/4-inch CCD) and white LED lamps into the tube. We observed roots on both the left and the right side of each tube. We determined the root length per unit area of the soil profile photographed by this minirhizotron method (MRLD; cm cm^{-2}) by analyzing the digital photographs using the line-intersection method (Tennant, 1975).

Results

1. Field experiment

(1) Root growth

RLD and RWD at 0–60 cm were highest in LMT, followed by NPB and YHM (Table 1). RWD at 30–60 cm was highest in LMT, but RLD at 30–60 cm did not differ significantly among the cultivars. The DRL ratio, which represents the ratio of root length at 30–60 cm to that at 0–60 cm, was the highest in YHM, followed by LMT and NPB, but the differences were not significant.

(2) Soil moisture profiles

Volumetric soil water content during the first half of the water-deficit period (from 89 to 103 DAS) changed only in the surface 30 cm and the pattern of the soil water depletion was similar among the three cultivars (data not shown). Fig. 1 shows the profiles of volumetric soil water content during the last half of the water-deficit period (from 121 to 145 DAS). All cultivars began to deplete soil moisture from the surface layer (10 to 20 cm in depth), but YHM also depleted water in deeper layers (30 to 40 cm in depth) earlier in the period of water stress than did the other cultivars; i.e., the tendency of rapid soil moisture depletion along the soil profile (e.g., 129 DAS; Figs. 1a,b,c). On the contrary, after 129 DAS (129–145 DAS), all cultivars showed similar change in soil water content along the profile. During the latter half of the water-deficit period, YHM tended to extract more water at a depth of 40 cm than did the other cultivars, although the difference was not significant ($P = 0.23$; Fig. 1d).

(3) Plant water status during the drought

The pre-dawn leaf water potential at 137 DAS was significantly higher in LMT than in YHM and NPB (Table 2). The leaf water potential at midday was lowest in YHM at both 129 and 137 DAS, and the difference was significant. LMT had consistently and significantly lower diffusion resistance than YHM and NPB (Fig. 2), and this difference in the resistance increased as the soil dried.

2. Lysimeter experiment

(1) Shoot and root growth

In the D1 treatment, TDM at 95 DAS was heavier in YHM than in NPB (321 vs. 229 g m^{-2}), but the difference was not significant ($P = 0.17$, $n = 3$). In the D2 treatment, TDM at 95 DAS did not differ between YHM and NPB (275 vs. 274 g m^{-2}). In the W treatment, the TDM of YHM was 283 g m^{-2} at 95 DAS. TDM of YHM among D1, D2 and W was not significantly different ($P = 0.64$).

The amount and distribution of destructively sampled root length of the cultivars did not differ between the D1 and D2 treatments (Fig. 3), as well as root dry weight (data not shown). The water regime also caused little difference in the RLD in YHM and in its distribution among the three soil layers (Fig. 3). However, YHM and NPB differed significantly in the distribution of root length; RLD was higher in NPB than in YHM at a depth of 0 to 15 cm ($P < 0.01$ in D1, $P = 0.06$ in D2 by t-test), but RLD below 15 cm was significantly higher in YHM than in NPB ($P = 0.05$ in D1, $P = 0.01$ in D2 by t-test).

The value of MRLD (y) at the 15–30 cm and 30–60 cm depth was correlated with the RLD (x) at these depths ($y = 0.29x + 0.08$; $n = 4$, $r = 0.97^*$); MRLD thus

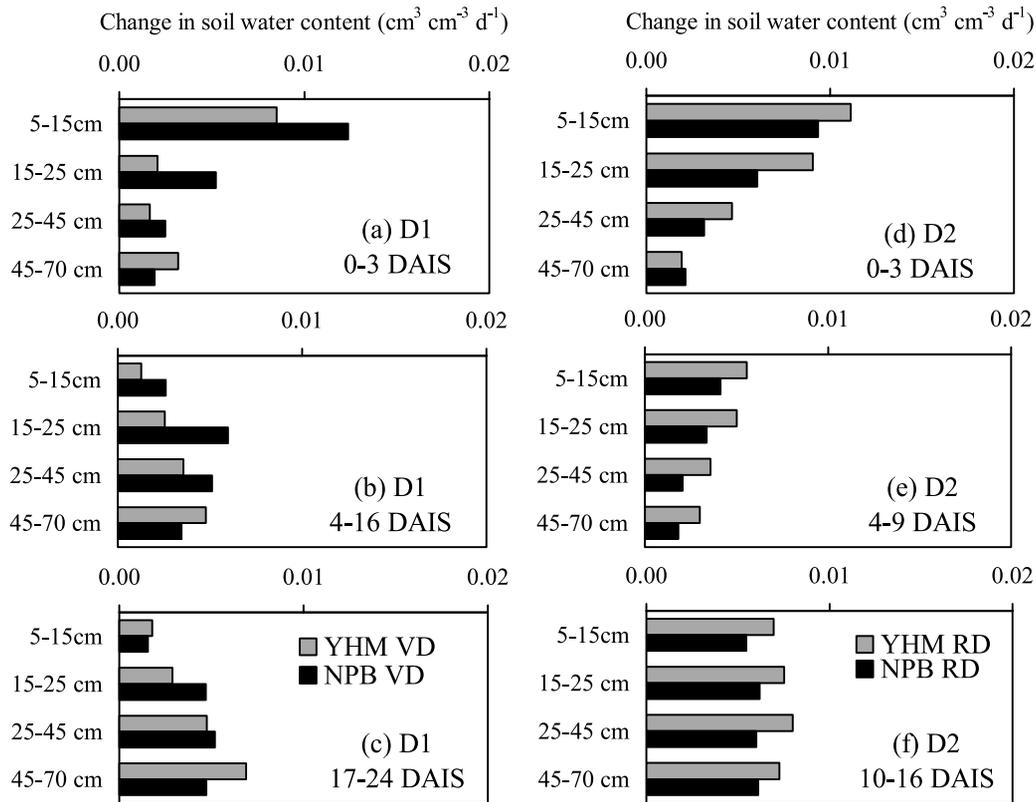


Fig. 6. Profiles of changes in soil water content in the plot with Yumeno-hatamochi [YHM] and Nipponbare [NPB] under drought of D1 (0-3 days after imposing stress [DAIS; a], 4-16 DAIS [b], 17-24 DAIS [c]) and D2 (0-3 DAIS [d], 4-9 DAIS [e], 10-16 DAIS [f]).

equaled approximately 29% of RLD below 15 cm. However, MRLD in the surface 10 cm of soil tended to be lower than that below the 10-cm layer, as is often the case in this method (Merrill and Upchurch, 1994; Samson and Sinclair, 1994; Ephrath et al., 1999). We could not monitor the rate of root elongation to the maximum rooting depths because both cultivars had already reached the bottom of at least one of the minirhizotron's acrylic tubes (i.e., a depth of 60 cm) by the first measurement at 56 DAS. However, the MRLD values in NPB were relatively low below 30 cm until at least 70 DAS, and maximum MRLD in NPB always occurred at a depth of 10 to 20 cm (Fig. 4). In contrast, the maximum MRLD in YHM was found at a depth of 20 to 30 cm after 70 DAS. MRLD in YHM was significantly higher than that in NPB from the earlier growth stages (70 and 84 DAS) at a depth of 20 to 30 cm, and the later growth stages (94 DAS) at a depth of 50 to 60 cm.

(2) Soil moisture profiles

The volumetric soil water content at a depth of 0 to 10 cm decreased from $0.48 \text{ cm}^3 \text{ cm}^{-3}$ to $0.35 \text{ cm}^3 \text{ cm}^{-3}$ and to $0.39 \text{ cm}^3 \text{ cm}^{-3}$ in D1 and D2 treatments, respectively, after imposition of drought stress, and the difference between YHM and NPB was little in both the D1 and D2 treatments (Fig. 5). Fig. 6 shows the

change in soil water content ($\text{cm}^3 \text{ cm}^{-3} \text{ d}^{-1}$) of each soil layer (5 to 15, 15 to 25, 25 to 45, and 45 to 70 cm). In the W treatment, the change in soil water content below 25 cm was smaller than that at a depth of 5–25 cm (data not shown). However, in both the D1 and the D2 treatments, the change in soil water content below 25 cm started to exceed that at a depth of 5–25 cm at about 4 DAIS. In D1, the soil water content at a depth of 5–15 cm decreased little for both cultivars between 4 and 24 DAIS, while the change in soil water content at a depth of 45 to 70 cm was the largest in the soil layers between 17 and 24 DAIS in both cultivars. Soil moisture change at a depth of 45 to 70 cm tended to be larger in the plot with YHM than NPB from 17 to 24 DAIS in D1. In the D2 treatment, the change in soil water content in a surface soil layer decreased with time after imposing stress, while that in a deeper soil layer increased in the plots with both cultivars. In both D1 and D2, the soil water depletion at a depth of 45 to 70 cm during the drying period was significantly correlated with the surface (0 to 10 cm in depth) soil moisture in the plots with both YHM ($r = -0.89^*$) and NPB ($r = -0.83^*$; Fig. 7), and soil moisture at a depth of 45 to 70 cm reduced more for YHM than NPB during drought stress.

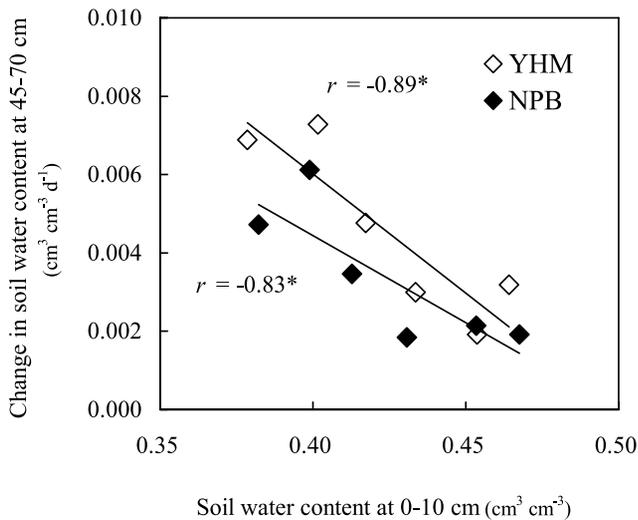


Fig. 7. Relationship between soil water content at 0-10 cm and changes in soil water content at 45-70 cm in the plot with Yumeno-hatamochi (YHM) and Nipponbare (NPB) under drought (D1 and D2). The data was the same as Fig. 6 for the changes in soil water content.

Discussion

1. Deep root development

Cultivar differences in deep root development was consistent to some extent but with some evidence of cultivar by environment interactions. YHM had a higher RLD at 30–60 cm depth than NPB in the lysimeter experiment (Fig. 3) and in a previous paper in which RLD was examined under rainfed upland conditions with adequate rainfall in 2002 (Kato et al., 2006a); this higher RLD at deeper soil layer in YHM resulted from a higher DRL ratio than for NPB (Kato et al., 2006a). On the other hand, in the field experiment, RLD at 30–60 cm depth did not differ among cultivars after the heading stage (Table 1). The deep root traits of YHM are derived from a tropical deep rooted rice cultivar, JC81 (Hirasawa et al., 1998), and it might be more affected by low air temperatures and low levels of solar radiation during the panicle-development stage in the field experiment, compared with LMT and NPB, resulting in lower RLD and RWD at 0–60 cm in YHM (Table 1). Greater distribution of roots in deeper soil layers was necessary for the development of a deep root system in the field, which confirms the results of Azhiri-Sigari et al. (2000) in pot experiments. YHM is used as a donor parent of deep root traits in a breeding program for drought resistance in upland rice in Japan (Manabe et al., 2005) and quantitative trait loci (QTLs) for deep root traits have been identified from a mapping population derived from YHM and a Japanese lowland rice cultivar. Although the numbers of QTLs for deep root characteristics in rice are regarded as putative drought resistance traits and would be useful for certain types

of drought (Champoux et al., 1995; Kamoshita et al., 2002a, b), elucidation of physiological mechanisms of deep root development (e.g. large partitioning into roots plus large partitioning into deep roots) and identification of environments in which deep root character is most fully expressed would be needed to better utilize the deep root traits and their QTLs for genetic improvement of drought resistance in rice.

The dynamics of root development was demonstrated by the minirhizotron experiment. NPB appears to have the longest roots that is comparable to that of YHM, since the deepest roots of both cultivars reached a depth of at least 60 cm by 56 DAS. In another study, we also observed that some roots of NPB had reached depths of more than 70 cm by 50 DAS, where a hardpan existed in the topsoil layer at our experimental site (Urasaki et al., 2002). However, YHM had a higher MRLD than NPB at depths below 20 cm, and this occurred at an earlier growth stage (Fig. 4). These results suggest that cultivar differences in the amount and ratio of deep roots are not necessarily associated with maximum rooting depth or maximum root length, which are often treated as important deep-root traits in pot experiments and hydroponic culture. Instead, it appears that differences in the number of adventitious roots that penetrate deeper soil layers, the proliferation of deep roots and assimilate supply to these deep roots would be more important. Morphological studies of the determinants of root elongation into deep soil layers may help guide the genetic improvement of rice root systems.

The effects of water regimes on root development were not necessarily explicit in our study. RLD at 95 DAS did not differ between the control and drought treatments for YHM at all depths in the lysimeter experiment (Fig. 3), though this might be partly because the water stress was not very lengthy or intense enough. Compared with the results of our previously reported experiment, in which there was adequate rainfall (Kato et al., 2006a), YHM had smaller RWD under the water stress in the present field experiment, but the other two cultivars did not. The development of deep roots was slightly smaller under the water stress in the present field experiment than under more favourable water supply in the previous experiment (Kato et al., 2006a) (e.g., 0.9 vs. 1.4 km m⁻² of RLD in deeper layer and 13% vs. 17% of DRL ratio, on the average of the three cultivars). In previous studies with rice in pots or root boxes, RWD were reduced under water deficit compared with well-watered conditions, though the proportion of deep roots were substantially increased (Azhiri-Sigari et al., 2000; Price et al., 2002; Kamoshita et al., 2004). In rainfed lowlands where hydrological conditions can change drastically from anaerobic (flooding) to aerobic (drought), Ingram et al. (1994) pointed the importance of dynamic root responses to water regimes. In upland

fields, the extent of any adaptive changes in deep root development (i.e. partitioning of biomass) in response to declining surface soil moisture content may not be as large as those that are often reported in pot experiments. Limitation of the assimilate supply under water deficit conditions would probably limit the amounts of assimilate translocation to roots and suppress root development (Boonjung, 1993). Nevertheless, the differences among cultivars in some of the root traits were consistent; by comparison with YHM, the deep root system of NPB always developed poorly. Our results support the suggestion of Lilley and Fukai (1994a) that the inherent root growth of cultivars rather than the adaptive responses of deep root morphology to water deficits is most important in upland fields, when drought levels are mild.

2. Root growth and change in soil water content along the profile

We monitored the profile of soil water content at the whole-canopy level under drought conditions in the lysimeter experiment. Both NPB and YHM more relied on soil water from deeper layers in response to reduction in the moisture content of surface soil (Fig. 6, 7). Interestingly, soil moisture change at a depth of 45 to 70 cm tended to be greater in YHM than in NPB under drying of the surface soil (Fig. 7). This would be primarily due to higher root length density at the 30 to 60 cm depth in YHM than in NPB (Fig. 3). These results suggested that the deeper root development of YHM gave this cultivar an advantage over NPB under conditions of intermittent drought. This supports the results of Kamoshita et al. (2000) in a pot experiment, where genotypes with a higher root length density at a depth of 30 to 40 cm extracted more soil water from deeper soil under drought.

These findings from the lysimeter experiment did not agree with the field experiment in which water content of soil in the surface layers (a depth of 10 to 20 cm) continued to decline below $0.25 \text{ cm}^3 \text{ cm}^{-3}$ until the end of drying period (Fig. 1), suggesting the possibility that the rice plants continued to take up some soil water from the surface layer in the field experiment. However, the soil water content of soil in the surface layer might be affected by a larger amount of soil evaporation in the field experiment with the wider row spacing (35 cm) and longer drying period than the lysimeter experiment (25 cm). We did not quantify the vertical physical soil water movement from deeper to shallower soil layers, and this might also affect the difference between the two experiments; the vertical soil water movement might be greater in the field experiment consisting of the 2 soil layers than the lysimeter experiment.

Total aboveground biomass might also affect canopy water use when the surface soil was relatively wet, considering from rapid soil moisture depletion

along the soil profile with YHM compared with other cultivars (121–129 DAS; Fig. 1). The large differences among the cultivars in total aboveground biomass and hence in transpirational demand may confuse the effect of rooting pattern on the extraction of soil water during the drying period (Lilley and Fukai, 1994a). Thus, the advantage offered by a deep root system depends not only on the severity of the drought conditions (Kamoshita et al., 2004) but also on shoot size, which determines the potential amount of soil water that is extracted under the water stress that can occur in uplands.

3. Plant water status

In the field experiment, LMT maintained better plant water status than YHM and NPB, with a higher midday leaf water potential and a lower diffusion resistance (Table 2; Fig. 2). The larger total aboveground biomass and more rapid extraction of available soil water by YHM worsened its water status, as expected (Lilley and Fukai, 1994b; Mitchell et al., 1998). NPB also tended to have a larger leaf area than LMT during the last stage of the drying period (139 DAS) (Kato et al., 2006a), and this might increase its transpiration and have a more negative effect on plant water status in NPB than in LMT. However, plant characteristics other than deep root development and total aboveground biomass may be associated with plant water status during the drying period. LMT has been reported to maintain higher leaf water potential during drought stress (Jongdee et al., 2002), but not in relation to its total aboveground biomass (Sibounheuang et al., 2001). LMT had much thicker adventitious roots and stems than NPB according to a visual assessment in this study. This root thickness might be associated with increased xylem diameter and, thus, improved water conductivity (Passioura, 1982; Yambao et al., 1992), and this might also have contributed to the observed difference in plant water status between LMT and NPB in the present study.

LMT maintained a larger number of spikelets per panicle than YHM and NPB and attained the highest harvest index in the field experiment (Kato et al., 2006b). This may be resulted from the cultivar's ability to maintain a relatively good water status, since plant water status during reproductive stages is closely associated with both spikelet sterility (Garrity and O'Toole, 1994) and spikelet formation and abortion due to differences in physiological metabolism, such as a greater translocation of assimilates to young panicles (Saini and Westgate, 2000).

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* In Japanese with English abstract.

** In Japanese.