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Functional roles of the plasticity of root system development in biomass production and water uptake under rainfed lowland conditions

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ABSTRACT

Fluctuation of soil moisture conditions between wet and dry is a normal occurrence in rainfed lowland and irrigated rice fields where water saving production systems are implemented, which can constrain rice productivity. In this study, we evaluated the functional roles of root plasticity for water uptake and dry matter production under such fluctuating water stress conditions. Introgression lines (INLs) of IR64, whose yield performances were previously evaluated in aerobic fields, were evaluated in the field and greenhouse under soil culture conditions using slant tube and root box methods. Under field conditions, greater root system development of INLs YTH183 and YTH304 in shallow soil layers contributed to greater shoot dry matter production than that of IR64. Furthermore, the line YTH183 responded sharply to rewatering after drought in slant tube and root box systems by increasing root elongation and branching, which contributed to its higher shoot dry matter production and water extraction compared to IR64. Such growth responses to the different soil water regimes reflect the plastic root growth response of this INL. These results imply that the plasticity in root system development in response to rewatering after drought contributed to the promotion of shoot dry matter production. Since the INLs in this study are highly genetically similar, future work will focus on pinpointing the genetic control of rice root plasticity under rainfed lowland conditions.

1. Introduction

The soil environment in agricultural fields rarely stays constant but continues to change with time, in addition to being spatially heterogeneous. The topsoil of rainfed lowland rice fields is often exposed to frequent wet and dry cycles caused by irregular rainfall (Wade et al., 1999a). Likewise, irrigated rice fields in which water-saving technology such as aerobic rice and alternate wetting and drying are employed (Bouman et al., 2005) may also experience transient anaerobic and flooded to aerobic and dry conditions. Such soil moisture fluctuations typically reduce rice growth and production compared with continuously flooded conditions (Belder et al., 2005; Matsuo and Mochizuki, 2009). A rapid response of root traits to these fluctuating soil water regimes was proposed as one of the important physiological traits for adaptation (Ingram et al., 1994; Suralta et al., 2010; Niones et al., 2012).

Several studies have demonstrated increased root length density at depth to be associated with greater water extraction from deep soil layers (Wade et al., 1999b; Lilley and Fukai, 1994; Okada et al., 2002; Bernier et al., 2009; Henry et al., 2011; Henry, 2012). However, roots are commonly shallowly distributed in rainfed lowlands, which is thought to be due to the presence of a hardpan that impedes deep rooting (Clark et al., 2002; Samson et al., 2002). Therefore the capacity to adapt to cycles of wet and dry conditions may be linked with the ability of roots to proliferate quickly in the subsurface layers of soil in response to rewatering (rainfall) after periods of drought (Bañoc et al., 2000a, 2000b).

The promotion of root system development in response to various soil resources conditions can be considered a type of phenotypic plasticity, in which a plant alters its phenotype in response to changing environmental conditions (O'Toole and Bland, 1987; Lynch, 1995; Yamauchi et al., 1996; Wang and Yamauchi, 2006). Previously, we reported that phenotypic plasticity in root system development is a key trait for plant adaptation to water stress such

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as continuous drought (Kano et al., 2011; Kano-Nakata et al., 2011), drought and recovery (Azhiri-Sigari et al., 2000; Kamoshita et al., 2000; Subere et al., 2009), and fluctuating soil moisture conditions (Bañoc et al., 2000a, 2000b; Suralta et al., 2008a, 2008b, 2010; Suralta and Yamauchi, 2008; Niones et al., 2012). In this study, we characterized the effects of plastic root system development in different soil layers on water uptake, photosynthesis, and dry matter production in field, tube, and root box studies.

2. Materials and methods

2.1. Plant materials

Introgression rice lines (INLs) derived from crosses between IR64 (*indica*) and 10 donor varieties including 9 new plant type (NPT) lines and Hoshiaoba (as known as Chugoku146) (Fujita et al., 2009, 2010b) whose yield performance was previously evaluated in aerobic fields were used for this experiment. From the original 334 INLs, we selected representative 21 INLs to cover their phenotypic variation. LTK3, which is a near-isogenic line of IR64 with low tiller number (Fujita et al., 2010a) was also included, as well as KDML105 and NSG19 (*indica*) which are popular in the rainfed areas of Northeast Thailand for their drought tolerance (Wade et al., 2000; Azhiri-Sigari et al., 2000; Bañoc et al., 2000a, 2000b).

2.2. Field evaluation

Two field experiments were conducted in the dry seasons (DS) of 2008 and 2009 at the International Rice Research Institute (IRRI), Los Baños, Laguna, Philippines (14°13′N, 121°15′E). The aim was to analyze the response of IR64 INLs when grown under drought-prone rainfed lowland conditions as compared with continuously flooded conditions (control). Thirteen genotypes – IR64, KDML105, NSG19 and 10 INLs (YTH13, YTH16, YTH160, YTH183, YTH186, YTH197, YTH259, YTH264, YTH304 and LTK3) – were grown in 2008. Twenty-four genotypes – IR64, KDML105, NSG19 and 21 INLs (YTH13, YTH16, YTH63, YTH73, YTH88, YTH125, YTH146, YTH160, YTH183, YTH186, YTH243, YTH246, YTH259, YTH264, YTH272, YTH288, YTH302, YTH304, YTH323, YTH339 and LTK3) – were grown in 2009. Seeds were sown in a field seed bed and were transplanted to the experimental field after 3 weeks. In 2008, transplanting dates were 29 January for the rainfed treatment and 19 January for the flooded control. In 2009, the transplanting date was 19 January for both the rainfed and flooded conditions. For the rainfed treatment in both field seasons, the fields were irrigated for 2 weeks after transplanting for plant establishment and then allowed to drain at 30 days after transplanting (DAT). Experiments were laid out in a randomized complete design with four replications. The dimension of each plot was 2.5 m long and 3 rows wide with 0.25 m × 0.25 m spacing. Rainfall was recorded at agrometeorological stations operated by the IRRI Climate Unit during the experiment.

Several physiological traits were measured under rainfed conditions. Stomatal conductance was measured at 58 DAT in 2008 and at 64 DAT in 2009 using a Li-1600 porometer (Li-Cor Biosciences, USA) on the abaxial side of the topmost fully developed leaf. Leaf rolling (IRRI, 1996) was scored visually at 54 DAT in 2008 and at 64 DAT in 2009 using a scale of 0 (no rolling) to 9 (severe rolling). In 2009, canopy temperature was measured at 64 DAT under the rainfed condition. Thermal images were acquired at mid-day using an NEC TH7800 infrared camera (NEC Avio Infrared Technologies Co. Ltd., Tokyo, Japan) from a 3.5-m-tall ladder positioned 10 m in front of the plots. Canopy temperature was determined using the line tool (one line selected per planted row) in Report Generator v. 1.7 software (NEC Avio Infrared Technologies Co. Ltd., Tokyo, Japan).

Roots were sampled with a 20 cm × 20 cm monolith sampler at 75 DAT in 2008 and at 71 DAT in 2009. The soil monoliths were divided into four increments in 2008 (0–10 cm, 10–20 cm, 20–30 cm and 30–45 cm) and three sections in 2009 (0–15 cm, 15–30 cm and 30–45 cm). In addition, a 4-cm diameter core sampler was used to collect soil samples to a depth of 60 cm and the cores were divided into 0–15 cm, 15–30 cm and 30–45 cm at 61 DAT in 2009. Monoliths were centered over one planted hill, and cores were sampled at the mid-point between rows and hills. The sampled roots were carefully washed using 1.5 mm mesh screen and stored in 50% ethanol for further root measurements. Root samples were scanned (Epson V700, CA, USA) and analyzed using WinRhizo v. 2007d (Regent Instruments, Quebec, Canada) to determine the root length. The root length density was calculated as the root length per unit volume of soil from which roots were extracted. The plants were harvested at 75 DAT in 2008 and at 71 DAT in 2009. Shoots were oven-dried at 70 °C for three days and weighed, and the panicle was separated from the rest of the shoot.

2.3. Characterization of root response to rewatering: slant tube experiment

A slant-tube experiment was conducted at the glasshouse of IRRI in the DS of 2008. Five genotypes – IR64, KDML105, NSG19 and 2 INLs (YTH183, YTH304) – were grown in the plastic tubes with height of 100 cm and inner diameter of 7 cm. The tubes were arranged in a slanted position at 15° from vertical so that the root grew along the edge of the tubes to facilitate location of the root tip (Bañoc et al., 2000b).

Three soil moisture treatments were prepared, including well-watered (control), drought, and rewatered. Soil moisture was determined by measuring the net weight of the tubes every other day. In the control treatment, the soil in the tube was watered to maintain soil moisture at field capacity throughout the experiment. For the drought treatment, the soil was dried to 15% (w/w) of soil moisture contents (SMC) before planting. At sowing, the soil surface was watered just enough to wet the soil surface layer at a 2–3 cm depth to ensure seed germination. Watering was subsequently withheld throughout the experiment. For the rewatered treatment, drought was initiated as in the drought treatment, but the plants were watered in the same manner as in the control starting at 29 days after sowing (DAS).

The position of the deepest visible root tip was marked every other day on the tube to monitor the root elongation while the root axis elongation was measured manually using a ruler based on the marks traced on the tube (Bañoc et al., 2000b). Plants were sampled at 37 DAS; shoots were cut at the stem base and oven-dried at 70 °C for 3 days and the shoot dry weight was recorded. The root zone was divided by cutting the tubes into layers of 0–30 and >30 cm from the soil surface. Roots were carefully washed and preserved in ethanol solution for further measurements. The number of nodal roots was manually counted. Total root length was then determined using a root length scanner (Commonwealth Aircraft, Melbourne, Australia). The number of lateral roots per unit length of nodal root was manually counted.

2.4. Quantitative evaluation of root system development: root box experiment

To evaluate root system development and water uptake precisely, we conducted a root box experiment from 24 July to 27 August in 2009 in a vinyl house at the experimental field of Nagoya University, Japan (35°9′N, 136°56′E). The root box-pinboard method was used according to the protocols described by Kono et al. (1987). Three genotypes – IR64 and 2 INLs (YTH183, YTH304) – were grown. Three pre-germinated seeds from each