Roles of Root System Development and Function in the Growth and Yield under Waterlogged Condition in Common Wheat

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Abstract

Waterlogging stress substantially reduces the productivity of common wheat. Unavailability of oxygen to the roots is the major growth-limiting factor for plants exposed to waterlogging stress. The development and function of roots play significant roles in expression of waterlogging tolerance of wheat under such conditions. However, the mechanism of root function in the waterlogging tolerance is not clear yet. In this study, we, therefore, aimed to evaluate the roles of root system development and function in the growth and yield of wheat plants that were exposed to waterlogged condition at jointing stage. This study was conducted in 2009 at Aichi Agricultural Research Center experimental field. Plants were grown under two different conditions; control for rainfed upland conditions while in waterlogging treatment (WL), water level was maintained around 5 cm below the soil surface from jointing stage till maturity. Soil type of this field was andsol. We previously examined a set of germplasm (144 cultivars) collection, and selected Nishikazekomugi (high waterlogging tolerance), Iwainodaichi (moderate) and UNICULM (low). Grain yield of Nishikazekomugi in WL was 64% of control, while that of Iwainodaichi and UNICULM was 38 and 4%, respectively. The cultivars of greater watelogging tolerance further showed the ability to maintain higher stomatal conductance in WL, which should reflect higher root ability of soil water uptake. In fact, they showed higher root development as evaluated in total root length. Increase in nodal root porosity of Nishikazekomugi and Iwainodaichi in response to exposure to WL then contributed to the significant increase in total root length. Higher root porosity indicates greater root aerenchyma formation in response to waterlogging stress. These results indicated that the tolerant cultivars had higher ability of aerenchyma formation, which promoted root system development, and eventually contributed to the increase in shoot dry matter and grain yield under waterlogged conditions.

Keywords: aerenchyma, common wheat, hydraulic conductivity, porosity, waterlogging tolerance

Introduction

Common wheat is known to be susceptible to waterlogging, and the grain yield substantially decreases by excess moisture (Oyanagi *et al*, 2001) in most of the wheat producing countries such as UK (Belford and Cannel, 1979), Australia (Setter *et al*., 2009). In Japan, 27% of wheat-planted field (approximately 57,000 ha) is affected by excess moisture stress (Sakagami *et al*., 2010).

When the water table rises to or above the soil surface, roots surrounded by the waterlogged soil suffer from O_2 deficiency (Jackson *et al*., 1999; Malik *et al*., 2003). As one of mechanisms for waterlogging tolerance, aerenchyma in root provides a low-resistance internal diffusion pathway to supply O_2 to the root apex (Arikado, 1975; Colmer, 2003; Armstrong and Armstrong, 2005). Therefore, root aerenchyma formation under waterlogged condition may play important roles in waterlogging tolerance in wheat (Setter and Waters, 2003). Although wheat plants generally have low efficiency of root aerenchyma formation (Watkin *et al*., 1998), genotypic variations in its functional roles in the maintenance of waterlogging tolerance under waterlogged condition is not yet clear.

In this study, we examined if genotypes with high ability of root aerenchyma formation and root system development under waterlogging produce high dry matter and yield by evaluating the impacts of root aerenchyma formation on root development, stomatal conductance, photosynthetic rate and grain yield under waterlogged conditions, and compared with those under rainfed upland conditions in the field. Such hypothesis of this study was summarized in Figure 1. The objective of this study was, therefore, to examine the roles of root aerenchyma formation in the maintenance of waterlogging tolerance under waterlogged condition in wheat.

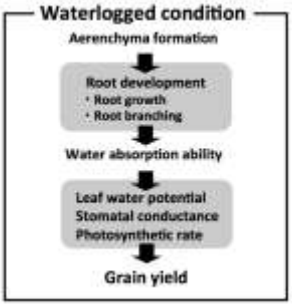


Figure 1. Schematic diagram of hypothetical mechanism of waterlogging tolerance in wheat.

Materials and Methods

Experiment design and Plant materials

A field experiment was conducted at Aichi Agricultural Research Center. Plants were grown under two different conditions e.i control for rainfed upland conditions while in waterlogging treatment (WL), water level was maintained around 5 cm below the soil surface from jointing stage till maturity. Soil type of this field was andsol.

The seeds were sown on December 3, 2008. The waterlogging treatment lasted for 50 days from April 13 to June 1, 2009. The plants were harvested on June 9, 2009 (188 days after sowing). Based on the results of our previous study (Hayashi *et al*., 2008) that examined a set of 144 cultivars collection, we selected three cultivars e.i. Nishikazekomugi (high waterlogging tolerance), Iwainodaichi (moderate) and UNICULM (low).

Grain Yield

Plants were harvested in six replicates for each cultivar. For shoots, after air-drying for about three weeks, leaves and stems were oven-dried and weighed, and the grains were threshed. After the grain moisture content was measured with a grain moisture tester, grains were weighed, and the yield components were determined.

Root Development

To determine total root length, after the harvest of shoots, roots were sampled in six replicates for each cultivar. At the end of waterlogging treatment, the roots were sampled with the round monolith method (Kang *et al*. 1994) by using stainless cylinder of 15 cm in diameter, and the soil cores of 20 cm in depth were taken. Soil samples were carefully washed to collect roots. After removing the debris, the roots were stained and arranged on water in a transparent plastic tray. They were then scanned to convert to a digitized image, and total root length was determined with the use of NIH Image ver. 1.62 and Root Length ver. 1.54 (Kimura, 1999).

Leaf Water Potential

We measured leaf water potential of the flag leaves in six replicates in each cultivar at -4, 4, 11, 16, 19, 28 and 34 days after the onset of waterlogging treatment. Leaf water potential was measured with thermocouple psychrometry using sample chambers (Model C-52, Wescor) and a microvoltmeter (Model HR-33T, Wescor). The sample chambers had been calibrated with NaCl solution of a known molarity in advance.

Stomatal Conductance and Photosynthetic Rate

We measured stomatal conductance and photosynthetic rate of the flag leaves in three replicates for each cultivar at -4, 4, 11, 16, 19, 28 and 34 days after the onset of waterlogging treatment. The measurements were conducted from 800 to 1300 on sunny days at PPFD of 1400 $\mu mol\ m^{-2}\ s^{-1}$ with a portable type apparatus for photosynthesis and transpiration measurements (LI-6400, LI-COR, Lincoln, NE, USA). Leaf temperature and CO_2 concentrations surrounding leaf was adjusted to be 28±1.7℃ and 400 $\mu mol\ mol^{-1}$, respectively. Measurement duration average was about 40 to 60 s. The leaf areas enclosed by chamber were from 3.0 to 6.0 cm^2.

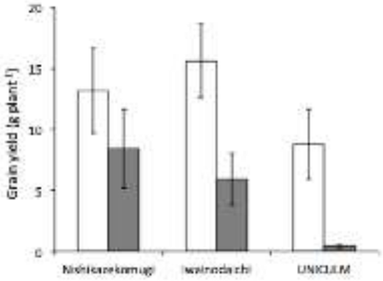
Root Porosity

We measured porosity of the nodal root in six replicates for each cultivar. Nodal root porosity was measured 50 days after the onset of waterlogging treatment.The nodal root axis was used for root porosity measurement following the microbalance method (Visser and Bögenmann, 2003; Suralta *et al*., 2010).

A 1-cm segment from the middle portion of each root was cut. From each plant (replicate), sixty 1-cm segments were further sampled. Each 1-cm root segment was cut with a sharp razor blade and gently blotted by rolling it with a small brush on tissue paper for about 2 s to remove adherent water. Then, to prevent weight loss by evaporation, the segments were transferred into a capsule with cover that had been tared on a microbalance. After closing the capsule, the segments were weighed (w1 in µg), transferred to a holder with small vials filled with water, and stored for 30 min. Up to 60 samples were weighed before they were infiltrated with tap water twice under vacuum for 30 min. After water infiltration, the root segments were blotted again on tissue paper for about 2 s and weighed in a capsule (w2 in µg). Using the specific weight (SW) obtained from larger samples, the porosity was calculated using the formula: Porosity (%; v : v) = $100 \times (w2 - w1) \times SW/w2$

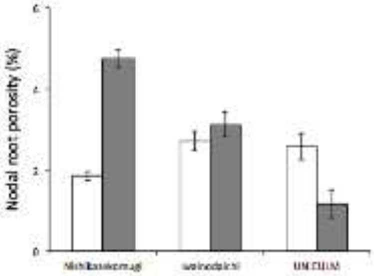
Results and Discussion

In this study, we evaluated the roles of root system development and function in the growth and yield of wheat plants that were exposed to waterlogged condition at jointing stage. Grain yield of Nishikazekomugi in WL was highest (64% of control), followed by Iwainodaichi (38%), and UNICULM (4%) (Figure 2). Nodal root porosity of Nishikazekomugi in WL was 284% of control, while that of Iwainodaichi and UNUCULM was 113% and 44%, respectively (Figure 3). Total root length of Nishikazekomugi in WL was 104% of control, while that of Iwainodaichi and UNICULM was 70 and 38%, respectively (Figure 4). These results showed that the cultivar with high porosity in response to exposure to WL tended to have greater total root length. Specifically, increase in nodal root porosity of Nishikazekomugi and Iwainodaichi contributed to the significant increase in total root length. Higher root porosity indicates greater root aerenchyma formation in response to waterlogging stress.



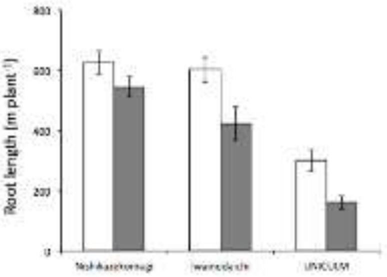
Data are means of 6 replicates. Vertical bar show standard errors (n=6). □ and ■ represents control and waterlogging conditions, respectively.

Figure 2. The effect of waterlogging stress on grain yield under rainfed upland (control) and waterlogged conditions.



Data are means of 60 replicates. Vertical bar show standard errors (n=60). □ and ■ represents control and waterlogging conditions, respectively.

Figure 3. The effect of waterlogging stress on nodal root porosity under rainfed upland (control) and waterlogged conditions.



Data are means of 6 replicates. Vertical bar show standard errors (n=6). □ and ■ represents control and waterlogging conditions, respectively.

Figure 4. The effect of waterlogging stress on root length under rainfed upland (control) and waterlogged conditions.

We also examined the effect of waterlogging stress on leaf water potential, stomatal conductance and photosynthetic rate. Leaf water potential of Nishikazekomugi maintained to the level of control for 16 days after waterlogging treatment onset, for 11 days in Iwainodaichi and for 4 days in UNICULM. Stomatal conductance of Nishikazekomugi maintained to the level of control for 16 days, for 16 days in Iwainodaichi and for 11 days in UNICULM. Likewise, photosynthetic rate of Nishikazekomugi maintained to the level of control for 16 days, for 11 days in Iwainodaichi and for 11 days in UNICULM. As stated above, the cultivars of greater root system development (greater total root length in WL) further showed the ability to maintain high leaf water potential and stomatal conductance, which maintained higher photosynthetic rate in WL.

These results indicated that the tolerant cultivars have higher ability of aerenchyma formation, which promotes root system development, and probably root hydraulic conductance, both of which, through high ability to provide water to shoot, eventually contributed to the increase in shoot dry matter and grain yield under waterlogged conditions.

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