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Root plasticity for maintenance of productivity under abiotic stressed soil environments in rice: Progress and prospects

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ABSTRACT

Roots play a number of important roles in crop adaptation to various abiotic stresses such as water stress. However, traits responsible for such adaptation may differ with environments. This paper reviews recent progress in our research on the functional roles of important root traits. We have been paying special attention to drought as well as to soil moisture fluctuations as prevailing water stresses, and the ability of the plant to change its development as environmental conditions change, which is known as phenotypic plasticity. We have been using various rice accessions/mapping populations such as the OryzaSNP panel, chromosome segment substitution lines (CSSL) derived from a Nipponbare and Kasalath cross, and IR64 introgression lines. The results consistently showed that, in addition to deep roots, the plasticity of root system development is a key trait for plant adaptation to water stress. We found that plasticity in the development of the entire root system as a function of the plasticity in lateral root development is important under progressive drought, while plasticity in lateral root development that is associated with aerenchyma formation is important under transient drought-to-waterlogged conditions. We quantitatively showed the contributions of root plasticity to dry matter production and yield through enhanced water uptake under such water stress. We also identified quantitative trait loci (QTLs) that are responsible for root plasticity. The importance of explicitly characterizing the nature of the stresses in the target areas is discussed in relation with designing an ideal root system, which is a primary requirement to define an actual breeding target for improving productivity in abiotic stress-prone soil environments. © 2016 Elsevier B.V. All rights reserved.

1. Introduction

Rice (*Oryza sativa* L.) is a major staple food crop for the world's population. Rice can be grown under irrigated (lowland) or rainfed (upland or lowland) conditions. Rainfed rice occupies about 45% of the global rice production area (Tuong and Bouman, 2003). Overall, there is an estimated global need for an additional 116 million tons of rice by 2035 compared to 439 million tons produced in 2010 (Seck et al., 2012). Although yields continue to increase in many areas across the globe, yields in other major rice production areas either never improved, stagnated or collapsed, which call for new investments (Ray et al., 2012). This may result in increasing yield performance of rice growing under less favorable conditions (Fischer et al., 2012). The world rice area is around 100 million hectares and 89% of it is in Asia, of which 45% lacks sources of irrigation and is therefore dependent on rainfall for most of the cropping season (Serraj et al., 2009). In rainfed rice areas, water stresses such as drought and fluctuating soil moistures are two of the limiting factors that substantially reduce rice production (Boling et al., 2004; Devereux, 2007; Pandey et al., 2007; Siopongco et al., 2008; Suralta et al., 2010; Gauchan and Pandey, 2012; Niones et al., 2012).

The root system, being the plant organ directly in contact with the soil, is the first line of defense for maintaining plant productivity under soil abiotic stresses. This paper reviews recent progresses of our research on the functional roles of root plasticity in rice with special emphasis on drought and soil moisture fluctuation as prevailing water stress conditions.

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Fig. 1. Comparison of responses in root system development between two anther culture-derived CT9993/IR62266 doubled haploid lines (DHLs) in rice to transient flooded-to-drought condition of soil moisture fluctuation treatment. The plants were grown in soil-filled boxes for 35 days under either continuously flooded or 21 days of waterlogging prior to transient progressive drought condition for another 14 days (Suralta et al., unpublished data).

2. Quantification of root plasticity

Phenotype plasticity is generally defined as the ability of a genotype to change its phenotypes as environmental conditions change (O'Toole and Bland, 1987). Specifically, root plasticity is defined as the ability of the root system to promote plant growth and development under changing soil conditions to mitigate the impact of stress and maintain greater plant productivity (Yamauchi et al., 1996; Wang and Yamauchi, 2006). An example of plasticity in root system development in rice is the promotion of L-type lateral roots under transient waterlogged-to-drought conditions (Fig. 1; Suralta et al., unpublished data). Two CT9993/IR62266 doubled-haploid lines (DHL) showed similar root system development under continuously waterlogged (control) conditions. However, under transient waterlogged-to-drought conditions of soil moisture fluctuation, while the two DHLs had similar reductions in nodal root production, DHL96 had greater ability to promote the production of L-type lateral roots than DHL98 specifically at the lower half of the soil profile (20-40 cm depth) (Fig. 1) where soil moisture is more available during progressive drought stress (Suralta et al., unpublished data).

Phenotypic plasticity can be quantified using different approaches. The most common methods of quantifying root plasticity are the coefficient of variation (CV; standard deviation/mean) (Guo et al., 2006) and the slope of the norm of reaction (slope of regression of dependent variable between two environments) (Huang et al., 2009). Other approaches such as plasticity index (Valladares et al., 2005) and environmental sensitivity score (Shimizu et al., 2010), have also been used. Most phenotypic plasticity studies have compared multiple plants of a genotype under different environments (Bañoc et al., 2000; Robinson 2001; Hodge, 2004; Kume et al., 2006). Root plasticity analysis can be done by comparing the roots of the same genotypes between water-stressed and non-stressed (control) conditions (Bañoc et al., 2000). Furthermore, the use of genetically similar lines such as recombinant inbred lines (RILs) (Zhu et al., 2010), CSSLs (Tran et al., 2014, 2015; Niones et al., 2012; Kano-Nakata et al., 2011; Kano et al., 2011; Suralta et al., 2010), introgression lines (INLs) (Kano-Nakata et al., 2013) and DHLs (Siopongco et al., 2005, 2006, 2009; Suralta et al., 2015) have resulted in precise quantitative evaluation and measurement of root plasticity with minimal effects of genetic confounding and, consequently, the precise analvsis of the OTL associated with root plasticity (Niones et al., 2013, 2015; Suralta et al., 2015). The latter approach of quantifying root plasticity has been extensively used in most of our researches cited in this review (e.g. Suralta et al., 2008a, 2008b, 2010; Kano-Nakata et al., 2011; Kano et al., 2011; Niones et al., 2012; Kano-Nakata et al., 2013; Niones et al., 2013; Tran et al., 2014; Niones et al., 2015; Tran et al., 2015). These studies identified lines that have the same shoot and root growth as the recurrent parent under control conditions but have greater root and shoot growth than the recurrent parent under stressed conditions. Plasticity can be calculated directly as the differences in root growth between the lines and their recurrent parent under stressed conditions (Suralta et al., 2008a, 2008b, 2010; Kano-Nakata et al., 2011; Kano et al., 2011; Niones et al., 2012; Kano-Nakata et al., 2013; Tran et al., 2014, 2015). The plasticity of a given root trait was calculated as the difference between mean values of the trait in stressed and non-stressed plants for each DHL in some of our studies (Wang et al., 2005; Suralta et al., 2015).

3. Water environment and root plasticity

3.1. Drought stress

Drought resistance in its physiological context is conventionally defined as being determined by dehydration avoidance and/or dehydration tolerance (Blum, 2005). Under rainfed lowland conditions, soil moisture usually fluctuates between waterlogged and aerobic (mild to severe drought) conditions at any stage of the crop growth due to erratic rainfall patterns (Wade et al., 1999; Bell and Seng, 2004; Boling et al., 2004, 2007; MacDonald et al., 2006; Fujihara et al., 2013). Root adaptations under fluctuating soil moisture stress may be more complicated than under either constant waterlogging conditions or progressive drought stress because of contrasting mode of root adaptation to either excess or deficit in soil moisture, respectively. Thus, increasing yield under fluctuating soil moisture stress is not easy because of the unexpected occurrence of progressive drought stress and transient waterlogging conditions at any stage of plant growth.

Under rainfed upland and lowland field conditions, soil moisture fluctuations or an interval occurrence in drought and/or rewetting events depend on rainfall patterns. Transpiration, stomatal conductance, photosynthesis, and plant growth may start to recover immediately after rewetting events but the extent and magnitude of the stimulation from rewatering was dependent on pre-drought intensity, duration (Xu et al., 2010), and genotypes (Bañoc et al., 2000; Suralta et al., 2010; Niones et al., 2012). Recoveries in transpiration rate and photosynthesis were associated with root plasticity in response to rewatering such as the promotion of nodal root elongation and lateral root production (Bañoc et al., 2000; Suralta et al., 2008b; Chai et al., 2010; Suralta et al., 2010; Kano-Nakata et al., 2013). Under rainfed lowland rice conditions, root plasticity in response to rewatering in terms of promoted lateral root production at the soil surface (0-20 cm soil depth) contributed to the increased capture of available water at the surface (Azhiri-Sigari et al., 2000; Kano-Nakata et al., 2013).

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