Quantitative evaluation of plastic root responses to contiguous water gradient in rice

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Abstract: Root plasticity is the key trait for plant adaptation to environmental stresses. To quantify phenotypic plasticity to its full extent in potential, it needs to be evaluated under contiguous environmental changes. For that purpose, we used the combination of chromosome segment substitution lines (Nipponbare/Kasalath CSSLs) and line source sprinkler (LSS) system of irrigation. For analysis, we first attempted to apply the coefficient of variation (CV) and norm of reaction that have been used as the conventional approaches, and then propose a new approach for quantification of root plasticity. Results revealed that CV was not linked to root plasticity under contiguous water gradient in this study. In contrast, norm of reaction was linked to root plasticity and better explained with curve than linear, especially for CSSL50 (the most plastic genotypes) under such gradient. Based on the norm of reaction with curve, root plasticity was calculated using the difference in total root length between CSSLs and the recurrent parent, Nipponbare. Further analysis of root plasticity in relation to dry matter production was also done. By applying the new approach, we confirmed that root plasticity expression was affected by the intensities of drought stress and genotypes, indicating that such root plasticity is genetically controlled. In addition, root plasticity effectively contributed to the dry matter production under the drought conditions and maximized at around 20% of soil moisture content (−0.04 MPa). By using CSSLs and LSS system, we successfully evaluated root plasticity under contiguous water gradient.

Keywords: chromosome segment substitution line, drought, line source sprinkler, root plasticity, total root length

Introduction

Crop environment is rarely constant but continues to change in the field. The ability of a plant to change its morphology as environmental conditions change is known as phenotypic plasticity (O’Toole and Bland 1987). Root plasticity that is expressed in response to such complex and heterogeneous soil environment is a key trait for plant adaptation (Suralta et al. 2016). In particular, we have shown that the plasticity of root system development is a key trait for plant adaptation to various types of water stress (Bañoc et al. 2000, Subere et al. 2009, Suralta et al. 2010, Kano et al. 2011, Niones et al. 2012, Tran et al. 2014, Kameoka et al. 2015, Menge et al. 2016).

In recent years, number of publications on phenotypic plasticity has been increasing tremendously (Forsman 2014). There are a number of approaches that have been used to quantify phenotypic plasticity. The reaction norm and the coefficient of variation (CV) are the two most commonly used quantification methods of plasticity. In the reaction norm method, the slope of regression of dependent variable between two environments is used, and this is the most immediate way to show the trait responses (Schlichting and Pigliucci 1998). Coefficient of variation is defined as a ratio of the standard deviation to the mean (Schlichting 1986).
Materials and methods

Plant materials

The data sets used in this study were obtained from the 54 CSSLs derived from Nipponbare and Kasalath crosses, as previously reported (Kano et al. 2011). The seeds were supplied by the Rice Genome Resource Center of the National Institute of Agrobiological Sciences, Japan (http://www.rgrc.dna.affrc.go.jp/ineNKCSSL54.html).

Experimental design and water treatments

Field experiments in the watertight experimental bed with LSS were conducted under a rain-out shelter at the experimental farm at Nagoya University, Nagoya, Japan (35°06'N 137°04'E) during the summer in 2005 and 2006, as previously described (Kano et al. 2011). Each row (= genotype) contained 8 plants with three replications and each replication was arranged in randomized complete block design with a spacing of 45 × 20 cm. A set of 54 CSSLs together with Nipponbare and Kasalath were transplanted at 25 days after sowing and grown in this field. Therefore, each genotype was exposed to and grown under various intensities of drought. The resulting water gradient manifested in the soil moisture connotes the “contiguous gradient” in this paper.

Measurements

The soil moisture content (SMC) at a soil depth of 12 cm at the base of each plant was measured by using Hydrosense (Decagon, Utah, USA) in % v/v (volumetric), and then converted into the value in % w/w (gravimetric). The fields were kept well-watered conditions by sprinkler irrigation for one week after transplanting for plant establishment. Thereafter, the drought stress was imposed by adjusting the irrigation pressure of the sprinkler and plants were grown under certain soil moisture conditions until when the experiment was terminated. The SMC values from wettest to driest of the soil perpendicular to the sprinkler pipe ranged from 7.1 to 33.9% w/w (–0.12 to 0 MPa) in 2005 and 6.4 to 43.8% w/w (–0.14 to 0 MPa) in 2006. The drought stress was imposed enough to elicit a plastic response in root development. We observed the plants grown further from the line source started to clearly became shorter than those closer to line source at around 26 days after transplanting (DAT) in 2005 and 30 DAT in 2006 (data not shown), and so judged that effect of contiguous water gradient treatment already started.

Bloor and Grubb (2004) in a research on shade-tolerant tropical rainforest seedlings, interpreted high CV as high plasticity in morphological traits in response to light environment. Furthermore, there are also different approaches that pay special attention to the root plasticity. Root plasticity, evaluated by the plant’s ability to proliferate roots under intermittent stress or upon recovery, is well demonstrated and this is important for enhanced nutrient capture under heterogeneous distribution of nutrients in the soil as represented by patch studies (Drew 1975, Robinson 2004, Hodge 2004). However, the plant’s ability to respond to contiguous environmental changes has yet to be documented. Under such changing environment, the optimal condition for plant growth will differ with different species and varieties.

In this study, therefore, we attempted to experimentally quantify the root plasticity that was expressed in response to contiguous water gradients by using the data set that was obtained from a series of field experiments with line source sprinkler (LSS) technique in rice (Kano et al. 2011). The LSS can maintain various water application rates across plots, thus allowing the assessment of the effect of different levels of water supply on the development of plants grown in contiguous plots (Hanks et al. 1976, Kano-Nakata et al. 2015). In addition, we used chromosome segment substitution lines (CSSLs) of rice for root plasticity evaluation in this study. The CSSLs are genetic resources that have the major genetic background of the recurrent parent with overlapping chromosome segments of the donor parent. With CSSLs, we can make quantitative evaluation and precise measurement of root plasticity with minimal effects of genetic confounding as compared with the conventional cultivar comparison or screening.

Therefore, the aim of this study was to show the advantages of the combination of LSS and CSSLs for the quantification of root plasticity as a new approach over other conventional approaches. We calculated root plasticity by using the difference in total root length between CSSLs and the recurrent. Based on the root plasticity calculation, we further analysed other parameters, such as contribution of root plasticity, efficiency of root plasticity and whole root plasticity. Through these analyses, we hypothesized that there is optimal soil moisture content that maximizes the expression of root plasticity depending on genotypes, and under such soil moisture conditions, root plasticity can contribute to maintain or promote dry matter production efficiently.

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to affect the plant growth by that time. Based on those observations, plants were harvested at 50 DAT in 2005 and 70 DAT in 2006. At those times, the plants grown under well-watered conditions as control near the sprinkler irrigation were already in ripening stage. The shoot samples were cut and oven-dried at 70°C for 72 hours and the dry weights were measured. The root system was extracted using a 15-cm diameter and 25-cm depth monolith stainless cylinder (Kang et al. 1994). The collected roots were washed free of soil in running water. In 2005, the total root length (TRL) of root samples was measured using a Comair root length scanner (Commonwealth Aircraft, Melbourne, Vic., Australia), while in 2006, the roots systems were scanned at 300 dpi (ES2000, EPSON) and scanned images were analyzed for TRL using NIH Image program (NIH Image. Version 1.62). For root measurements, the Comair root length scanner detected fewer fine roots than NIH image program (as described by Kato et al. 2010). Nevertheless, results obtained from both methods clearly showed the genotypic difference in TRL in responses to contiguous water gradient.

Plasticity analysis

To evaluate the environmental impact on root plasticity, 2 years data set were used across repeated field experiments. We selected two CSSLs (CSSL50 and CSSL34) among 54 CSSLs for plasticity analysis. CSSL50 and CSSL34 consistently showed no significant difference in plant growth including its phenology from Nipponbare when grown under well-watered conditions, but showed greatest/lowest shoot dry matter production as the drought intensified among 54 CSSLs for 2 years, respectively. We considered that these CSSLs are genetically similar with the recurrent parent, Nipponbare, except for the plant response under drought stress. Then the data for TRL and SDW were used for quantitative evaluation of root plasticity.

Firstly, CV was used to evaluate the plastic response for each genotype:

\[ CV = 100 \times \left( \frac{\text{standard deviation of TRL or SDW}}{\text{mean of TRL or SDW}} \right) \]

We also used the norm of reaction with slope and curve to show the responses of TRL and SDW of each genotype across a range of water gradient. Linear regressions and quadratic functions were applied to evaluate the genotypic variation in reaction norm. Based on the coefficient of determination \( R^2 \), curve reaction norm with

| Year | Genotype  | TRL  | SDW  |
|------|-----------|------|------|
|      | Mean (m plant\(^{-1}\)) | CV(%) | Mean (g plant\(^{-1}\)) | CV(%) |
| 2005 | Nipponbare | 40.3 a | 32.3 a | 15.5 b | 37.9 a |
|      | Kasalath  | 55.5 a | 28.8 a | 39.5 a | 32.7 a |
|      | CSSL34    | 38.6 a | 36.4 a | 16.9 b | 38.0 a |
|      | CSSL50    | 63.7 a | 22.0 a | 24.6 b | 30.3 a |
| 2006 | Nipponbare | 180.9 a | 16.2 a | 18.9 b | 29.0 a |
|      | Kasalath  | 200.8 a | 14.7 a | 32.3 a | 27.5 a |
|      | CSSL34    | 169.4 a | 22.2 a | 21.1 b | 27.4 a |
|      | CSSL50    | 220.5 a | 13.8 a | 25.9 ab | 27.2 a |

Data are from 3 replications and each replication contained 4–8 plants. Different letters indicate significant differences among the genotypes \( P < 0.05 \) by Tukey’s test.

| Year | Genotype  | TRL                  | SDW                  |
|------|-----------|----------------------|----------------------|
|      |           | Slope (Curves)       | Slope (Curves)       |
| 2005 | Nipponbare| 0.528 (0.528)        | 0.450 (0.523)        |
|      | Kasalath  | 0.001 (ns) (0.109 ns)| 0.229 (0.326)        |
|      | CSSL34    | 0.625 (0.691)        | 0.756 (0.822)        |
|      | CSSL50    | 0.001 (ns) (0.505)   | 0.045 (ns) (0.315)   |
| 2006 | Nipponbare| 0.621 (0.670)        | 0.694 (0.744)        |
|      | Kasalath  | 0.729 (0.746)        | 0.316 (0.316)        |
|      | CSSL34    | 0.526 (0.575)        | 0.636 (0.638)        |
|      | CSSL50    | 0.002 (ns) (0.282)   | 0.266 (0.332)        |

All regressions are significant \( P < 0.05 \) unless indicated by (ns).
quadratic function explained the estimated relationship between SMC and TRL/SDW better than slope reaction norm with linear regression (Table 2). Then, we decided to use quadratic function for further analysis.

By using the equation of regression curve, TRL was estimated at every 5% increase of SMC i.e., from 5 to 35%. Then, root plasticity based on the TRL was obtained by the difference between Nipponbare and CSSL:

\[
\text{Root plasticity} = \text{TRL (CSSL)} - \text{TRL (Nipponbare)}
\]

Then, the differences between Nipponbare and CSSL for SDW were regarded as the contribution of root plasticity to dry matter production, thus:

\[
\text{Contribution of root plasticity} = \text{SDW (CSSL)} - \text{SDW (Nipponbare)}
\]

Furthermore, to evaluate whether the plasticity can be exhibited effectively, the efficiency of root plasticity was estimated with the ratio of the contribution of root plasticity to the root plasticity:

\[
\text{Efficiency of root plasticity} = \frac{\text{Contribution of root plasticity}}{\text{Root plasticity}}
\]

For root plasticity quantification proposed in this paper, we also estimated whole root plasticity under contiguous water gradient. Based on the results of root plasticity data, total area between CSSL and Nipponbare was calculated by using an integral equation, which ranged from 10 to 30% of SMC in 2005 and 15 to 30% of SMC in 2006, where the root plasticity showed positive values for both genotypes. Thus, this area was regarded as whole root plasticity. In addition, we also detected the optimal SMC through differentiation, where the plant showed maximum value of root plasticity.

Statistical analysis

Difference in means were analysed by Tukey multiple range test \((P < 0.05)\). Multiple regression analysis was conducted to examine fitted curves of the relationships between SMC and TRL/SDW by using SPSS Statistics, version 17 (SPSS Inc., Chicago, Illinois, USA).

Results

As we previously reported, Nipponbare reduced both shoot dry matter production (SDW) and root growth (TRL) as drought intensified, while CSSL50 relatively

![Fig. 1. Total root length and shoot dry weight under continuous water gradients by LSS methods for Nipponbare (●), Kasalath (▲), CSSL34 (●), CSSL50 (○) in 2005 (a,c) and 2006 (b,d). Data are from 3 replications and each replication contained 4–8 plants. The data sources were derived from Kano et al. (2011).](image)
maintained shoot and root growth with increasing drought intensities (Fig. 1) (Kano et al. 2011). CSSL34 showed similar response as compared with Nipponbare. In contrast, Kasalath tended to be greater than Nipponbare in shoot dry matter production and root development at any SMC (Fig. 1).

Table 1 shows the mean value and CV value of TRL and SDW for 4 genotypes. Kasalath and CSSL50 showed higher TRL and SDW as compared to Nipponbare and CSSL34. In addition, CV value of Kasalath and CSSL50 tended to be smaller than that of Nipponbare and CSSL34. However, both mean and CV value were not significantly different among the genotypes in TRL and SDW, except for the mean SDW of Kasalath which was highest among the 4 genotypes for both years.

Based on the estimated relationship between TRL/SDW and SMC, reaction norm with slope and curve are shown in Figs. 2 and 3. Reaction norm with curve consistently shows a higher coefficient of determination ($R^2$) than reaction norm with slope so that norm of reaction was better explained by quadratic regression than linear for all the genotypes, except for Kasalath SDW in 2006 (Table 2). Nipponbare and CSSL34 apparently reduced TRL and SDW with increasing drought stress, and linear regression overlapped with quadratic regression. For Kasalath and CSSL50, the slope does not always
coincide with the curve. By the graphical analysis as we showed here, genotypic differences in shoot and root growth in response to contiguous water gradient were observed, although such responses were not clear with comparison of CV.

Table 3 shows the results of further analysis based on the estimated data from quadratic regression. Root plasticity peaked at 20% of SMC, while it was negative or small at 5, 10 and 35% of SMC. CSSL50 showed higher root plasticity than CSSL34 by 12.2 to 49.9 m plant\(^{-1}\) in 2005 and 31.4 to 86.2 m plant\(^{-1}\) in 2006, but root plasticity in CSSL50 was not observed at 35% of SMC in 2005. Then we evaluated the contribution of root plasticity to shoot dry matter production, which was calculated with the differences between Nipponbare and CSSLs in SDW. Contribution of root plasticity of CSSL50 was also higher than that of CSSL34 by 1.0 to 21.7 g plant\(^{-1}\) in 2005 and 1.8 to 6.7 g plant\(^{-1}\) in 2006, except for 35% of SMC in 2005. Furthermore, the contribution of root plasticity peaked in the range of 20 to 30% of SMC, whereas it increased as drought stress intensified for CSSL50 in 2005. We also examined whether the plastic root response efficiently contributed to the shoot dry matter production or not. The value of efficiency of root plasticity was not different between CSSL34 and CSSL50 at any SMC. Additionally, the effect of
drought intensity on this value was smaller than that on root plasticity and contribution of root plasticity.

Furthermore, whole root plasticity was calculated with integration (Table 3). CSSL50 showed 7.3 and 4.4 times larger total root plasticity than CSSL34 in 2005 and 2006, respectively. The peak SMC for maximized root plasticity expression ranged from 17.9 to 21.4% of SMC among genotypes for 2 years.

Discussion

We evaluated the root plasticity in response to contiguous water gradient with different approaches. Valladares et al. (2006) pointed out that the results of quantitative estimation of plasticity would vary depending on the approaches. The CV has been used as simple and quick estimator, and the data set with the smaller CV had less deviation than that with the larger CV. In our results, CSSL50 which had higher root plasticity tended to be smaller CV value than that of CSSL34 (smaller root plasticity), implying that CSSL50 might be stable under changing environment. But there was no significant difference in CV among genotypes, suggesting CV was not linked to plastic response in this study. The reaction norm is usually represented by slope (Schlichting and Pigliucci 1998). However, plastic responses to environment changes such as water gradient are generally complex and actually not linear (Fig. 2). Because root plasticity is hardly explained by a simple linear response, it is important to identify the best-fitted curve. Thus, the evaluation approach is the key to understand how phenotypic plasticity is regulated in response to stress.

As we mentioned before, we selected CSSL34 and CSSL50 that have the same shoot growth as their recurrent parent, Nipponbare under well-watered conditions as control. Thus, root plasticity can be calculated directly as the differences in TRL between CSSLs and Nipponbare, based on the norm of reaction with curve. We found that the root plasticity peaked at around 20% of SMC for both CSSL50 and CSSL34 under contiguous water gradient. Furthermore, we confirmed that root plasticity was affected by the intensities of drought stress and also differed with the CSSLs. (Table 2). Moreover, the whole plasticity in response to contiguous water gradient (Table 3) we proposed in

Table 3. Root plasticity analysis under contiguous water gradient by using 2 CSSLs in 2005 and 2006

| Year | Genotype | Soil moisture content (%) |
|------|----------|---------------------------|
|      |          | 5  | 10  | 15  | 20  | 25  | 30  | 35  |
| 2005 | Root plasticity (m plant⁻¹) | –8.0 | 0.9 | 6.5 | 8.8 | 7.7 | 3.3 | –4.3 |
|      | Contribution of plasticity (g plant⁻¹) | 0.3 | 0.4 | 0.7 | 1.3 | 2.1 | 3.1 | 4.4 |
|      | Efficiency of plasticity (m g⁻¹ plant⁻¹) | 0.0 | 0.4 | 0.1 | 0.1 | 0.3 | 0.9 | –1.0 |
|      | Root plasticity (m plant⁻¹) | 6.3 | 39.1 | 56.4 | 58.2 | 44.6 | 15.5 | –29.0 |
|      | Contribution of plasticity (g plant⁻¹) | 22.0 | 20.7 | 18.3 | 14.8 | 10.3 | 4.7 | –2.0 |
|      | Efficiency of plasticity (m g⁻¹ plant⁻¹) | 3.5 | 0.5 | 0.3 | 0.3 | 0.2 | 0.3 | 0.1 |
| 2006 | Root plasticity (m plant⁻¹) | –53.5 | –15.3 | 9.2 | 20.0 | 16.9 | 0.1 | –30.5 |
|      | Contribution of plasticity (g plant⁻¹) | –2.7 | 0.6 | 2.9 | 4.1 | 4.3 | 3.5 | 1.7 |
|      | Efficiency of plasticity (m g⁻¹ plant⁻¹) | 0.0 | 0.0 | 0.3 | 0.2 | 0.3 | 35.1 | –0.1 |
|      | Root plasticity (m plant⁻¹) | 32.6 | 59.5 | 73.5 | 74.6 | 62.9 | 38.3 | 1.0 |
|      | Contribution of plasticity (g plant⁻¹) | 1.2 | 6.3 | 9.5 | 10.8 | 10.2 | 7.8 | 3.5 |
|      | Efficiency of plasticity (m g⁻¹ plant⁻¹) | 0.0 | 0.1 | 0.1 | 0.1 | 0.2 | 0.2 | 3.7 |

Table 4. Whole root plasticity and peak SMC* of 2 CSSLs in 2005 and 2006

| Year | Genotype | Whole root plasticity (m plant⁻¹) | Peak SMC (%) |
|------|----------|---------------------------------|-------------|
| 2005 | CSSL50   | 958.5                           | 18.1        |
|      | CSSL34   | 131.2                           | 20.9        |
| 2006 | CSSL50   | 983.1                           | 17.9        |
|      | CSSL34   | 224.9                           | 21.4        |

*The SMC where the plant showed maximum value of root plasticity.
this study is a new parameter to understand the potential for root plasticity expression, which CSSL50 showed under such gradient. In our previous studies, the promoted development of root system of CSSL50 is mostly due to the plasticity of lateral roots under mild drought (Kano et al. 2011, Kano-Nakata et al. 2011, Tran et al. 2014).

Tanaka et al. (2000) proposed the idea of a hypothetical root that cannot exhibit root plasticity and they demonstrated that plastic root system development efficiently contributed to nitrogen acquisition in maize. In this study, Nipponbare was considered to be a hypothetical root as Tanaka et al. (2000) described. To evaluate the phenotypic plasticity experimentally, using the same sample is ideal for measurements. However, comparison between different plants is inevitable, especially with regards to root plasticity. Therefore, different samples of a given plant grown under a given environment were compared with those grown under different environment for measurements to confirm the root plasticity. Thus, by using CSSLs, we examined the quantitative evaluation on the role of root plastic responses to contiguous water gradient in rice. By comparing Nipponbare with CSSLs, we confirmed that root plasticity was affected by the intensities of drought stress and also affected by the genotypes indicating that such plastic root response is genetically controlled (Niones et al. 2015). By using these tools, the genetic control of phenotypic plasticity has been clarified through the precise quantitative evaluation and measurement of root plasticity with minimal effects of genetic confounding (Lacaze et al. 2009, Sandhu et al. 2016).

In the present study, we used SDW as an index of contribution of root plasticity, but were not measure directly. However, on root plasticity in relation to water uptake and nutrient uptake are needed to explain the functional role of root plasticity in dry matter production. In this aspect, we previously confirmed the role of root plasticity in enhancing water uptake and contribution to dry matter production by using the root box-pinboard method (Kano-Nakata et al. 2011). Furthermore, a large amount of photosynthates may be necessary for roots to exhibit their plasticity, and aboveground growth and root development are competing for current photosynthates as more than 50% of plant photosynthates produced daily may be respired by the roots (Lambers et al. 1996). Rajaniemi (2007) also pointed out that root plasticity may not always be beneficial because root growth and maintenance also represent costs to the plant. Further study is in progress to examine quantitatively the root metabolic cost in relation to plastic root response to water stress.

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Dr. Shiro Mitsuya has been studied at Nagoya University, Japan. His research focuses on salinity tolerance in crops.

Dr. Akira Yamauchi has been studying the functional roles of root system in crop production focusing on plasticity as a key trait for the plants’ adaptation to unfavorable conditions such water stress, nutrient deficiency and the identification of root ideo-type under each environment.