



# Functional roles of root plasticity and its contribution to water uptake and dry matter production of CSSLs with the genetic background of KDML105 under soil moisture fluctuation

Stella Owusu-Nketia, Jonaliza Lanceras Siangliw, Meechai Siangliw, Theerayut Toojinda, Apichart Vanavichit, Noppon Ratsameejanphen, Mathurada Ruangsiri, Sararin Sriwiset, Roel Rodriguez Suralta, Yoshiaki Inukai, Shiro Mitsuya, Mana Kano-Nakata, Dinh Thi Ngoc Nguyen, Kabuki Takuya & Akira Yamauchi

To cite this article: Stella Owusu-Nketia, Jonaliza Lanceras Siangliw, Meechai Siangliw, Theerayut Toojinda, Apichart Vanavichit, Noppon Ratsameejanphen, Mathurada Ruangsiri, Sararin Sriwiset, Roel Rodriguez Suralta, Yoshiaki Inukai, Shiro Mitsuya, Mana Kano-Nakata, Dinh Thi Ngoc Nguyen, Kabuki Takuya & Akira Yamauchi (2018) Functional roles of root plasticity and its contribution to water uptake and dry matter production of CSSLs with the genetic background of KDML105 under soil moisture fluctuation, *Plant Production Science*, 21:3, 266-277, DOI: [10.1080/1343943X.2018.1477509](https://doi.org/10.1080/1343943X.2018.1477509)

To link to this article: <https://doi.org/10.1080/1343943X.2018.1477509>



© 2018 The Author(s). Published by Informa UK Limited, trading as Taylor & Francis Group.



Published online: 23 May 2018.



Submit your article to this journal [↗](#)



Article views: 1052



View related articles [↗](#)



Citing articles: 4 View citing articles [↗](#)

# Functional roles of root plasticity and its contribution to water uptake and dry matter production of CSSLs with the genetic background of KDML105 under soil moisture fluctuation

Stella Owusu-Nketia<sup>a</sup>, Jonaliza Lanceras Siangliw<sup>b</sup>, Meechai Siangliw<sup>b</sup>, Theerayut Toojinda<sup>b</sup>, Apichart Vanavichit<sup>b</sup>, Noppon Ratsameejanphen<sup>b</sup>, Mathurada Ruangsiri<sup>b</sup>, Sararin Sriwiset<sup>b</sup>, Roel Rodriguez Suralta<sup>c</sup>, Yoshiaki Inukai<sup>d</sup>, Shiro Mitsuya<sup>a</sup>, Mana Kano-Nakata<sup>a,e</sup>, Dinh Thi Ngoc Nguyen<sup>a,f</sup>, Kabuki Takuya<sup>a</sup> and Akira Yamauchi<sup>a</sup>

<sup>a</sup>Graduate School of Bioagricultural Sciences, Nagoya University, Nagoya, Japan; <sup>b</sup>Rice Gene Discovery Unit, BIOTEC, NSTDA, Kasetsart University, Kamphangsaeen Campus, Nakhon Pathom, Thailand; <sup>c</sup>Agronomy, Soils and Plant Physiology Division, Philippine Rice Research Institute (PhilRice), Muñoz, Philippines; <sup>d</sup>International Center for Research and Education in Agriculture, Nagoya University, Nagoya, Japan; <sup>e</sup>Institute for Advanced Research, Nagoya University, Nagoya, Japan; <sup>f</sup>Faculty of Agronomy, Vietnam National University of Agriculture, Hanoi, Vietnam

## ABSTRACT

Soil moisture fluctuation (SMF) stress due to erratic rainfall in rainfed lowland (RFL) rice ecosystems negatively affect production. Under such condition, root plasticity is one of the key traits that play important roles for plant adaptation. This study aimed to evaluate root plasticity expression and its functional roles in water uptake, dry matter production and yield under SMF using three chromosome segment substitution lines (CSSLs) with major genetic background of KDML105 and a common substituted segment in chromosome 8. The CSSLs showed greater shoot dry matter production than KDML105 under SMF, which was attributed to the maintenance of stomatal conductance resulting in higher grain yield. The root system development based on total root length of the CSSLs were significantly higher than that of KDML105 due to the promoted production of nodal and lateral roots. These results implied that the common substituted segments in chromosome 8 of the 3 CSSLs may be responsible for the expression of their root plasticity under SMF and contributed to the increase in water uptake and consequently dry matter production and yield. These CSSLs could be used as a good source of genetic material for drought resistance breeding programs targeting rainfed lowland condition with fluctuating soil moisture environments and for further genetic studies to elucidate mechanisms underlying root plasticity.

## ARTICLE HISTORY

Received 26 February 2018  
Revised 7 May 2018  
Accepted 11 May 2018

## KEYWORDS

Chromosome segment substitution line (CSSL); rainfed lowland (RFL); rice; root plasticity

## Introduction

In rainfed lowland rice ecosystem, soil moisture fluctuation (SMF) stress (Niones, Suralta, Inukai, & Yamauchi, 2012; Owusu-Nketia et al., 2018; Suralta, Inukai, & Yamauchi, 2008b, 2010) which is different from stress due to simple/progressive drought usually occurs due to erratic rainfall. The SMF is a result of the alternate recurrences of waterlogging and water deficit. Such condition can affect root development and its physiological functions (Bañoc, Yamauchi, Kamoshita, Wade, & Pardales, 2000b; Niones et al., 2012; Suralta et al., 2010; Suralta & Yamauchi, 2008), soil nutrient availability (Iijima, Morita, Zegada-Lizarazu, & Izumi, 2007; Kondo, Singh, Agbisit, & Murty, 2005; Suralta et al., 2010; Tran et al., 2014) as well as shoot growth, causing severe yield losses particularly when the drought period coincides with the reproductive stage (O' Toole, 1982;

Venuprasad et al., 2009; Verulkar et al., 2010). For the adaptation of rice plants to such rainfed lowlands, several roots traits have been shown to be desirable such as deep roots, strong roots that can penetrate hardpan (Cairns, Impa, O'Toole, Jagadish, & Price, 2011; Clark, Ferraris, Price, & Whalley, 2008; Wade et al., 2015). In this aspect, the root plasticity is one of the key traits for plant growth under changing environmental conditions such as soil moisture stresses (O'Toole & Bland, 1987; Suralta et al., 2016; Wang & Yamauchi, 2006).

In rice, the root plasticity such as promoted lateral root development were shown to be exhibited in response to varying water-deficit stress intensities (Kameoka, Suralta, Mitsuya, & Yamauchi, 2015; Kano, Inukai, Kitano, & Yamauchi, 2011; Kano-Nakata et al., 2013; Kano-Nakata, Inukai, Wade, Siopongco, & Yamauchi, 2011; Menge et al., 2016; Tran et al., 2014), continuous cycles of alternating

waterlogged and drought stress (Niones et al., 2012; Owusu-Nketia et al., 2018), rewatering after drought (Bañoc, Yamauchi, Kamoshita, Wade, & Pardales, 2000a; Sandhu et al., 2016; Siopongco, Yamauchi, Salekdeh, Bennett, & Wade, 2005; Wade, Kamoshita, Yamauchi, & Azhiri-Sigari, 2000) and transient drought preceded by waterlogged and vice versa (Suralta et al., 2010; Suralta & Yamauchi, 2008), and to contribute to the maintenance of dry matter production and yield under such conditions.

Khao Dawk Mali 105 (KDML105) is an elite cultivar of aromatic rice mainly grown in rainfed lowland areas of North and Northeast Thailand which are prone to abiotic and biotic stresses such as salinity, drought, submergence, diseases and pest (Jantaboon et al., 2011; Jongdee, Pantuwan, Fukai, & Fischer, 2006; Kanjoo et al., 2012; Siangliw, Jongdee, Pantuwan, & Toojinda, 2007; Toojinda, Siangliw, Tragoonrung, & Vanavichit, 2003; Toojinda et al., 2005). Several studies have been carried out on the improvement of KDML105 under such stresses to increase grain yield. Through marker-assisted selection, the development of pyramiding lines tolerant to submergence and resistant to brown plant hopper (Korinsak et al., 2016), backcrossed introgression lines tolerant to drought (Siangliw et al., 2007) as well as chromosome segment substitution lines (CSSLs) tolerant to drought and salinity (Kanjoo et al., 2011, 2012) have been reported.

KDML105 was shown to be susceptible to severe water deficit conditions (Cabuslay, Ito, & Alejar, 2002; Kanjoo et al., 2012; Kumar et al., 2006). A series of our studies showed that KDML105 is well adapted to the rainfed lowland conditions (Azhiri-Sigari, Yamauchi, Kamoshita, & Wade, 2000; Fukai & Cooper, 1995; Kamoshita, Wade, & Yamauchi, 2000; Kano-Nakata et al., 2013; Wade, Fukai, Samson, Ali, & Mazid, 1999) where not solely simple/progressive drought but SMF stress is also a major constraint to production. It has quick responses in root development particularly in the promoted production of lateral roots under various water stress conditions. For instance, under SMF conditions, it can increase its efficiency in converting dry matter to root length to promote production of lateral and nodal roots, which supports leaf expansion (Bañoc et al., 2000a, 2000b). Kameoka et al. (2015) also reported that KDML 105 has the ability to promote lateral root production at the shallow soil layer despite of higher water availability in deep soil, which indicates its high adaptability to the conditions of limited soil depth or impermeable hardpan where soil moisture is available mainly in shallow layer. In addition, we also pointed out the functional significance of plasticity in root aerenchyma formation during the wet period under SMF condition

(Suralta et al., 2008b; Niones et al., 2012), which was shown to promote lateral development during the subsequent dry period under the same condition. As a consequence, such ability to promote lateral root development due to plasticity, which may be associated with plasticity in aerenchyma formation could be important trait for enhancing water and nutrient uptake during water deficit periods under SMF condition. This can lead to the improvement of KDML105 by increasing the biomass production and hence the yield.

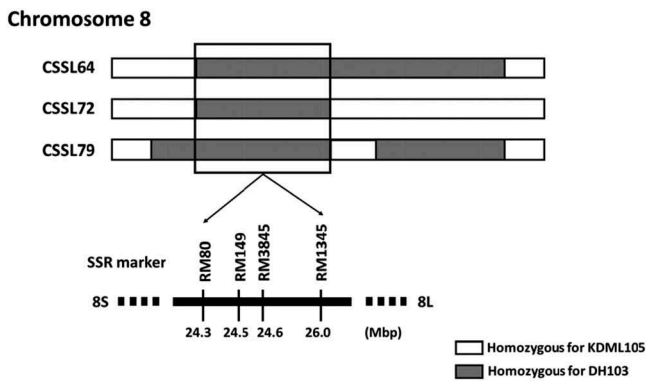
Chromosome segment substitution lines (CSSLs) is a novel mapping population since they are genetic resources containing major genetic background similar to that of the recurrent parent but with introgressed chromosome segments from the donor. CSSLs have been used to effectively identify root plasticity traits, with reduced confounding effects by the variation in genetic backgrounds due to other traits, in response to water deficit of different intensities (Kano et al., 2011; Tran et al., 2014) and SMF conditions (Niones et al., 2012; Suralta et al., 2008b; Suralta & Yamauchi, 2008). Kanjoo et al. (2012) developed CSSLs carrying drought tolerant (DT) QTLs on chromosomes 1, 4 and 8 (Lanceras, Pantuwan, Jongdee, & Toojinda, 2004) in the genetic background of KDML105. These CSSLs showed better adaptation and higher yield than the recurrent parent, KDML105 under drought stress conditions although the mechanism of such adaptation has not yet been studied. In this aspect, we assumed that root plasticity may be involved as one of the major mechanisms.

In this study, we hypothesized that selected KDML105 CSSLs with common substituted segments on chromosome 8 would produce more dry matter and yield more under SMF stress conditions, which could be attributed to the expression of root system plasticity. Thus, this study aimed to evaluate root plasticity expression of the selected CSSLs of KDML105 under SMF condition and its functional roles in water uptake, dry matter production and grain yield.

## Materials and methods

### Plant materials

We used three CSSLs (CSSL64, CSSL72 and CSSL79) selected from 90 CSSLs, which had higher grain yield under drought stress condition than their irrigated counterparts (Kanjoo et al., 2012). The three selected CSSLs carry substituted segments from double haploid line, IR58586-F2-CA-31 (DH103), derived from a cross between CT9993-5-10-1-M (CT9993) and IR62266-42-6-



**Figure 1.** The graphical map of CSSL64, CSSL72 and CSSL79 genotypes showing the KDML105 with substituted chromosome segments from the double haploid line, IR58586-F2-CA-31 (DH103) genome on chromosome 8. The *solid white square* represents KDML105 segment while the *solid grey segment* represents DH103 segment.

2 (IR62266) on chromosome 8 in a genetic background of KDML105 (Siangliw et al., 2007) (Figure 1).

### Field experiment

The selected CSSLs; CSSL64, CSSL72, CSSL79 together with their recurrent parent, KDML105 were evaluated under two soil moisture treatments: continuously waterlogged (CWL as control) and rainfed lowland (RFL) conditions with soil moisture fluctuation (SMF) during the wet season in 2016. The experiment was conducted at the experimental field of Kasetsart University, Kamphaengsaen Campus, Thailand (14.0236° N, 99.9749° E) using a randomized complete block design (RCBD) with four replications. The experimental plot size was 20 m × 5 m with spacing of 0.2 m for each treatment plot. The soil used was heavy clay. Chemical fertilizers, NPK 46-0-0 was applied at 17 days after transplanting (DAT), and NPK 16-18-2 applied at 42–52 DAT at a rate of 90 kg N ha<sup>-1</sup>.

Seeds of each genotype were put in paper bags and placed in an oven at 50°C for 48 h to break dormancy prior to sowing. The seeds were then sown in black plastic trays with soil under well-watered conditions. Twenty-eight day old healthy seedlings of each genotype were transplanted in the field at one seedling per hill on the 29th August, 2016. The transplanted seedlings were allowed to recover from transplanting shock for 28 days with frequent watering after which the seedlings were exposed to two water treatments; CWL and RFL conditions, and grown until maturity.

### Soil moisture treatments

In CWL, the water level was maintained at 5 cm depth above the soil surface from transplanting until maturity.

In RFL, the field was irrigated similar to that of the CWL until 28 days after transplanting (DAT) and then the water was drained and shifted its water supply purely from the rainfall.

Soil water potential was recorded using a soil tensiometer (Daiki soil and moisture, Daiki Rika Kogyo Co., Japan). The soil O<sub>2</sub> concentration was measured with a soil oxygen meter (E.M.J., Decagon, Utah, USA). Six soil tensiometers and one oxygen sensor were installed at 20 cm soil depth in RFL plot only.

The heading date was recorded as the number of days when 50% of the panicles of all plants in a plot already emerged (55 DAT).

### Stomatal conductance measurements

The stomatal conductance was measured at heading (55 DAT) and 15 days after heading (DAH) using a leaf porometer (Decagon, Utah, USA) between 10:00 and 14:00 h.

### Shoot and root measurements

The shoot and root samples were collected at heading (55 DAT) and 15 DAH. Shoots were cut from the base and oven-dried at 80°C for 48 h before recording the dry weight. The root system was extracted as described by Niones et al. (2012) and Kano et al. (2011) using a monolith stainless cylinder (20 cm diameter × 40 cm height) (Kang, Morita, & Yamazaki, 1994) up to 20 cm soil depth. The collected root samples were washed free of soil with gentle running water and stored in 70% ethanol for further measurements. The number of nodal roots at the base was manually counted. For the total root length (TRL) measurements, root samples were spread evenly on a transparent tray without overlapping. Digital images were then taken using an image scanner (EPSON Perfection V700 Photo) at 400 dpi resolution. The TRL was analyzed using WinRhizo software (Regent Instruments Inc., Saint-Foy, Canada) (Kameoka et al., 2015; Menge et al., 2016). A pixel threshold value of 175 was set for the root length analysis (Nguyen et al., 2018; Suralta et al., 2018). The root lengths were analyzed according to their diameter classes to estimate the total length of lateral roots having a diameter of <0.3 mm (Yamauchi, Pardales, & Kono, 1996).

### Yield and yield component measurements

Forty eight plants per genotype per water treatment were sampled at maturity (35 DAH) for the yield and yield components measurements. Panicles were separated from the shoots, counted and oven-dried at 80°C for 48 h before weighing. The spikelets were manually separated from the panicles. The spikelets were classified into filled (with developed grains) and unfilled

(without developed grains) spikelets and counted separately. The 1000 grains were collected from each sample to record the 1000 grain weight. Yield was determined as the weight of filled grains per plant (adjusted to 14% grain moisture content).

### Statistical analysis

Differences between mean values were compared using the least significant difference (LSD) test at  $p < 0.05$  level to compare genotypes within each water treatment using Microsoft Excel Statistics 2013 for Windows. The relationships between root traits and shoot traits were determined using regression analysis.

### Pot experiment

To accurately evaluate the water uptake of the three CSSLs (CSSL64, CSSL72, and CSSL79) and their recurrent parent, KDML105, plastic pots (20 cm in height and 25 cm in diameter) were used. Each plastic pot was filled with 6.0 kg of air-dried heavy clay soil and placed under greenhouse of Rice Gene Discovery Unit, Kasetsart University, Kamphangsaeen Campus, Thailand using RCBD with four replications.

Seeds of each genotype were put in paper bags and placed in an oven at 50°C for 48 h to break the dormancy prior to sowing. Ten seeds per genotype were directly sown in the plastic pots on the 22nd August, 2016. The seedlings were thinned to one seedling per pot at 20 days after sowing (DAS). Each pot represented one replication.

### Soil moisture treatments

The plants were exposed to two water treatments; CWL (as control) and SMF (as stress) conditions. In CWL, the water level was maintained at 5 cm depth above the soil surface from sowing until the end of the experiment. In SMF, the plants were first waterlogged similar to that of the CWL until 30 DAS. Thereafter, the water was drained until the leaves started to roll (52 DAS), and then rewatered back to 5 cm water level above the soil surface (Niones et al., 2012; Owusu-Nketia et al., 2018) for ten days. This was done repeatedly until the termination of the experiment at 85 DAS (20 DAH). The pots were weighed daily using a digital balance to record the wet mass of the soil until leaf rolling. The water uptake for each plant per pot was calculated as the proportion of water weight estimated as the difference between the wet weights of the soil excluding the pot on a given day to the dry weight of soil (Suralta, Lucob, Perez, Niones, & Nguyen, 2015).

### Shoot and root measurements

The shoot and root samples were collected at 85 DAS. Shoots were cut from the base and oven-dried at 80°C for

48 h before weighing. The root samples were washed free of soil with gentle running water. The cleaned root samples were stored in 70% ethanol for further measurements described in the field experiment.

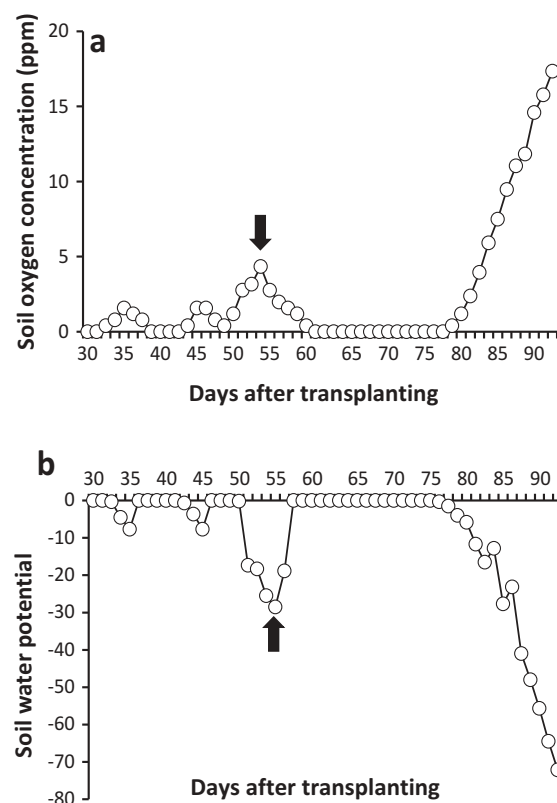
Root measurements were carried out in a similar manner described in Field Experiment.

## Results

### Field experiment

#### Soil moisture fluctuation dynamics

The soil water potential and oxygen concentration dynamics under RFL conditions are shown in Figure 2. Soil water potential and oxygen concentration were recorded from 27 DAT until 90 DAT. The soil water potential fluctuated from 0.0 to -7.6 kPa with oxygen concentration of 1.6 ppm from 30 to 35 DAT, after which the soil oxygen concentration dropped to 0 ppm. The soil water potential then dropped to -7.4 kPa with soil oxygen concentration of 1.5 ppm at 45 DAT. Afterwards, the soil oxygen concentration decreased to 1.2 ppm with water potential of 0.0 kPa at 50 DAT due to rainfall. During the heading stage at



**Figure 2.** Soil oxygen concentration (a) and soil water potential (b) under rainfed lowland (RFL) condition in field experiment. An arrow symbol indicates the heading time for the three selected CSSLs and KDML105 genotypes.

55 DAT, the soil water potential dropped to  $-29.0$  kPa with soil oxygen concentration of 4.3 ppm. The soil oxygen concentration and soil water potential then dropped to 0.0 ppm and 0.0 kPa, respectively at 74 DAT. However, due to absence of rain, the soil oxygen concentration increased to 17.3 ppm with soil water potential of  $-72.0$  kPa from 75 DAT to the termination of the experiment at 90 DAT.

### Shoot growth and development

Generally, all the CSSLs had a significant increase in shoot dry weight (SDW) under RFL, relative to their CWL counterparts while KDML 105 showed reduction. Specifically, CSSL64 increased SDW by 17 and 28% at heading and 15 DAH, respectively. Likewise, CSSL72 had significant increase by 19% at heading stage and 10% at 15 DAH. Furthermore, CSSL79 had significant increase in SDW by 18 and 21% at heading and 15 DAH respectively. On the other hand, KDML 105 had reduced SDW by 19 and 16% under RFL relative to its CWL counterpart at heading and 15 DAH, respectively (Tables 1 and 2). The three CSSLs (CSSL64, CSSL72 and CSSL79) produced similar SDW with the recurrent parent, KDML 105 at heading and 15 DAH under CWL (Tables 1 and 2). Under RFL, on the other hand, these CSSLs produced significantly greater SDW by 43% (CSSL64), 36% (CSSL72) and 44% (CSSL79) than KDML105 at heading stage. Furthermore, these CSSL also produced significantly greater SDW by 62% (CSSL64), 34% (CSSL72) and 50% (CSSL79) than KDML105 at 15 DAH (Tables 1 and 2).

Moreover, the CSSLs had an increase in number of tillers under RFL relative to CWL conditions while

**Table 1.** Shoot dry weight, tiller number, stomatal conductance and root traits of three selected CSSLs and their recurrent parent KDML 105 grown under continuous waterlogged (CWL) and rainfed lowland (RFL) conditions at heading stage in field experiment.

Soil moisture treatment Genotype	SDW (g plant <sup>-1</sup> )	TN (No. plant <sup>-1</sup> )	gs (mmol m <sup>-2</sup> s <sup>-1</sup> )	TRL (cm plant <sup>-1</sup> )	LRL (cm plant <sup>-1</sup> )	NRN (No. plant <sup>-1</sup> )
<i>CWL</i>						
CSSL 64	54.0a	16a	423.3a	12876a	8862 a	462a
CSSL72	50.3a	17a	419.5a	13504a	9339 a	432a
CSSL79	53.9a	15a	398.9a	12978a	8742 a	443a
KDML105	52.8a	16a	413.2a	13179a	9359 a	450a
<i>RFL</i>						
CSSL 64	63.3a	20a	391.5a	12065a	10564a	415a
CSSL72	60.5a	19a	454.9a	12400a	11041a	399a
CSSL79	64.2a	18a	407.9a	12731a	11253a	428a
KDML105	44.2b	14b	231.4b	8020b	7085b	223b

Values are means of four replicates. In a column, means followed by the same letters are not significantly different at LSD<sub>0.05</sub> level within each treatment. *SDW*: shoot dry weight; *TN*: number of tillers; *gs*: stomatal conductance; *TRL*: total root length; *LRL*: total lateral root length; *NRN*: total number of nodal roots.

**Table 2.** Shoot dry weight, tiller number, stomatal conductance and root traits of three selected CSSLs and their recurrent parent KDML 105 grown under continuous waterlogged (CWL) and rainfed lowland (RFL) conditions at 15 DAH in field experiment.

Soil moisture treatment Genotype	SDW (g plant <sup>-1</sup> )	TN (No. plant <sup>-1</sup> )	gs (mmol m <sup>-2</sup> s <sup>-1</sup> )	TRL (cm plant <sup>-1</sup> )	LRL (cm plant <sup>-1</sup> )	NRN (No. plant <sup>-1</sup> )
<i>CWL</i>						
CSSL 64	68.9a	15a	357.7a	19774a	13682a	511a
CSSL72	65.8a	14a	368.9a	18860a	12921a	480a
CSSL79	67.4a	15a	376.5a	20138a	14116a	476a
KDML 105	63.8a	15a	345.7a	18899a	13018a	468a
<i>RFL</i>						
CSSL 64	88.7a	18a	398.9a	17336a	15642a	464a
CSSL72	73.6a	16a	433.8a	16357a	14847a	432a
CSSL79	82.0a	16a	402.5a	17227a	15603a	456a
KDML 105	54.6b	11b	277.3b	9896b	8791b	256b

Values are means of four replicates. In a column, means followed by the same letters are not significantly different at LSD<sub>0.05</sub> level within each treatment. *SDW*: shoot dry weight; *TN*: number of tillers; *gs*, stomatal conductance; *TRL*: total root length; *LRL*: total lateral root length; *NRN*: total number of nodal roots.

KDML105 had reduced tillering (Tables 1 and 2). Furthermore, there were no significant differences in tillering ability between the CSSLs and KDML 105 under CWL. On the contrary, the CSSLs significantly produced higher number of tillers than KDML 105 under RFL both at heading and 15 DAH. Under both water treatments, the tiller production of the genotypes was slightly reduced at 15 DAH as compared with heading stage.

### Stomatal conductance

In CWL, the stomatal conductance of CSSL64, CSSL72 and CSSL79 was not significantly different among genotypes regardless of growth stages (Tables 1 and 2). In contrast, these CSSLs had significantly higher stomatal conductance than KDML105 at heading during drought stress and even at 15 DAH during rewatering (occurrence of rainfall). In general, under RFL, the CSSLs maintained their stomatal conductance after rewatering whereas that of KDML105 was reduced at 15 DAH as compared with CWL.

### Root system development

Root system development based on TRL was not significantly different among CSSLs and KDML105 under CWL (Tables 1 and 2). On the contrary, the CSSLs had significantly greater root system than KDML105 under RFL. Compared to KDML105, CSSL64, CSSL72 and CSSL 79 had significantly greater TRL by 50, 54 and 58%, respectively, at heading and by 75, 65 and 74%, respectively at 15 DAH.

Also, for nodal root production (Tables 1 and 2), there were no significant differences between the CSSLs and KDML105 under CWL. Under RFL condition, the number of nodal roots (NRN) of the genotypes

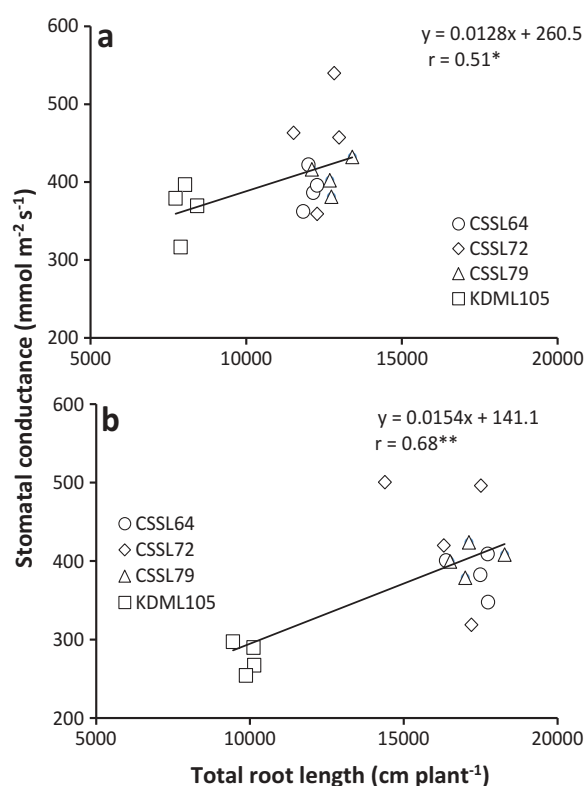
slightly increased from heading to 15 DAH although the CSSLs showed significantly higher nodal root production than KDML105. CSSL64 had significantly higher nodal root production than KDML105 by 86% at heading and 81% at 15 DAH. CSSL72 showed significantly higher NRN than KDML105 by 78 and 68%, respectively, at heading and 15 DAH. Also, CSSL79 had significantly higher NRN than KDML105 by 91 and 78% at heading and 15 DAH, respectively.

### Correlation among root and shoot traits

The correlations between TRL and stomatal conductance (Figure 3), TRL and SDW (Fig. 44), and stomatal conductance and SDW (Figure 5) of the three selected CSSLs were positive and significant at heading and 15 DAH under RFL conditions.

### Yield and yield components

The yield and yield components of the CSSLs and KDML105 are presented in Table 3. There were no significant differences among the genotypes under CWL condition. Under RFL condition, CSSL64, CSSL72 and CSSL79 had significantly higher yields as well as the yield components such as total number of spikelets,



**Figure 3.** Relationship between total root length and stomatal conductance of three selected CSSLs and their recurrent parent KDML105 grown under rainfed lowland (RFL) conditions in field experiment at heading (a) and grain filling (b) stages. \* and \*\* significant at  $p < 0.05$  and  $p < 0.01$ .

**Table 3.** Yield and yield components of three selected CSSLs and their recurrent parent KDML105 grown under continuous waterlogged (CWL) and rainfed lowland (RFL) conditions in field experiment.

Soil moisture treatment	TNS (No. plant <sup>-1</sup> )	FS (No. plant <sup>-1</sup> )	1000 GW (g)	PN (No. plant <sup>-1</sup> )	% FS	GY (g plant <sup>-1</sup> )
<b>CWL</b>						
CSSL 64	666a	598a	26.4b	10a	89.8a	15.7a
CSSL72	690a	638a	27.4ab	11a	92.5a	16.3a
CSSL79	606a	581a	27.7a	11a	95.8a	14.8a
KDML 105	645a	590a	26.9ab	10a	91.5a	15.4a
<b>RFL</b>						
CSSL 64	858a	776a	26.3b	16a	90.4a	18.8a
CSSL72	828a	757a	27.9a	15a	91.4a	18.4a
CSSL79	757a	690a	27.3ab	14a	91.1a	17.9a
KDML 105	608b	438b	26.1ab	8b	72.0b	10.7b

Values are means of four replicates. In a column, means followed by the same letters are not significantly different at  $LSD_{0.05}$  level within each treatment. TNS: total number of spikelet; FS: filled spikelet; GW: grain weight; PN: number of panicles; GY: grain yield.

filled number of spikelets, percentage filled spikelets and the number of panicles than KDML105. However, there were no significant differences in 1000 grain weight among the genotypes except CSSL64, which was significantly lower than CSSL72.

### Pot experiment

#### Shoot dry matter production, root system development and water uptake

For shoot and root growth of the genotypes, a similar trend was observed as in Field Experiment. Under CWL condition, there were no significant differences among genotypes for SDW, TRL and NRN (Table 4). The CSSLs, CSSL64, CSSL72 and CSSL79 had significantly higher SDW, TRL and NRN than KDML105 under SMF

**Table 4.** Shoot dry weight, total water uptake and root traits of three selected CSSLs and their recurrent parent KDML105 grown under continuous waterlogged (CWL) and soil moisture fluctuation (SMF) conditions in pot experiment.

Soil moisture treatment	SDW (g plant <sup>-1</sup> )	TWU (g plant <sup>-1</sup> )	TRL (cm plant <sup>-1</sup> )	NRN (No. plant <sup>-1</sup> )
<b>CWL</b>				
CSSL 64	7.71a	-	7964a	51a
CSSL72	7.58a	-	7845a	49a
CSSL79	7.60a	-	8006a	53a
KDML 105	8.01a	-	8094a	53a
<b>SMF</b>				
CSSL 64	9.42a	1935a	11030a	82a
CSSL72	8.95a	2008a	10026a	79a
CSSL79	9.06a	2095a	12787a	86a
KDML 105	7.12b	1698b	7885b	50b

Values are means of four replicates. In a column, means followed by the same letters are not significantly different at  $LSD_{0.05}$  level within each treatment. SDW: shoot dry weight; TWU: total water uptake; TRL: total root length; NRN: number of nodal roots. Total water use was not measured in CWL.

condition. CSSL64 had significantly higher SDW, TRL and NRN than KDML105 by 32, 47 and 64%, respectively, under SMF condition. Likewise, CSSL72 showed significantly greater SDW by 25%, TRL by 34% and NRN by 58% than KDML105 under SMF. Again, under SMF, CSSL79 showed significantly higher SDW, TRL and NRN by 27, 70 and 72%, respectively than KDML105.

Also, CSSL64, CSSL72 and CSSL79 showed significantly greater production of SDW, TRL and NRN under SMF than CWL condition. For instance, CSSL64 had higher SDW, TRL and NRN under SMF than CWL by 22, 38 and 60%, respectively. Under SMF, CSSL72 showed significantly higher SDW by 18%, TRL by 27% and NRN by 61% than under CWL condition. Similarly, CSSL79 had significantly greater SDW by 18%, TRL by 62% and NRN by 62% under SMF than CWL condition. In contrast, KDML105 had significant reduction in SDW and TRL by 12 and 8%, respectively, under SMF as compared with CWL. There was also reduction in NRN under SMF by 6% compared with CWL although not significant (Table 4).

The total water uptake of the CSSLs, CSSL64, CSSL72 and CSSL79 under SMF condition was significantly higher than their recurrent parent, KDML105 (Table 4).

#### ***Correlation among root and shoot traits and water uptake***

The TRL of the three selected CSSLs and KDML105 was positively and significantly correlated with total water uptake (Figure 7(a)). There was also significant and positive relationship between total water uptake and SDW (Figure 7(b)).

#### **Discussion**

In this study, CSSLs carrying substituted segments on chromosomes 8 in KDML105 genetic background were evaluated for root plasticity expression under SMF condition and its functional roles in water uptake, dry matter production and grain yield. We found out that these CSSLs performed better than their recurrent parent in terms of root and shoot growth under only RFL condition in the field and SMF condition in pot experiment but not under favorable CWL conditions. Moreover, these CSSLs had the ability to increase root and shoot growth under RFL, relative to CWL conditions. This indicates that the introgressed segments into the genetic background of KDML105 may have QTLs which could be responsible for the expression of root plasticity responses to SMF and consequently increased water uptake during the transient drought periods and the overall dry matter production.

Several studies have shown the reduction in shoot dry matter production and grain yield of rice plants grown under SMF condition (Belder, Spiertz, Bouman, Lu, & Tuong, 2005; Niones et al., 2012; Owusu-Nketia et al., 2018; Suralta et al., 2008b, 2010) while such fluctuating soil moisture environment including aerobic culture could cause increase in dry matter production (Katsura, Okami, Mizunuma, & Kato, 2010) as well as grain yield (Kato, Okami, & Katsura, 2009) as compared with flooded conditions. In this study, CSSL64, CSSL72 and CSSL79 had significantly higher grain yield than the recurrent parent, KDML105 under RFL condition but not under CWL condition (Table 3). This increase in grain yield could be attributed to increase in yield components such as number of panicles, total number of spikelets and filled spikelets. The significantly higher number of filled spikelets led to a decrease in percentage spikelet sterility and hence the higher grain yield. These results of increased yield and yield components of the three CSSLs under RFL condition was consistent with the previous studies by Kanjoo et al. (2012), in which these three CSSLs showed increased grain yield also under drought stress. On the other hand, the yield reduction of KDML105 under RFL condition was found to be caused by increased number of unfilled spikelets and high percentage spikelet sterility. During the heading stage (55 DAT), the soil became dry and the water potential reached at  $-29.0$  kPa (Figure 2). KDML 105 had significantly shorter TRL and thus most probably shallower root system under RFL conditions than CWL conditions while the three CSSLs maintained their root system development under RFL conditions at heading stage (Table 1). These facts indicate that KDML 105 exhibited less plasticity in root system development in response to RFL conditions, which could have adversely caused spikelet sterility.

In addition, the maintenance or increase in dry matter production under SMF condition could result in higher grain yield (Katsura et al., 2010; Niones et al., 2012; Owusu-Nketia et al., 2018; Suralta et al., 2010). The significant increase in shoot dry matter production of CSSL64, CSSL72 and CSSL79 under SMF conditions as compared with CWL in both experiments in this study contributed to their higher grain yields than KDML105 (Tables 1 and 2). This can be attributed to the increased production of tillers (Kanjoo et al., 2012) as well as water uptake and stomatal conductance (Kano-Nakata et al., 2013; Nguyen et al., 2018; Suralta et al., 2015; Tran et al., 2014). The significant and positive relationships between stomatal conductance and shoot dry matter (Figure 5), under RFL condition in the field and that of total water uptake and shoot dry matter production (Figure 7(b)) under SMF in pot experiment indicate

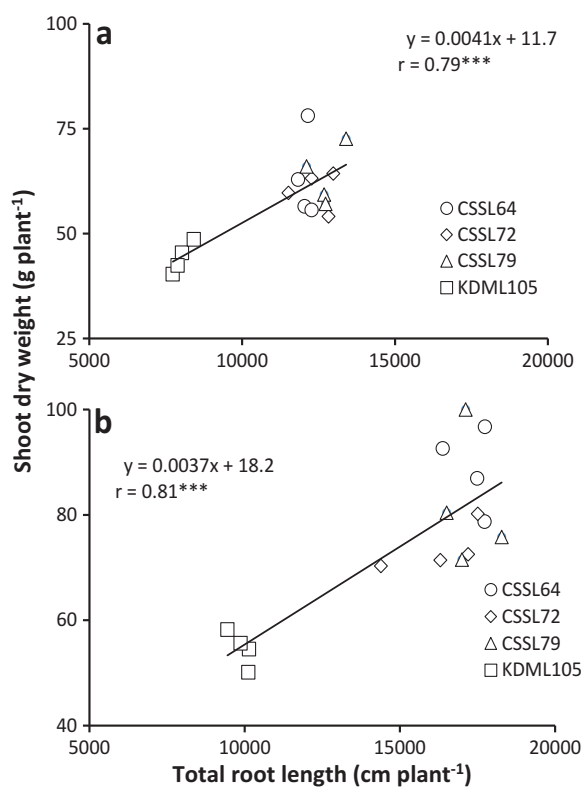


that water uptake and stomatal conductance enhanced dry matter production and consequently the grain yield of CSSL64, CSSL72 and CSSL79, which was significantly higher than that of KDML105. This maintenance or increase in stomatal conductance which subsequently increased water supply to the leaves could be a consequence of promoted root growth under SMF conditions. Significant and positive relationships between TRL and stomatal conductance (Figure 3), TRL and shoot dry matter production and grain yield (Figures 4 and 6(a)) as well as TRL and total water uptake (Figure 7 (a)) of CSSL64, CSSL72 and CSSL79 under SMF conditions suggest that water uptake, stomatal conductance and dry matter production were enhanced by increased root length due to the expressed plasticity.

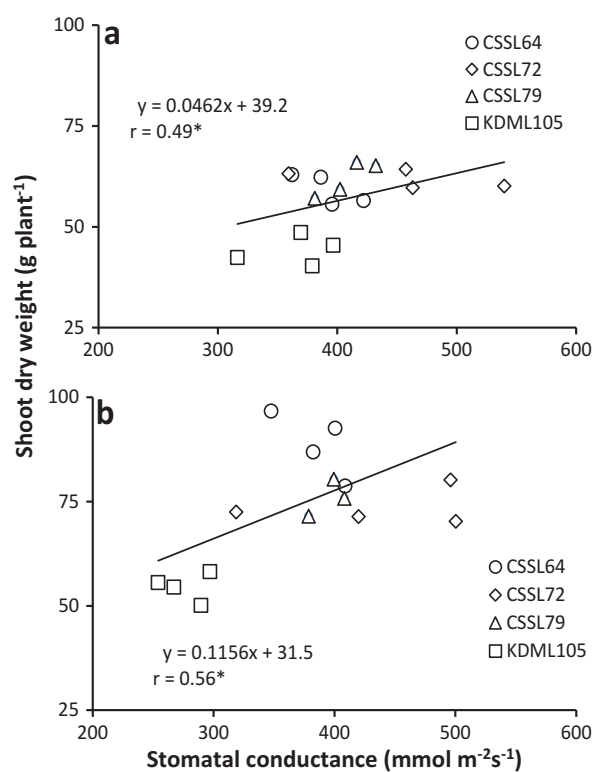
Previous studies have shown experimental evidences of genotypic variations in root plasticity expressed in response to heterogeneous soil environments for the adaptation of rice plants (Bañoc et al., 2000a; Siopongco et al., 2008; Kano-Nakata et al., 2013; 2017; Kameoka et al., 2015; Menge et al., 2016; Niones et al., 2012; Nguyen et al., 2018; Owusu-Nketia et al., 2018; Suralta et al., 2010, 2016, 2018; Tran et al., 2014). In this study,

the CSSLs showed no significant differences in root system development with the recurrent parent under CWL in both experiments. In contrast, root system development in terms of total root length of CSSL64, CSSL72 and CSSL79 were significantly greater than KDML105 under SMF condition. The greater root system of the CSSLs was due to the promoted nodal root production from the tillers and elongation, and promoted lateral root elongation (Tables 1 and 2). These observations were similar to those reported by Niones et al. (2012), Kano-Nakata et al. (2013) and Owusu-Nketia et al. (2018).

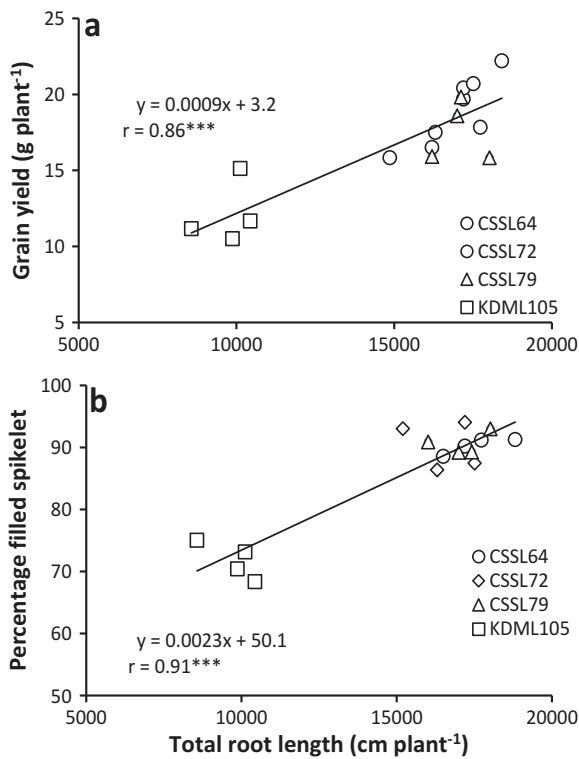
These results infer that the root plasticity resulting in promoted nodal root development and increased total root length of which lateral roots constitute greater portion (Wang, Siopongco, Wade, & Yamauchi, 2009; Yamauchi, Kono, & Tatsumi, 1987), could play a major role in the adaptation of rice plants to soil moisture fluctuation conditions (Bañoc et al., 2000a, 2000b; Niones et al., 2012; Owusu-Nketia et al., 2018). Thus, the ability of the plant to maintain greater root system (Bañoc et al., 2000b) under progressive drought stress in soil moisture fluctuation conditions can result in



**Figure 4.** Relationship between total root length and shoot dry weight of three selected CSSLs and their recurrent parent KDML105 grown under rainfed lowland (RFL) conditions in field experiment at heading (a) and grain filling (b) stages. \*\*\* significant at  $p < 0.001$ .



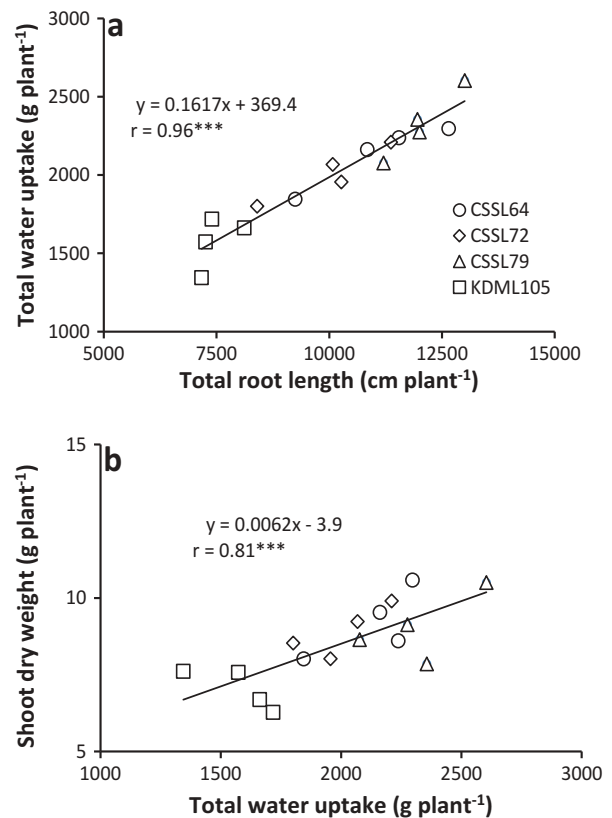
**Figure 5.** Relationship between stomatal conductance and shoot dry weight of three selected CSSLs and their recurrent parent KDML105 grown under rainfed lowland (RFL) conditions in field experiment at heading (a) and grain filling (b) stages. \* significant at  $p < 0.05$ .



**Figure 6.** Relationship between total root length and grain yield (a), and total root length and percentage filled spikelet (b) of three selected CSSLs and their recurrent parent KDML105 grown under rainfed lowland (RFL) conditions in field experiment. \*\*\* significant at  $p < 0.001$ .

increase in root surface area, thereby enhancing water uptake (Kano-Nakata et al., 2013; Kato et al., 2011; Kato, Kamoshita, Yamagishi, Imoto, & Abe, 2007; Siopongco et al., 2005; Siopongco, Yamauchi, Salekdeh, Bennett, & Wade, 2006; Suralta et al., 2010). This could lead to maintenance of dry matter production and yield. In addition, there were significant and positive correlation between TRL and grain yield (Figure 6(a)) as well as TRL and percentage filled spikelet (Figure 6(b)) of particularly CSSL64, CSSL72 and CSSL79 under RFL condition. These results suggest that the promoted root development due to plasticity contributed to increase in grain yield through grain filling.

Moreover, the similar performance of the three CSSLs under SMF condition could be due to the common substituted segments on chromosome 8 (Figure 1), which are derived from DH103 allele and introgressed into KDML105 genetic background. These common substituted segments may regulate root plasticity in response to SMF stress condition. Such regulation could have contributed to the greater root system (Tables 1 and 2) of the CSSLs as a result of promoted and elongated nodal and lateral roots,



**Figure 7.** Relationship between total root length and total water uptake (a), and total water uptake and shoot dry weight (b) of three selected CSSLs and their recurrent parent KDML105 grown under soil moisture fluctuation (SMF) condition in pot experiment. \*\*\* significant at  $p < 0.001$ .

which led to increase in water uptake and consequently the dry matter production and yield. Furthermore, the common substituted segments coincided with QTLs for biological yield, panicle number and plant height (Lanceras et al., 2004), harvest index (Bernier et al., 2007), root to shoot ratio (Champoux et al., 1995), and deep root biomass (Courtois et al., 2013) under constant drought stress conditions using other rice mapping populations. Likewise, the substituted segments of the CSSLs also overlapped with QTLs associated with specific water use (Kato, Hirotsu, Nemoto, & Yamagishi, 2008), root volume (Qu et al., 2008), and root number (Ray et al., 1996; Zheng et al., 2000). However, QTLs detected under SMF condition for root number (Owusu-Nketia et al., 2018; Suralta et al., 2015) and total root length (Suralta et al., 2015) did not coincide with the substituted segments of the CSSLs on chromosome 8. This suggests that these QTLs regulating root development may be dependent on specific rice mapping population. The common substituted regions of the CSSLs could play important roles in adaptation to soil moisture fluctuation stress which occurs in rainfed

lowland areas. However, further genetic analysis on detection of QTLs using these CSSLs is still needed to confirm the location and validate the effect of QTLs for root plasticity.

## Conclusion

In our study, CSSLs carrying DT-QTL on chromosomes 4 and 8 were evaluated for the expression of root plasticity and its functional roles in water uptake, dry matter production and yield. The CSSLs, CSSL64, CSSL72 and CSS79 showed greater shoot dry matter production than KDML105, which were credited to their increase in tiller production as well as higher stomatal conductance and water uptake. In addition, the root system development of the CSSLs expressed as total root length were higher than KDML105 due to the promoted nodal and lateral roots production and elongation under rainfed condition. Interestingly, under rainfed condition, the shoot dry weight of the CSSLs were higher than that of the flooded condition and this could be attributed to the introgressed DT-QTL segment thereby leading to increase in yield. Therefore, such genetic variation in the expression of root plasticity is essential in improving the adaptability of rice plants grown under fluctuating soil moisture environments such as rainfed lowlands and could be useful genetic material for breeding programs for rainfed lowland rice.

## Acknowledgments

This research was funded by the Grant-in-Aid for Scientific Research (No. 15H02644) from the Japan Society for the Promotion of Science, and partially supported by the Japan Science and Technology Agency (JST)/Japan International Cooperation Agency (JICA) and Science and Technology Research Partnership for Sustainable Development (SATREPS). We are very thankful to the staff and students of Rice Gene Discovery Unit, Kasetsart University, Kamphangsaen Campus, Thailand for their enormous support with conducting the experiments.

## Disclosure statement

No potential conflict of interest was reported by the authors.

## Funding

This research was funded by the Grant-in-Aid for Scientific Research (No. 15H02644) from the Japan Society for the Promotion of Science, and partially supported by the Japan Science and Technology Agency (JST)/Japan International

Cooperation Agency (JICA) and Science and Technology Research Partnership for Sustainable Development (SATREPS).

## References

- Azhiri-Sigari, T., Yamauchi, A., Kamoshita, A., & Wade, L. J. (2000). Genotypic variation in response of rainfed lowland rice to drought and rewetting. II. Root growth. *Plant Production Science*, 3, 180–188.
- Bañoc, D. M., Yamauchi, A., Kamoshita, A., Wade, L. J., & Pardales, J. R., Jr. (2000a). Dry matter production and root system development of rice cultivars under fluctuating soil moisture. *Plant Production Science*, 3, 197–207.
- Bañoc, D. M., Yamauchi, A., Kamoshita, A., Wade, L. J., & Pardales, J. R., Jr. (2000b). Genotypic variations in response of lateral root development to fluctuating soil moisture in rice. *Plant Production Science*, 3, 335–343.
- Belder, P., Spiertz, J. H. J., Bouman, B. A. M., Lu, G., & Tuong, T. P. (2005). Nitrogen economy and water productivity of lowland rice under water-saving irrigation. *Field Crops Research*, 93(2–3), 169–185.
- Bernier, J., Kumar, A., Ramaiah, V., Spaner, D., & Atlin, G. (2007). A large-effect QTL for grain yield under reproductive-stage drought stress in upland rice. *Crop Science*, 47(2), 507–516.
- Cabuslay, G. S., Ito, O., & Alejar, A. A. (2002). Physiological evaluation of responses of rice (*Oryza sativa* L.) to water deficit. *Plant Science*, 163(4), 815–827.
- Cairns, J. E., Impa, S. M., O'Toole, J. C., Jagadish, S. V. K., & Price, A. H. (2011). Influence of the soil physical environment on rice (*Oryza sativa* L.) response to drought stress and its implications for drought research. *Field Crops Research*, 121(3), 303–310.
- Champoux, M. C., Wang, G., Sarkarung, S., Mackill, D. J., O'Toole, J. C., Huang, N., & McCouch, S. R. (1995). Locating genes associated with root morphology and drought avoidance in rice via linkage to molecular markers. *Theoretical and Applied Genetics*, 90(7–8), 969–981.
- Clark, L. J., Ferraris, S., Price, A. H., & Whalley, W. R. (2008). A gradual rather than abrupt increase in soil strength gives better root penetration of strong layers. *Plant and Soil*, 307, 235–242.
- Courtois, B., Audebert, A., Dardou, A., Roques, S., Ghneim-Herrera, T., Droc, G., ... Ahmadi, N. (2013). Genome-wide association mapping of root traits in a japonica rice panel. *PLoS One*, 8(11), e78037.
- Fukai, S., & Cooper, M. (1995). Development of drought-resistant cultivars using physio-morphological traits in rice. *Field Crops Research*, 40, 67–86.
- Iijima, M., Morita, S., Zegada-Lizarazu, W., & Izumi, Y. (2007). No-tillage enhanced the dependence on surface irrigation water in wheat and soybean. *Plant Production Science*, 10, 182–188.
- Jantaboon, J., Siangliw, M., Im-Mark, S., Jamboonsri, W., Vanavichit, A., & Toojinda, T. (2011). Ideotype breeding for submergence tolerance and cooking quality by marker-assisted selection in rice. *Field Crops Research*, 123, 206–213.
- Jongdee, B., Pantuwan, G., Fukai, S., & Fischer, K. (2006). Improving drought tolerance in rainfed lowland rice: An example from Thailand. *Agricultural Water Management*, 80, 225–240.
- Kameoka, E., Suralta, R. R., Mitsuya, S., & Yamauchi, A. (2015). Matching the expression of root plasticity with soil

- moisture availability maximizes production of rice plants grown in an experimental sloping bed having soil moisture gradients. *Plant Production Science*, 18, 267–276.
- Kamoshita, A., Wade, L. J., & Yamauchi, A. (2000). Genotypic variation in response of rainfed lowland rice to drought and rewatering. III. Water extraction during drought period. *Plant Production Science*, 3, 189–196.
- Kang, S. Y., Morita, S., & Yamazaki, K. (1994). Root growth and distribution in some japonica-indica hybrid and japonica type rice cultivars under field conditions. *Japanese Journal of Crop Science*, 63(1), 118–124.
- Kanjoo, V., Jearakongman, S., Punyawaew, K., Siangliw, J. L., Siangliw, M., Vanavichit, A., & Toojinda, T. (2011). Co-location of quantitative trait loci for drought and salinity tolerance in rice. *Thai Journal of Genetics*, 4, 126–138.
- Kanjoo, V., Punyawaew, K., Siangliw, J. L., Jearakongman, S., Vanavichit, A., & Toojinda, T. (2012). Evaluation of agronomic traits in chromosome segment substitution lines of KDML105 containing drought tolerance qtl under drought stress. *Rice Science*, 19, 117–124.
- Kano, M., Inukai, Y., Kitano, H., & Yamauchi, A. (2011). Root plasticity as the key root trait for adaptation to various intensities of drought stress in rice. *Plant and Soil*, 342, 189–196.
- Kano-Nakata, M., Gowda, V. R. P., Henry, A., Serraj, R., Inukai, Y., Fujita, D., ... Yamauchi, A. (2013). Functional roles of the plasticity of root system development in biomass production and water uptake under rainfed lowland conditions. *Field Crops Research*, 144, 288–296.
- Kano-Nakata, M., Inukai, Y., Siopongco, J. D. L. C., Mitsuya, S., & Yamauchi, A. (2017). Quantitative evaluation of plastic root responses to contiguous water gradient in rice. *Plant Root*, 11, 70–78.
- Kano-Nakata, M., Inukai, Y., Wade, L. J., Siopongco, J. D., & Yamauchi, A. (2011). Root Development, water uptake, and shoot dry matter production under water deficit conditions in two cssls of rice: Functional roles of root plasticity. *Plant Production Science*, 14, 307–317.
- Kato, Y., Henry, A., Fujita, D., Katsura, K., Kobayashi, N., & Serraj, R. (2011). Physiological characterization of introgression lines derived from an indica rice cultivar, IR64, adapted to drought and water-saving irrigation. *Field Crops Research*, 123, 130–138.
- Kato, Y., Hirotsu, S., Nemoto, K., & Yamagishi, J. (2008). Identification of QTLs controlling rice drought tolerance at seedling stage in hydroponic culture. *Euphytica*, 160(3), 423–430.
- Kato, Y., Kamoshita, A., Yamagishi, J., Imoto, H., & Abe, J. (2007). Growth of rice (*Oryza sativa* L.) cultivars under upland conditions with different levels of water supply. *Plant Production Science*, 10, 3–13.
- Kato, Y., Okami, M., & Katsura, K. (2009). Yield potential and water use efficiency of aerobic rice (*Oryza sativa* L.) in Japan. *Field Crops Research*, 113, 328–334.
- Katsura, K., Okami, M., Mizunuma, H., & Kato, Y. (2010). Radiation use efficiency, N accumulation and biomass production of high-yielding rice in aerobic culture. *Field Crops Research*, 117, 81–89.
- Kondo, M., Singh, C. V., Agbisit, R., & Murty, M. V. R. (2005). Yield Response to urea and controlled-release urea as affected by water supply in tropical upland rice. *Journal of Plant Nutrition*, 28, 201–219.
- Korinsak, S., Siangliw, M., Kotcharek, J., Jairin, J., Siangliw, J. L., Jongdee, B., ... Toojinda, T. (2016). Improvement of the submergence tolerance and the brown planthopper resistance of the Thai jasmine rice cultivar KDML105 by pyramiding Sub1 and Qbph12. *Field Crops Research*, 188, 105–112.
- Kumar, R., Sarawagi, A. K., Ramos, C., Amarante, S. T., Ismail, A. M., & Wade, L. J. (2006). Partitioning of dry matter during drought stress in rainfed lowland rice. *Field Crops Research*, 96(2–3), 455–465.
- Lanceras, J. C., Pantuwan, G., Jongdee, B., & Toojinda, T. (2004). Quantitative trait loci associated with drought tolerance at reproductive stage in rice. *Plant Physiology*, 135, 384–399.
- Menge, M. D., Kameoka, E., Kano-Nakata, M., Yamauchi, A., Asanuma, S., Asai, H., ... Makihara, D. (2016). Drought-induced root plasticity of two upland NERICA varieties under conditions with contrasting soil depth characteristics. *Plant Production Science*, 19, 389–400.
- Nguyen, D. T. N., Suralta, R. R., Kano-Nakata, M., Mitsuya, S., Owusu-Nketia, S., & Yamauchi, A. (2018). Genotypic variations in the plasticity of nodal root penetration through the hardpan during soil moisture fluctuations among four rice varieties. *Plant Production Science*, 21(2), 93–105.
- Niones, J. M., Suralta, R. R., Inukai, Y., & Yamauchi, A. (2012). (2012). Field evaluation functional roles of root plastic responses on dry matter production and grain yield of rice under cycles of transient soil moisture stresses using chromosome segment substitution lines. *Plant and Soil*, 359, 107–120.
- O' Toole, J. C. (1982). Adaptation of rice to drought prone environments. In J. C. O'Toole (Ed.), *Drought resistance in crops with emphasis on rice* (pp. 195–213). Los Baños: International Rice Research Institute.
- O'Toole, J. C., & Bland, W. L. (1987). Genotypic variation in crop plant root systems. *Advances in Agronomy*, 41, 91–145.
- Owusu-Nketia, S., Inukai, Y., Ohashi, S., Suralta, R. R., Doi, K., Mitsuya, S., ... Yamauchi, A. (2018). Root plasticity under fluctuating soil moisture stress exhibited by backcross inbred line of a rice variety, Nipponbare carrying introgressed segments from KDML105 and detection of the associated QTLs. *Plant Production Science*, 21(2), 106–122.
- Qu, Y., Mu, P., Zhang, H., Chen, C. Y., Gao, Y., Tian, Y., ... Li, Z. (2008). Mapping QTLs of root morphological traits at different growth stages in rice. *Genetica*, 133(2), 187–200.
- Ray, J. D., Yu, L., McCouch, S. R., Champoux, M. C., Wang, G., & Nguyen, H. T. (1996). Mapping quantitative trait loci associated with root penetration ability in rice (*Oryza sativa* L.). *Theoretical and Applied Genetics*, 92(6), 627–636.
- Sandhu, N., Raman, K. A., Torres, R. O., Audebert, A., Dardou, A., Kumar, A., & Henry, A. (2016). Rice root architectural plasticity traits and genetic regions for adaptability to variable cultivation and stress conditions. *Plant Physiology*, 171(4), 2562–2576.
- Siangliw, J. L., Jongdee, B., Pantuwan, G., & Toojinda, T. (2007). Developing KDML105 backcross introgression lines using marker-assisted selection for QTLs associated with drought tolerance in rice. *Science Asia*, 33, 207–214.
- Siopongco, J. D. L. C., Sekiya, K., Yamauchi, A., Egdane, J., Ismail, A. M., & Wade, L. J. (2008). Stomatal responses in rainfed lowland rice to partial soil drying; Evidence for root signals. *Plant Production Science*, 11, 28–41.

- Siopongco, J. D. L. C., Yamauchi, A., Salekdeh, H., Bennett, J., & Wade, J. L. (2006). Growth and water use response of doubled-haploid rice lines to drought and rewatering during the vegetative stage. *Plant Production Science*, 9, 141–151.
- Siopongco, J. D. L. C., Yamauchi, A., Salekdeh, H., Bennett, J., & Wade, L. J. (2005). Root growth and water extraction responses of double haploid rice lines to drought and rewatering during the vegetative stage. *Plant Production Science*, 9, 141–151.
- Suralta, R. R., Inukai, Y., & Yamauchi, A. (2008b). Utilizing chromosome segment substitution lines (CSSLs) for evaluation of root responses to transient moisture stresses in rice. *Plant Production Science*, 11, 457–465.
- Suralta, R. R., Inukai, Y., & Yamauchi, A. (2010). Dry matter production in relation to root plastic development, oxygen transport, and water uptake of rice under transient soil moisture stresses. *Plant and Soil*, 332(1), 87–104.
- Suralta, R. R., Kano-Nakata, M., Niones, J. M., Inukai, Y., Kameoka, E., Tran, T. T., ... Yamauchi, A. (2016). Root plasticity for maintenance of productivity under abiotic stressed soil environments in rice: Progress and prospects. *Field Crops Research*. doi:10.1016/j.fcr.2016.06.023
- Suralta, R. R., Lucob, N. B., Perez, L. M., Niones, J. M., & Nguyen, H. T. (2015). Developmental and quantitative trait loci analyses of root plasticity in response to soil moisture fluctuation in rice. *Philippine Journal of Crop Science*, 40(2), 12–24.
- Suralta, R. R., Niones, J. M., Kano-Nakata, M., Tran, T. T., Mitsuya, S., & Yamauchi, A. (2018). Plasticity in nodal root elongation through the hardpan was triggered by rewatering during soil moisture fluctuation stress in rice. *Scientific Reports*, 8(1), 4341.
- Suralta, R. R., & Yamauchi, A. (2008). Root growth, aerenchyma development, and oxygen transport in rice genotypes subjected to drought and waterlogging. *Environmental and Experimental Botany*, 64(1), 75–82.
- Toojinda, T., Siangliw, M., Tragoonrung, S., & Vanavichit, A. (2003). Molecular genetics of submergence tolerance in rice: QTL analysis of key traits. *Annals of Botany*, 91, 243–253.
- Toojinda, T., Tragoonrung, S., Vanavichit, A., Siangliw, J. L., Paln, N., Jantaboon, J., ... Fukai, S. (2005). Molecular breeding for rainfed lowland rice in the Mekong region. *Plant Production Science*, 8(3), 330–333.
- Tran, T. T., Kano-Nakata, M., Takeda, M., Menge, D., Mitsuya, S., Inukai, Y., & Yamauchi, A. (2014). Nitrogen application enhanced the expression of developmental plasticity of root systems triggered by mild drought stress in rice. *Plant and Soil*, 378, 139–152.
- Venuprasad, R., Bool, M. E., Dalid, C. O., Bernier, J., Kumar, A., & Atlin, G. N. (2009). Genetic loci responding to two cycles of divergent selection for grain yield under drought stress in a rice breeding population. *Euphytica*, 167, 261–269.
- Verulkar, S. B., Mandal, N. P., Dwivedi, J. L., Singh, B. N., Sinha, P. K., Mahato, R. N., ... Kumar, A. (2010). Breeding resilient and productive genotypes adapted to drought-prone rainfed ecosystem of India. *Field Crops Research*, 117, 197–208.
- Wade, L. J., Bartolome, V., Mauleon, R., Vasant, V. D., Prabakar, S. M., Chelliah, M., ... Henry, A. (2015). Environmental response and genomic regions correlated with rice root growth and yield under drought in the oryzaSNP panel across multiple study systems. *PLoS ONE*, 10, 4.
- Wade, L. J., Fukai, S., Samson, B. K., Ali, A., & Mazid, M. A. (1999). Rainfed lowland rice: Physical environment and cultivar requirements. *Field Crops Research*, 64(1–2), 3–12.
- Wade, L. J., Kamoshita, A., Yamauchi, A., & Azhiri-Sigari, T. (2000). Genotypic variation in response of rainfed lowland rice to drought and rewatering. I. Growth and water use. *Plant Production Science*, 3, 173–179.
- Wang, H., Siopongco, J., Wade, L. J., & Yamauchi, A. (2009). Fractal analysis on root systems of rice plants in response to drought stress. *Environmental and Experimental Botany*, 65, 338–344.
- Wang, H., & Yamauchi, A. (2006). Growth and function of roots under abiotic stress soils. In B. Huang (Ed.), *Plant–Environment Interactions* (3rd ed., pp. 271–320). New York: CRC Press, Taylor and Francis Group, LLC.
- Yamauchi, A., Kono, Y., & Tatsumi, J. (1987). Quantitative analysis on root system structure of upland rice and maize. *Japanese Journal of Crop Science*, 56, 608–617.
- Yamauchi, A., Pardales, J. R., Jr., & Kono, Y. (1996). Root system structure and its relation to stress tolerance. In O. Ito, K. Katayama, C. Johansen, J. V. D. K. Kumar Rao, J. J. Adu-Gyamfi, & T. J. Rego (Eds.), *Roots and nitrogen in cropping systems of the semi-arid tropics* (pp. 211–234). Tsukuba: Japan International Research Center for Agriculture Sciences.
- Zheng, H. G., Babu, R. C., Pathan, M. S., Ali, L., Huang, N., Courtois, B., & Nguyen, H. T. (2000). Quantitative trait loci for root-penetration ability and root thickness in rice: Comparison of genetic backgrounds. *Genome*, 43(1), 53–61.