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Genetic control of root architectural traits in KDML105 chromosome segment substitution lines under well-watered and drought stress conditions

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ABSTRACT

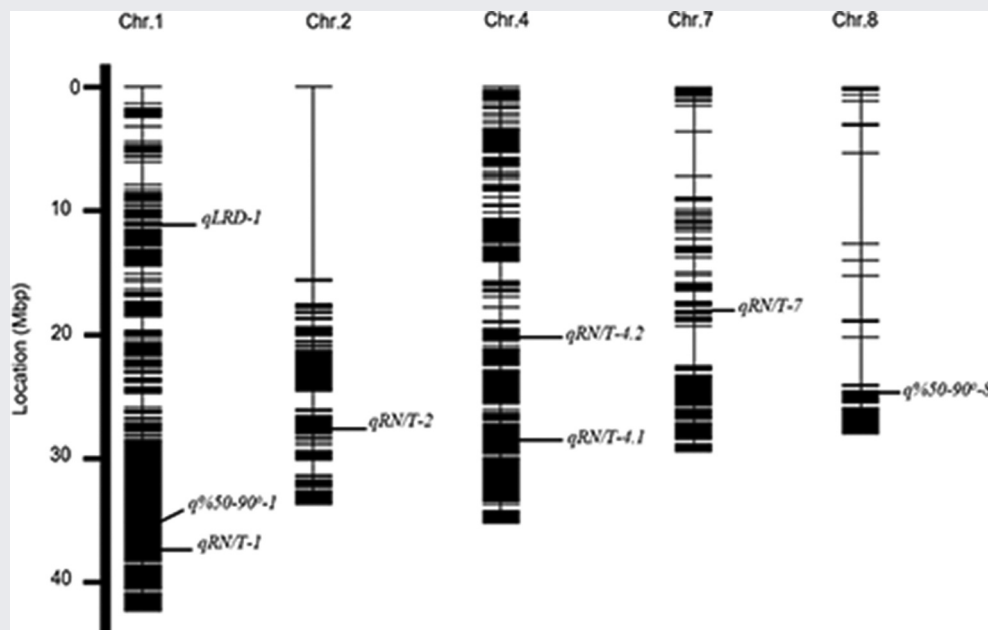
Drought is a major constraint in rainfed rice production and root architectural traits are important breeding targets for improving productivity under drought stress. A set of chromosome segment substitution lines (KDML105-CSSLs) and KDML105 were grown in the wet season at two sites (Rice Gene Discovery (RGD) and Ubon Ratchathani Rice Research Center (URRC)) in Thailand under well-watered (WW) and drought stress (DS) treatments. RGD is characterized by having a heavy clay soil type while URRC's soil has a high percentage of sand and characterized by infertility. Root architecture traits varied within the population at both sites and exhibited plasticity in response to drought as affected by location by water regime interaction. Lateral root density increased by 77% with drought at RGD but decreased by 18% at URRC. The proportion of nodal roots that elongated more vertically increased under drought stress by 21%, at RGD. Root number per tiller was negatively associated with tiller number and biomass at RGD under drought, while lateral root density was negatively associated with biomass under drought at URRC. Eight QTL were identified for the number of nodal roots per tiller, lateral root density, and nodal root growth angle. Several candidate genes were identified by annotating the genes within the QTL regions. Our study presented genetic insights into root architectural traits with potential use in rice breeding programs for drought tolerance.

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 Supplemental data for this article can be accessed [here](#).

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Introduction

Rice is a staple food for more than half of the world's population and it is a crucial product of Thailand (Kawasaki, 2010). Approximately 75% of the agricultural area in Northeast (NE) Thailand is used for cultivation of rainfed lowland rice (Jongdee et al., 2006). Drought is a major limiting factor in rice production, especially in NE Thailand, due to unpredictable seasonal rains (Jongdee, 2001; Prapertchob et al., 2007). Drought, particularly when it occurs at panicle initiation and flowering, can devastate yield (A. Kumar et al., 2008; United Nations Convention to Combat Desertification, 2014). The magnitude of yield loss depends on the duration of drought, the stage of crop growth (Gana, 2011), and the severity of drought stress (S. Kumar et al., 2014). Drought stress during vegetative growth, especially booting (Pantuwan et al., 2002), flowering and terminal periods can interrupt floret initiation, causing spikelet sterility and slow grain filling, resulting in lower grain weight and ultimately poor paddy yield (Acuña et al., 2008; Kamoshita et al., 2004). In Thailand, rice yield losses due to drought are estimated 55–68% (Polthanee & Promkhambut, 2014). Continuous decline in rainfall has been observed in the country from 2010 to 2016 (Thaiturapaisan, 2016), and future rice production is likely to suffer even greater reductions unless more tolerant cultivars can be developed.

In rice root system, roots are mainly classified as 1) seminal roots 2) mesocotylar roots and 3) crown root. Crown roots are also called nodal roots (Rebouillat et al., 2009) as they emerge from the nodes on the stem and tillers arranged in one or two rows. Lateral roots can appear on any primary root, including embryonic and crown roots. The morphological and architectural characteristics of roots are closely associated with determining rice shoot growth and overall production, particularly under stress (Uga et al., 2013; Yang et al., 2012). The plant's access to water is determined by its root system, thus improving root traits to increase the uptake of soil moisture and maintain productivity under drought stress is an important objective (De Dorlodot et al., 2007). Gowda et al. (2011) outlined rice root system architectural traits and their functional roles in penetrating, exploring, and absorbing moisture and nutrients from the soil. Deeper root systems are thought to be desirable under drought stress, since they permit acquisition of water in the deep soil layer (Gowda et al., 2011; Henry et al., 2011). Several traits can contribute to deeper rooting. An allele of the QTL *DRO1* conferring deeper root growth angle improves performance under drought (Uga et al., 2013). Gao and Lynch (2016) found that low crown root number in maize improved performance

under drought stress by increasing root depth and deep-water acquisition. Fewer crown roots permit allocation of resources to greater root elongation, increasing rooting depth. Lynch (2013) suggested that reduced lateral root density may have a similar effect in increasing elongation rather than proliferation. Maize with fewer but longer lateral roots performed better under drought conditions and displayed improved capture of water in the deep soil layer under stress (Zhan & Lynch, 2015; Zhan et al., 2015). Root plasticity in response to changing soil moisture could be important for rice plants under drought stress (Bañoc et al., 2000; O'Toole & Bland, 1987). Several studies have demonstrated the contribution of root architectural plasticity to yield or biomass increase. Drought response of nodal root number and total root length or root length density (Kano-Nakata et al., 2011; Tran et al., 2015), lateral root length and/or branching (Hazman & Brown, 2018; Kano et al., 2011; Kano-Nakata et al., 2013; Suralta et al., 2010) and deep rooting (Hazman & Brown, 2018) has been observed to improve shoot biomass. Plastic response to drought stress has also been observed for number of nodal roots (Gao & Lynch, 2016), lateral root branching frequency, angles of roots (Schneider & Lynch, 2020) and lateral root branching density and length (Schneider & Lynch, 2020; Zhan et al., 2015) in maize, and deep rooting in wheat (Ehdaie et al., 2012; Wasson et al., 2012). Phenotypic selection of root plasticity might be a viable strategy for breeding programs, however, selection must occur in specific targeted environments or under specific edaphic stresses (Schneider & Lynch, 2020).

In rice, quantitative trait loci (QTL) for root architectural traits such as root angle, root number, and root depth distribution have been identified in various mapping populations (Hu & Xiong, 2014). For root number, Ali et al. (2000) identified two QTL within F₇ recombinant inbred population derived from IR58821 × IR52561 located on chromosome 3 and 7. Hemamalini et al. (2000) found five QTL for total root number under well-watered condition which located on chromosomes 1, 6, 7, 10. Uga et al. (2013) identified *DEEPER ROOTING 1 (DRO1)*, a rice quantitative trait locus controlling root growth angle on chromosome 9. B. S. Zheng et al. (2003) found QTL for several root architecture traits under flooded and upland conditions. Brigitte Courtois et al. (2009) conducted a meta-analysis of QTL for root architectural traits to identify regions found to be significant across multiple studies.

Chromosome segment substitution lines (CSSL) can be used for QTL detection of complex traits in plants and may resolve the issues of precise mapping of QTL

by blocking background genetic noise (Doi et al., 1997; Kubo et al., 2002). So far, several CSSL populations have been developed in rice and used to detect QTL for drought-related traits (Kanjoo et al., 2011) and root architecture traits such as root number (Zhou et al., 2016) and root growth angle (Uga et al., 2015). In this study, we used CSSLs of KDML105 (KDML105-CSSLs) with DT-QTL (DT, drought tolerant) segments in the genetic background of KDML105. KDML105 is a jasmine rice which is of particular importance in Thailand. The KDML105-CSSL population was developed by Kanjoo (2012) to assist breeding of more drought-tolerant jasmine rice. We used this population to identify QTL for root morphological and architectural traits in well-watered and drought conditions at two sites in Thailand. We hypothesize that this population exhibits variation in root architectural traits, that they respond to drought and are genetically controlled.

Materials and methods

Plant materials

One hundred and thirty-five KDML105-CSSLs were used for phenotypic screening of root traits. The KDML105-CSSL population was derived from a cross between KDML105 and two doubled haploid (DH) lines, namely IR68586-F2-CA-31 (DHL103), and IR68586-F2-CA-143 (DH212), which were derived from the cross between CT9993 and IR62266. The KDML105-CSSLs were originally found to carry segments of the DH lines on chromosomes 1, 3, 4, 8, and 9 (Kanjoo, 2012; Siangliw et al., 2007). The KDML105-CSSL population was developed by using SSR markers in marker-assisted selection targeting these regions at generations BC₅F₂ to BC₅F₄ in 2012 (Kanjoo, 2012). More than 500 SSR markers were screened for polymorphism and there were 18, 19, 23, 10, and 16 SSR markers that cover the QTL regions on chromosomes, 1, 3, 4, 8, and 9, respectively. The 135 KDML105-CSSLs were genome scanned using SSR markers to determine the KDML105 genome recovered. The genome scan showed that an average of 96% of the KDML105 genome had been recovered in the CSSLs. In the BC₅F₇ generation, the KDML105-CSSL population was subjected to genotyping by sequencing (see section on genotyping of CSSLs below) and the called SNPs revealed that there were introgressions in the genome other than the regions of the QTL which were not found in the genome scan at BC₅F₃/F₄ generation using SSR markers.

Crop management and drought imposition

The experiments were conducted at Rice Gene Discovery (RGD), BIOTEC, at Kasetsart University, Kamphaengsaen Campus, Nakhon Pathom, Thailand (14°02'69.6"N, 99° 97'46.9"E) and Ubon Ratchathani Rice Research Center (URRC), Ubon Ratchathani, Thailand (15°19'55.2"N, 104° 41'27.9"E). The soil at RGD has a clay texture (65.7% clay, 23.30% silt, and 11.0% sand) while URRC soil is sandy (74% sand, 15% silt and 11% clay). At RGD, a total of 135 KDML105-CSSLs and KDML105 were sown on August 13, 2016, and seedlings were transplanted in puddled field at 30 days after sowing (DAS) at a spacing of 25 × 25 cm in a randomized complete block design with 3 replications. Fertilizer formulas 16–18–2 and 46–0–0 were mixed and applied at a rate of 94 kg/ha (58.3 kg/ha N, 16.9 kg/ha P and 1.9 kg/ha K) at 49 DAS. The mean air temperature ranged from 25.3 to 29.3°C. The highest and lowest relative humidity recorded during experiment was 94.5 to 72.2%. No extremely high temperature or extremely low relative humidity was recorded, therefore heat stress was not a confounding factor. Standing water was maintained for the duration of experiment in the well-watered treatment. In the drought stress field, water was drained at maximum tillering stage, at 57 DAS. Soil water potential was monitored in the drought stress field using tensiometers (DIK-8334 pF Meter, Daiki Rika Kogyo Corporation, Japan) installed at a depth of 18 cm. Tensiometer readings were recorded every day, and showed that water deficit occurred from 83 to 87 DAS with a minimum tensiometer reading of –80 kPa when the plants are at booting stage. In general, the drought stress was mild due to rainfall interruptions during the experiment (Figure 1(a)).

At URRC, the 135 KDML105-CSS lines were planted in the field and in the rainout shelter. For the field experiment, seeds were sown on September 6, 2016 and transplanted in puddled field at 30 DAS using a randomized complete block design with 3 replications at a spacing of 25 × 25 cm. Drought was imposed by draining out the water at panicle initiation stage, 66 DAS. The plants experienced a 13-day rain-free period after draining (Figure 1(b)). Soil moisture was measured by the gravimetric method at two depths (5–10 cm and 25–30 cm below the soil surface). The soil moisture decreased by 38% and 34% at 5–10 cm and 25–30 cm depths, respectively (Figure 1(b)). The mean air temperature ranged from 24.8 to 29.7°C, and the range of relative humidity was 61 to 92%.

URRC rainout shelter (ROS) has a dimension of 14.8 m length × 1.8 m width × 0.5 m height. It contains soil that were taken from the field which is sandy. In the rainout

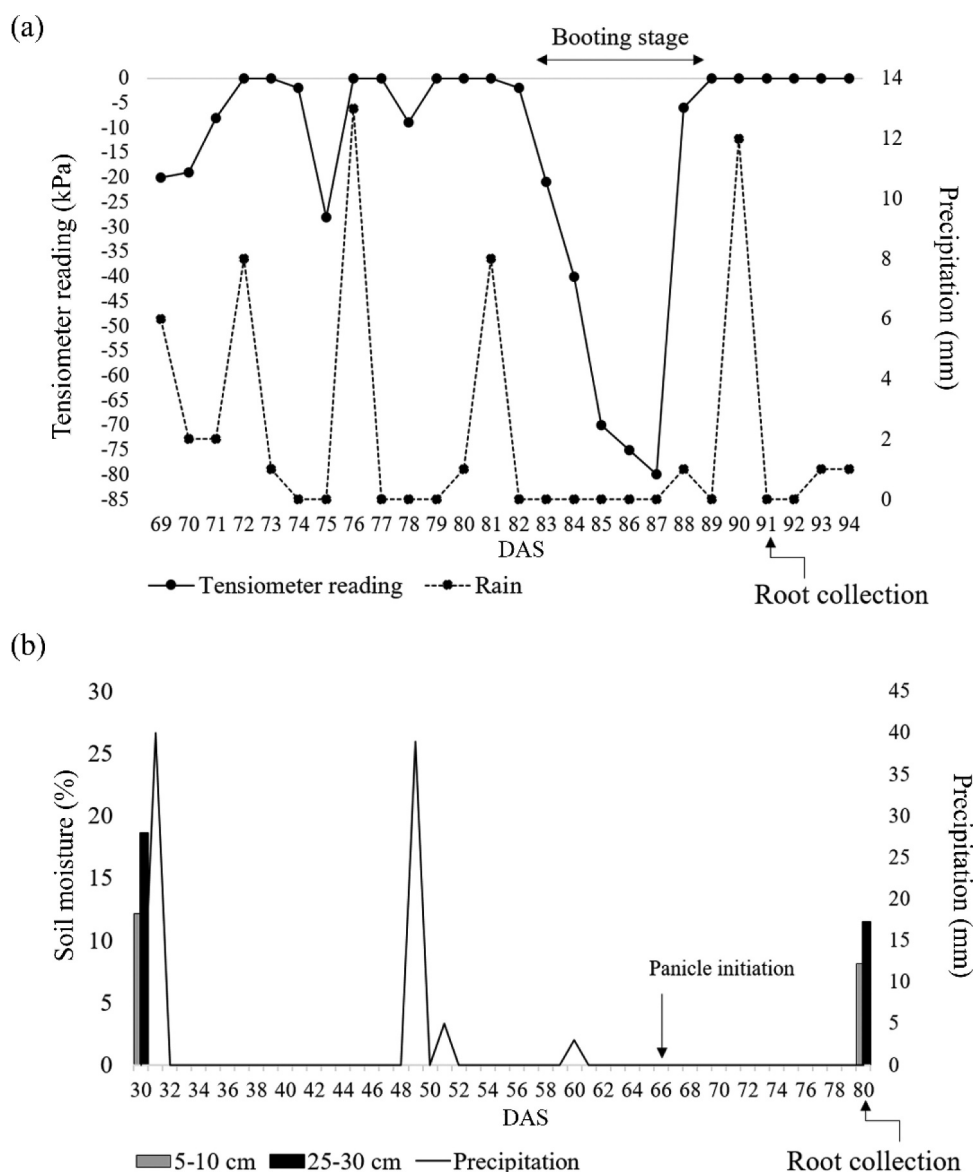


Figure 1. Drought imposition in 2016 wet season field experiments. (a) Soil water potential and rainfall at RGD. Tensiometer readings showed water deficit in the field between 83 and 87 DAS. (b) Rainfall and soil moisture (%) at 5–10 cm and 25–30 cm soil depth at transplanting (30 DAS) and root harvest (80 DAS) at URRC.

shelter facility with puddled soil adapting lowland environment, the 135 KDML105-CSSLs and KDML105 were sown on September 6, 2016 directly into plastic mesh baskets with upper and lower diameter of 21.5 cm and 17 cm, respectively, height of 23 cm and with pore size of 6×1 cm and the plastic baskets were buried in the soil. An RCB design with 2 replications at a spacing of 25×25 cm was used in this experiment. Drought stress was imposed at 65 DAS by draining out the water. The duration of drought stress was 14 days.

Root sampling and screening

Root sampling and analysis of nodal root number per tiller and lateral root density were the same at RGD and at URRC. Two root samples were collected from the field after 2 weeks of drought stress by using a 14 cm and 20 cm diameter monolith at RGD and at URRC, respectively. Roots were collected at 20 cm soil depth, washed, and stored in 70% ethanol. Nodal root number per tiller (RN/T) was measured by counting roots in a third of the root crown. The root number was multiplied by three

and divided by the number of tillers to obtain RN/T. Three nodal roots of similar length (10 cm in length from base) were selected and scanned by image scanner (EPSON PERFECTION V700 PHOTO, Seiko Epson Corporation, Japan) at 600 dpi resolution. Lateral roots were counted from the three scanned nodal roots to assess the lateral root density (LRD) per 10 cm. The basket method (Uga et al., 2013) was used to determine root angle and root distribution. At RGD, plastic baskets were truncated cones with 21.5 cm upper diameter, 14 cm lower diameter and 11.5 cm height and hole's size of 0.3 × 0.3 cm. The baskets were buried under the soil surface before transplanting. For root collection, baskets were excavated and the nodal roots that pass through the basket pores were counted at various angles. The angle was determined based on the hole that the root penetrated. The nodal roots penetrating the basket at from 0° to 50° from horizontal were pooled together to represent the horizontal root distribution while those existing the basket at from 50° to 90° from horizontal represented the vertical root distribution. Number of roots per range of angles was divided by total root number and converted to percentage of root distribution. At URRC, roots emerging at 0°-30°, 30°-60°, and 60°-90° were counted in a plastic basket (with upper and lower diameter of 21.5 and 17 cm, respectively, height of 23 cm and with pore size of 6 × 1 cm) and the soil with the roots were cut based on the angles set above. The soil was washed off for each segment and the roots were counted. Number of roots per range of angles was divided by total root number and converted to percentage of root distribution.

Phenotyping agronomic traits

Agronomic traits were collected to assess the extent of drought in each environment. Tiller number (TN) and plant height (PH) were recorded before root sampling at 92 DAS. PH was measured by using a meter stick and the height of the plant was determined from three plants by measuring the height from the soil surface to the tip of the longest leaf while TN was manually counted using the same plants. Shoot dry weight (SDW) was determined for the same plants from which PH and TN were recorded. The shoots were cut off and placed in a nylon bag, sun dried for 5 days and SDW was determined by weighing the dried shoots individually. At RGD, twelve plants (0.4 m²) were harvested for yield (YLD), and one hundred seed weight (100SW) from the yield samples was determined by weighing 100 fully filled grains. Yield was not obtained in URRC. Leaf rolling scores were recorded at 86 and 89 DAS at RGD and at 72 DAS in URRC. Leaf drying scores were recorded at URRC

at 72 DAS following the Standard Evaluation System for Rice (SES) (IRRI, 2013). Recovery score at URRC was recorded 10 days after applying irrigation and scoring was based on SES (IRRI, 2013). For drought stress plasticity, values for each phenotype were calculated using single replicates from drought stress (DS_{rep}) and mean values from well-watered (WW_{mean}) according to the formula:

$$\text{Droughtstressplasticity} = \frac{DS_{rep} - WW_{mean}}{WW_{mean}} \quad (1)$$

Statistical analysis

Analysis of variance (ANOVA), combined analysis using two-way ANOVA with randomized block design, least significant difference (LSD), broad-sense heritability (H^2), path coefficient and Pearson's r correlation were analyzed by Genstat 19th Edition software (Payne, 2009) for all treatments. Principle Component Analysis (PCA) was analyzed using 'factoextra' R package (Kassambara, 2017). Path analysis was performed using genotypic correlation considering shoot dry weight (SDW) as the response variable and other traits as predictor variables. Each variable was transformed to the new standardized version to construct path diagram using regression by Genstat 19th Edition software (Payne, 2009).

Genotyping and QTL analysis

Genotyping by sequencing (GBS) was done twice by digesting with two sets of enzymes namely *MseI*/*PstI* (set 1) and *ApeKI* (set 2) and barcoded sequencing was carried out using the Ion Proton PII chip which can pool 24 samples per chip. The sequence data were mapped with the japonica genome (*Nipponbare*) using Tmap and HaplotypeCaller in GATK (v3.2.2) was used to call the variants (McKenna et al., 2010). The parental genomes were sequenced with Illumina paired end technique obtained from National Center for Genetic Engineering and Biotechnology, Thailand. GBS SNPs were then filtered on allele read depth per SNP using a binomial test and compared to the parental genome sequence to select SNPs that were consistent between the two methods and a sample call rate of at least 50%. A total of 27,353 SNPs was called and these were further filtered by removing SNP markers with more than 10% missing values and monomorphic markers. The final genotype data contained 6,140 SNPs. The genetic map of the KDML105-CSSL population was constructed (Tables S1) using 6,140 SNP markers. The mean distance between markers was 124.5 kb/SNP. For the QTL analysis, 6,140 SNP markers were used and significant QTL

were selected based on LOD (>4.0) score by single marker analysis (SMA) method. The QTL were analyzed using R package 'qtl' (Broman et al., 2003) using a backcross for 5 generations model with significance thresholds from 1,000 permutations to access the QTL location, number, effect, bounding markers and variation explained by each QTL. The QTL regions were identified using the 'lodint' functions.

QTL co-localization and identification of candidate genes

TropGENE-DB (Ruiz et al., 2004) was used to identify the QTL co-localized with the QTL identified in this study. Candidate genes were identified within the significant QTL identified for root traits. The candidate genes were searched *in silico* from 1 Mb upstream and downstream of the significant SNP associated with the trait in each QTL using Rice Annotation Project Database (RAP-DB) (Sakai et al., 2013).

Results

Root architectural traits in KDML105-CSSLs

Phenotypic variation was observed in root and shoot traits collected from two locations in Thailand, Rice Gene Discovery (RGD), BIOTEC and Ubon Ratchathani Rice Research Center (URRC) (Figures 2, Figures 3 and Figures 4). Drought reduced nodal root numbers by an average of 11% at RGD which was due to declines in both tiller number and root number per tiller (Table 1). On the other hand, at URRC, drought stress increased nodal root number by 61% on average (Table 2). Plasticity in nodal root number per tiller was significant at both sites (Tables 1 and Tables 2) although more KDML105-CSSLs responded to drought by increasing nodal root number at URRC (-0.12 to 1.76). Combined analysis of nodal root number per tiller further confirms that responses of genotypes in different environments and conditions were different and plastic response to

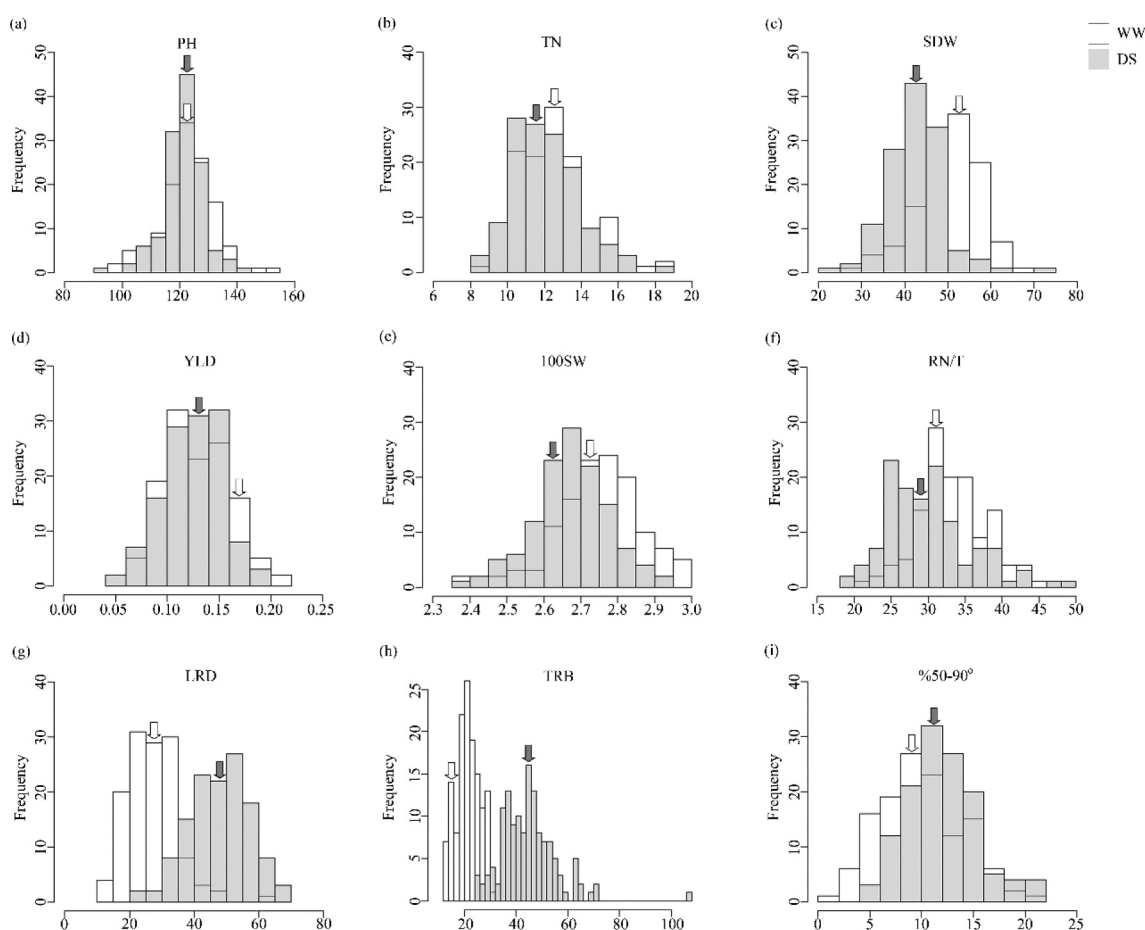


Figure 2. Frequency distribution of shoot and root traits from RGD field experiment in 2016. (a) Plant height (PH); (b) Tiller number (TN); (c) Shoot dry weight (SDW); (d) Yield (YLD); (e) One hundred seed weight (100SW); (f) Root number per tiller (RN/T); (g) Lateral root density (LRD); (h) Total root number from basket (TRB); (i) percent of roots at 50°–90° (%50–90°). White and grey bars represent well-watered (WW) and drought stress (DS) conditions, respectively. White and grey arrows indicate values for KDML105 under WW and DS, respectively.

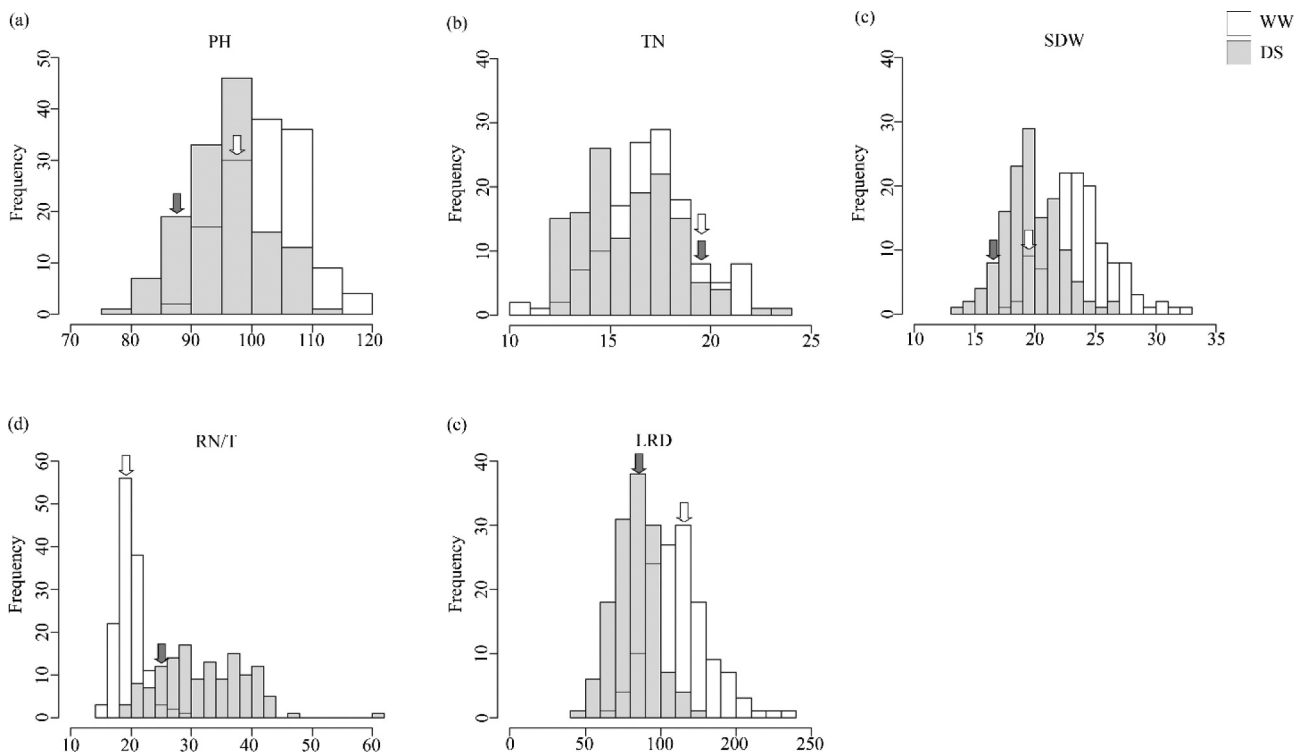


Figure 3. Frequency distribution of shoot and root traits from URRC field experiment in 2016. (a) Plant height (PH); (b) Tiller number (TN); (c) Shoot dry weight (SDW); (d) Root number per tiller (RN/T); (e) Lateral root density (LRD). White and grey bars represent well-watered (WW) and drought stress (DS) conditions, respectively. White and grey arrows indicate values for KDML105 under WW and DS, respectively.

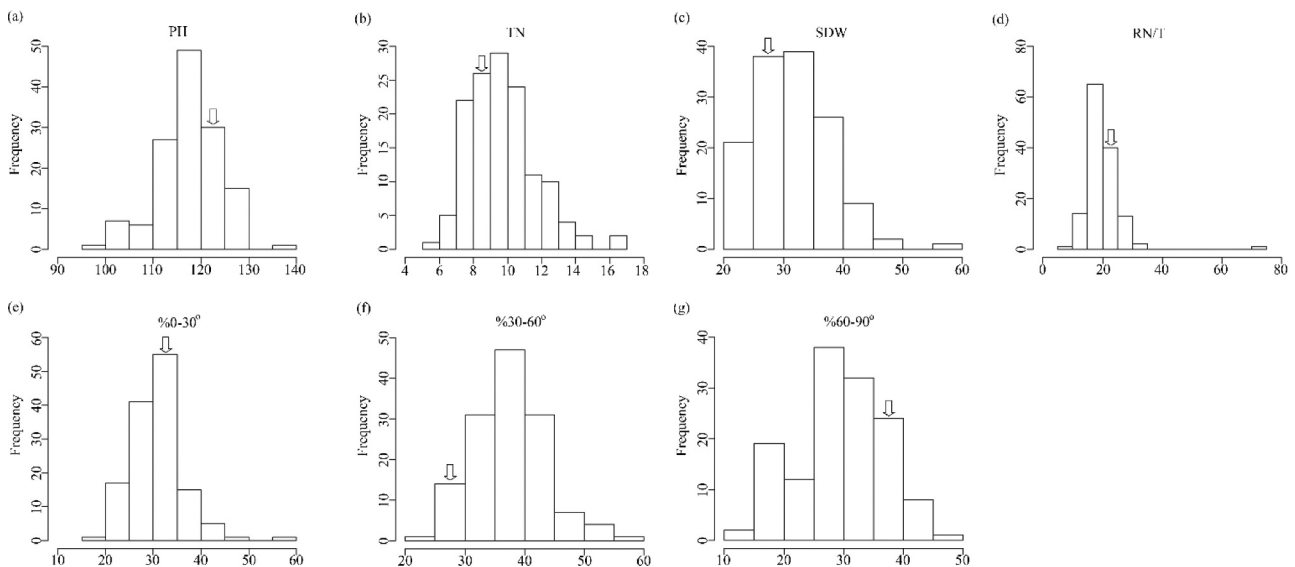


Figure 4. Frequency distribution of shoot and root traits from URRC rainout shelter drought experiment in 2016. (a) Plant height (PH); (b) Tiller number (TN); (c) Shoot dry weight (SDW); (d) Root number per tiller (RN/T); (e) percent of root at 0°-30° (%0-30°); (f) percent of root at 30°-60° (%30-60°); (g) percent of root at 60°-90° (%60-90°). White arrows indicate values for KDML105.

drought was significantly different at the two locations (Table S2).

There was more variation in lateral root density among CSSLs at URRC than at RGD, and lateral root

density was 4.2 times greater than at RGD (Tables 1 and Tables 2) at WW condition. At URRC, lateral root density was 26% greater in flooded compared with drought stress treatments (Table 2, Figure 3). Unlike

Table 1. ANOVA, means, ranges, and heritability of agronomic, productivity, root characters, and drought stress plasticity traits of KDML105-CSSLs population and recurrent parent KDML105 grown under well-watered and drought stress conditions at RGD in wet season 2016.

Traits	Trt	KDML105	KDML105-CSSLs population										
			Mean	±	LSD	Ranges	F-value	G effect	F-value	T effect	F-value	GxT	H ²
Phenotypic traits													
PH	WW	124.9	122.5		12.1	92 to 153	8.55	**	7.73	**	3.25	**	0.89
	DS	120.6	121.2		9.0	94 to 141	6.92	**					0.85
TN	WW	13	13	±	4	9 to 19	3.71	**	6.24	ns	2.75	**	0.69
	DS	13	12	±	3	8–18	3.49	**					0.7
SDW	WW	54.4	50.3	±	17.3	28.0 to 65.1	3.06	**	114.4	**	2.96	**	0.62
	DS	40.1	42.5	±	25.3	23.2 to 74.0	3.40	**					0.59
YLD	WW	0.172	0.135	±	0.008	0.063 to 0.208	1.72	**	1.01	ns	1.37	**	0.4
	DS	0.13	0.13	±	0.007	0.045 to 0.204	1.46	**					0.26
100SW	WW	2.75	2.75	±	0.16	2.35 to 3.00	5.78	**	167.8	**	2.75	**	0.83
	DS	2.65	2.67	±	0.17	2.37 to 2.94	17.12	**					0.94
RN/T	WW	30.4	33.3	±	9.1	21.7 to 49.2	3.86	**	67.7	**	2.07	**	0.71
	DS	27.9	29.8	±	11.7	18.8 to 49.5	2.34	**					0.53
LRD	WW	25.7	26.9	±	14.8	11.3 to 61.8	3.59	**	1,281	**	3.23	**	0.68
	DS	46.5	47.7	±	13.4	24.2 to 68.5	3.74	**					0.73
TRB	WW	17	22	±	17.1	12 to 31	0.85	ns	1153	**	2.46	**	0.00
	DS	44	45	±	3.4	24 to 107	3.38	**					0.35
%50–90°	WW	7.8	9.9	±	10.5	0.0 to 20.5	4.10	**	55.17	**	4.91	**	0.75
	DS	11	12	±	7.6	4.5 to 22.0	6.32	**					0.83
LR86	DS	0.9	0.7		0.8	0.0 to 1.3	1.11	ns					0.16
LR89	DS	1.1	1.2		0.8	0.7 to 2.0	1.05	ns					0.06
Drought stress plasticity													
pPH_R		–0.04	–0.01	±	0.07	–0.16 to 0.15	6.83	**					0.85
pTN_R		–0.03	–0.01	±	0.25	–0.33 to 0.66	5.07	**					0.80
pSDW_R		–0.28	–0.16	±	0.37	–0.67 to 0.83	3.77	**					0.56
pYLD_R		–0.24	0.02	±	0.56	–0.70 to 1.53	2.80	**					0.64
p100SW_R		–0.04	–0.03	±	0.04	–0.15 to 0.15	10.43	**					0.90
pRN/T_R		–0.08	–0.09	±	0.32	–0.43 to 0.52	2.69	**					0.63
pLRD_R		0.80	0.91	±	0.56	–0.31 to 0.52	9.82	**					0.90
pTRB_R		1.62	1.18	±	0.88	–0.21 to 4.65	6.63	**					
p%50–90°_R		0.37	0.45	±	0.71	–0.87 to 3.88	11.71	**					0.90

PH, plant height (cm); TN, tiller number (no.); SDW, shoot dry weight (g); YLD, yield (kg/0.4 m²); 100SW, one hundred seed weight (g); RN/T, root number per tiller; LRD, lateral root density (number per 10 cm); TRB, total root number from basket (no.); %50–90°, percent of roots at 50°–90°; LR86, leaf rolling at 86 DAS (score); LR89, leaf rolling at 89 DAS (score); Trt, treatment; G, genotype effect; T, treatment effect; GxT, genotype by treatment effect; H² = broad sense heritability; WW, well-watered; DS, drought stress. *, ** and ns represent significant differences at 0.05, 0.01 levels and no significant difference, respectively; pRN/T_R, pRN/T_R, pTRB_R, p50–90°_R, pPH_R, pTN_R, pSDW_R, pYLD_R, p100SW_R are plasticity traits in RGD.

URRC, lateral root density was greater under drought than under flooded conditions at RGD (Table 1 and Figure 2(g)). Significant variation in plasticity was observed for lateral root density (Tables 1 and Tables 2). Combined analysis revealed that both site and drought treatment affected lateral root density and plasticity varied significantly between environments (Table S2).

Nodal root growth angle distribution varied among CSSLs at both sites (Tables 1 and Tables 2). Nodal root angles were assessed by position of emergence from a basket, and therefore included only roots that elongated enough to emerge from the basket. Approximately 5.6% of nodal roots emerged from the basket in WW treatment, and 14.7% of nodal roots emerged from the basket under drought, so that there were twice as many roots emerging from the baskets under drought compared with the WW treatment (Figure S1). Drought increased the nodal root numbers emerging at every angle increment at RGD (Figure S1). However, the greater increase in root number emerging

at depth resulted in a 21% increase in the proportion of nodal roots that elongated more vertically (>50°) under drought compared with WW (Table 1 and Figure 2(h)). Root growth angles at URRC were only evaluated under drought in rainout shelter (ROS) which contains soil that were taken from the field which is sandy adapting to the rainfed environment. Large genotypic variation in number and percentage of roots classified as shallow (0°–30°), medium (30°–60°) and deep (60°–90°) was observed (Figure 4). More roots were identified in the medium angle class (30°–60°) and roots tended to be more vertical than at RGD, with 30% of roots emerging at >60° (Table 2).

In order to assess the effects of drought stress on performance at each location, shoot parameters were collected. Plant height, tiller number, and shoot dry weight varied significantly among KDML105-CSS lines at both sites (Tables 1 and Tables 2). Drought stress slightly decreased plant height, tiller number, and shoot dry weight overall, and there were significant genotype by treatment interactions for each of these variables at both sites (Tables 1 and

Table 2. ANOVA, means, ranges, and heritability of agronomic, productivity, root characters, and drought stress plasticity traits of KDML105-CSSLs population and recurrent parent KDML105 grown in the field under well-watered and drought stress conditions and in rainout shelter at URRC in wet season 2016.

Traits	Trt	KDML105	KDML105-CSSLs population										
			Mean	±	LSD	Ranges	F-value	G effect	F-value	T effect	F-value	GxT	H ²
Phenotypic traits													
PH	WW	95.5	102.2	±	5.9	87 to 120	13.59	**	488.0	**	3.02	**	0.92
	DS	88.2	95.6	±	9.0	79 to 114	6.17	**					0.60
TN	WW	19	18	±	3	10 to 24	3.95	**	73.34	**	2.20	**	0.75
	DS	19	16	±	4	13 to 24	3.96	**					0.51
SDW	WW	19.9	23.5	±	4.3	17.9 to 32.3	3.19	**	436.9	**	2.61	**	0.68
	DS	18.9	19.6	±	4.4	13.4 to 26.7	2.46	ns					0.09
RN/T	WW	19.3	19.8	±	3.1	14.7 to 28.0	4.43	**	4,531	**	13.52	**	0.76
	DS	25.3	31.8	±	12	19.3 to 60.0	15.22	ns					0.64
LRD	WW	111.9	112	±	54	67.9 to 187.7	1.23	*	247.0	**	1.14	ns	0.17
	DS	91.7	83.2	±	32	46.1 to 122.7	1.68	**					0.55
LR72	DS	1.6	1.6	±	1.5	1.0 to 3.0	1.18	ns					0.12
LD72	DS	3.3	2.9	±	1.9	1.0 to 4.3	1.08	ns					0.08
RCEV	DS	1.8	2	±	1.6	1.0 to 4.6	1.77	**					0.43
Phenotypic traits in rainout shelter													
PH	DS	126.7	117.4	±	10.2	96 to 138	15.98	**					0.91
TN	DS	8	9.8	±	3.2	6 to 17	5.20	**					0.77
SDW	DS	28.5	31.5	±	12.0	20.5 to 55.1	6.63	*					0.79
RN/T	DS	28.0	20.4	±	6.2	6.0 to 75.0	8.18	**					0.73
%0–30°	DS	31.3	30.9	±	12	19.8 to 56.6	4.62	**					0.68
%30–60°	DS	29	37.6	±	12	24.3 to 57.2	5.35	**					0.74
%60–90°	DS	39.2	29.5	±	14	13.6 to 48.7	8.48	**					0.77
Drought stress plasticity													
pPH_U		-0.076	-0.11	±	0.33	-0.47 to 0.12	1.08	ns					0.07
pTN_U		0.02	-0.06	±	0.20	-0.44 to 0.49	4.36	**					0.77
pSDW_U		-0.14	-0.16	±	0.19	-0.44 to 0.35	4.18	**					0.75
pRN/T_U		0.38	0.61	±	0.25	-0.12 to 1.76	20.02	**					0.94
pLRD_U		-0.18	-0.24	±	0.28	-0.63 to 0.20	2.91	**					0.66

PH, plant height (cm); TN, tiller number (no.); SDW, shoot dry weight (g); RN/T, root number per tiller; LRD, lateral root density (number per 10 cm); %0–30°, percent of root at 0°–30°; %30–60°, percent of root at 30°–60°; %60–90°, percent of root at 60°–90°; LR72, leaf rolling at 72 DAS (score); LD72, leaf drying at 72 DAS (score); RCEV, recovery (score); Trt, treatment; G, genotype effect; T, treatment effect; GxT, genotype by treatment effect; H² = broad sense heritability; WW, well-watered; DS, drought stress. *, ** and ns represent significant differences at 0.05, 0.01 levels and no significant difference, respectively; pTN/T_U, pLRD_U, pPH_U, pTN_U and pSDW_U are plasticity traits in URRC.

Tables 2). Combined analysis revealed significant effects of growth environments and drought on shoot traits (Table S2). CSSLs were on average smaller (less dry weight) and shorter but had more tillers at URRC, and drought had similar effects on shoot dry weight (16% reduction) at the two sites (Table S2). At URRC, KDML105 suffered less reduction (5%) in shoot biomass with drought than the mean of the CSSL population (16%), while at RGD, KDML105 had greater reduction in shoot biomass (26%) than the mean of the CSSL population (16%).

At RGD, CSSLs showed large genotypic variation in 100 seed weight and yield. CSSLs showed an average of 3.7% yield reduction under stress at RGD and there was a significant interaction of drought treatment with genotype (Table 1). Yield data were not collected at URRC. KDML105 suffered more biomass reduction (–26%) and yield loss (>–24%) with drought than the overall population and demonstrated a greater change in proportion of nodal roots that elongated more vertically (41% change vs 21% for the population), though KDML105 had more

horizontal root angles than the mean of the overall population, particularly in the irrigated treatment.

Correlation of traits

Genotypes with fewer tillers tended to have more roots per tiller under well-watered and drought conditions at both sites (Table S3). Root number per tiller was not correlated with shoot biomass or yield except under well-watered conditions at URRC, where there was a negative correlation. At RGD, lateral root density was not correlated with productivity traits or other root traits. At URRC, there was a negative correlation of lateral root density with shoot biomass under both well-watered and drought conditions (Table S3).

Negative correlations were identified between the proportion of nodal roots that elongated more vertically and 100 seed weight and yield under well-watered conditions at RGD. Under drought at RGD, the 100 seed weight was positively correlated with root number per

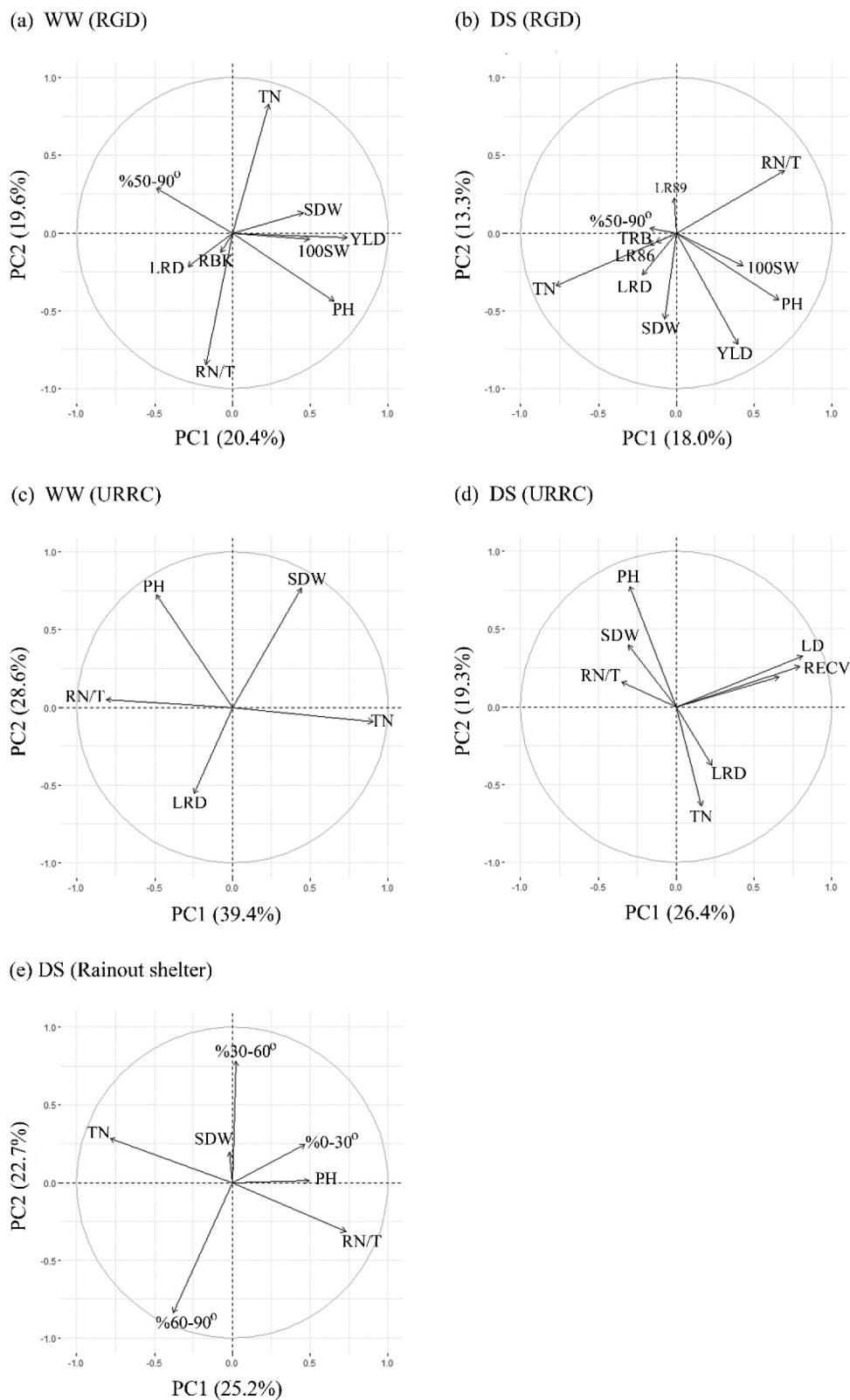


Figure 5. Principal component analysis of phenotypic traits for well-water at RGD (a), drought stress at RGD (b), well-water at URRC (c), drought stress at URRC (d) and drought stress in rainout shelter at URRC (e).

tiller. Root number per tiller influenced plant recovery at URRC (Table S3). The lower the recovery score, the better the plant recovery.

PCA of root architecture and productivity traits

Principal component analysis (PCA) was carried for each location and treatment (Figure 5 and Table S4). Under

well-watered conditions at RGD, percent vertical roots (%50–90°) contributed to PC1, while tiller number and root number per tiller contributed to PC2 and lateral root density to PC3. Under drought, root number per tiller contributed to PC1, lateral root density contributed to PC2, and percent vertical roots contributed to PC3. In the field experiment at URRC, the only root trait contributing to variation under well-watered conditions was lateral root density, while under drought, lateral root density contributed to PC3. In the rainout shelter, where all plants were subject to drought, the first PC was affected by the distribution of nodal root growth angle.

Path coefficient analysis of shoot dry weight

Path analysis was used to determine the direct and indirect traits contributing to shoot dry weight at different locations and drought conditions. In all locations and conditions, plant height was a direct contributor to shoot dry weight (Figure 6) signifying an allometric relationship. Allometric relationships between root traits and productivity traits were not significant (Table S5). Root architectural traits also contributed directly to shoot dry weight (Figure 6). In the well-watered treatments at both sites, proportion of nodal roots that elongated more vertically, lateral root density, and root number per tiller were negative contributors to shoot

biomass. Under drought stress, root number per tiller was negatively associated with shoot biomass at RGD but positively associated with shoot biomass in the rain-out shelters at URRC, while lateral root density was negatively associated with shoot biomass in the URRC field experiment.

QTL analysis of root architectural traits

A total of eight QTL for root traits were identified at RGD and URRC (Table 3). Five QTL were identified for RN/T. One QTL on chromosome 4, *qRN/T-4.1*, contributed by the donor conferring greater root number per tiller, was identified in the well-watered treatment at RGD with a phenotypic variation explained (PVE) of 23.2% and LOD score of 7.28. Another QTL on chromosome 4, *qRN/T-4.2* identified in the well-watered treatment at URRC was also contributed by the donor with LOD score of 6.8 and explained 7.6% of the phenotypic variation for root number per tiller. *qRN/T-4.1* and *qRN/T-4.2* were 8.3 to 9.7 Mbp apart, thus they are considered different loci. Under drought condition at URRC, three QTL for RN/T (*qRN/T-1*, *qRN/T-2* and *qRN/T-7*) were detected on chromosomes 1, 2, and 7. KDML105 allele increased root number per tiller in chromosome 1 while the donor allele contributed to the other QTL. These identified QTL explained phenotypic variation (PVE) from 14.1% to 21.0% with LOD scores ranging from 5.8

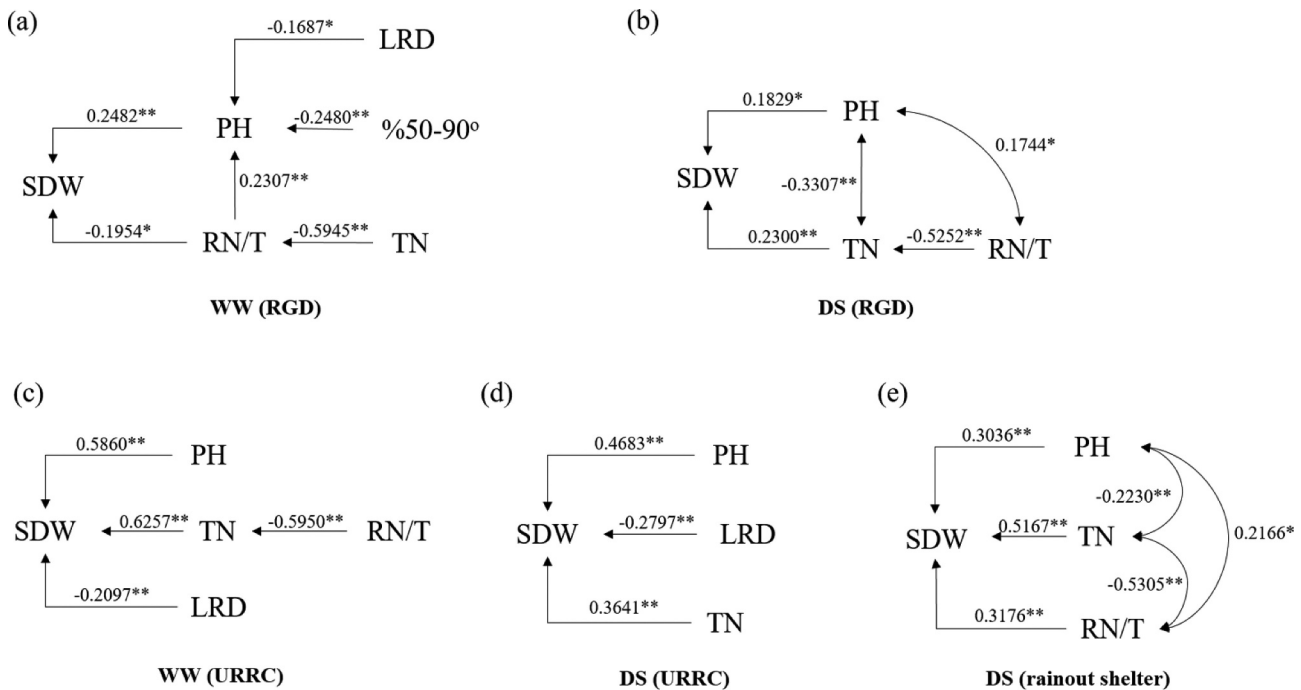


Figure 6. Path coefficient analysis. (a) Well-watered condition at RGD. (b) Drought stress condition at RGD. (c) Well-watered condition at URRC. (d) Drought stress condition at URRC. (e) Drought stress condition in rainout shelter at URRC. * and ** indicate significance at the 0.05 and 0.01 levels, respectively.

Table 3. QTL analysis of root architectural traits and drought stress plasticity from well-watered and drought conditions in RGD and URRC.

Location	QTL	Traits	Chr.	Marker name	Start (bp)	End (bp)	Size (Mb)	LOD	PVE (%)	Allele
RGD (WW)	<i>qRN/T-4.1</i>	RN/T	4	4_31188042	29,809,856	31,261,400	1.5	7.28	23.2	Donor
	<i>q%50-90°-1</i>	%50-90°	1	M1_35944104	32,966,983	40,215,261	7.3	4.01	6.95	Donor
RGD (DS)	<i>qLRD-1</i>	LRD	1	1_11007976	10,601,209	11,498,233	0.9	7.75	24.09	KDML105
	<i>q%50-90°-8</i>	%50-90°	8	8_26330490	25,432,956	26,990,071	1.6	4.79	12.58	Donor
URRC (WW)	<i>qRN/T-4.2</i>	RN/T	4	4_21529095	21,521,073	21,532,818	0.01	6.83	7.64	Donor
URRC (DS)	<i>qRN/T-1</i>	RN/T	1	1_39800030	39,707,928	39,819,532	0.11	6.91	20.99	KDML105
	<i>qRN/T-2</i>	RN/T	2	2_28818290	20,823,582	32,249,957	11.4	5.8	14.11	Donor
	<i>qRN/T-7</i>	RN/T	7	7_23772926	19,334,046	23,859,829	4.5	5.8	17.66	Donor

RN/T, root number per tiller; LRD, lateral root density; %50-90°, percent of roots at 50°-90°; WW, well-watered; DS, drought stress; LOD, logarithm of the odds ratio; PVE, phenotypic variation explained.

to 6.9. Only one QTL for LRD (*qLRD-1*) was identified on chromosome 1 under drought stress at RGD. This QTL explained 24.1% of the phenotypic variation and greater values were contributed by KDML105 with LOD 7.8. Two QTL were identified for percentage of vertical roots on chromosomes 1 (*q%50-90°-1*) and 8 (*q%50-90°-8*) under well-watered and drought conditions at RGD, respectively. Both QTL were contributed by the DT donor and the PVE ranged from 7.0 to 12.6%.

Discussion

Drought tolerance is comprised of various morphological, biochemical, and molecular characteristics (Pandey & Shukla, 2015). Morphological traits such as root traits can improve access to deep soil moisture play a major role in increasing yield under drought stress. Nodal roots form the scaffolding of the rice root system, and their larger diameter has been associated with penetration ability (Clark et al., 2008; Nguyen et al., 1997). Lateral roots ramifying from the nodal roots form the majority of the absorptive surface of rice plants, and contribute to deep root length density and drought tolerance (Sandhu et al., 2016). Root angles determine how quickly roots become deep, thereby affecting drought tolerance (Uga et al., 2013). This paper describes the response of the KDML105-CSSL population to drought stress and examines how root architectural traits contributed to stress tolerance. QTL for nodal root number per tiller, lateral root density, and root vertical distribution were mapped in KDML105-CSSLs population. This population was previously shown to vary for drought tolerance under mild stresses (Kanjoo et al., 2012). The yield reduction of KDML105-CSSLs ranged from 2 to 50% under mild stress and the lines with increased grain yield under stress had introgressed DT-QTL in chromosomes 1, 4, and 8 suggesting that KDML105-CSSLs carrying DT-QTL segments were adapted to mild drought stress (Kanjoo et al., 2012). Similar to Kanjoo et al. (2012), reduction in yield and

biomass was experienced under drought stress in this study. This variation was confirmed in this study at two sites in Thailand under well-watered and mild drought stress treatments.

The mild drought stress that developed at both RGD and URRC affected agronomic and productivity traits. Plant height, tiller number, shoot dry weight, 100 grain weight, and yield decreased due to the effects of drought, as expected (Tables 1 and Tables 2). Although the reduction in shoot biomass with drought was similar at the two sites, root system responses differed. At RGD, there were fewer roots per tiller with drought, LRD was greater, and roots shifted to proportionally vertical distribution. At URRC, there was a 61% increase in the number of roots per tiller with drought, but LRD was less (Tables 1 and Tables 2). In maize, reduction in the number of nodal roots results in deeper rooting, improved stomatal conductance, and improved photosynthesis (Gao & Lynch, 2016), and similar benefits were found in lines with less dense lateral roots compared with lines with greater lateral root density (Zhan et al., 2015). We found benefits of fewer RN/T at RGD, but LRD was not significant in our path analysis (Figure 6). On the other hand, LRD was negatively associated with shoot biomass under drought at URRC, while RN/T was not significant in the path analysis for that site, despite the large increase in nodal root numbers with drought. It is possible that both reduced nodal root number and reduced lateral root density are strategies to conserve metabolic resources for axial root elongation, but the relative benefits probably depend on the soil type and the timing and duration of the drought. Moreover, the nodal root number and lateral root branching was decreased under aerobic condition (Kato & Okami, 2011) indicating rice roots had responded to aerobic conditions as though they were under drought stress. At URRC, plant recovery was influence by RN/T (Table S3) thus the maintenance or increase in roots after stress is a sign of good recovery.

The soil at RGD has high clay content and drought developed at the booting stage. While the role of soil type in lateral root proliferation has not received much

research attention, increased lateral root density in response to drought was observed in previous studies (Hazman & Brown, 2018; Henry et al., 2011; Kameoka et al., 2016; Kano-Nakata et al., 2011). In contrast, at URRC with sandy soil, LRD decreased with drought, though LRD was much greater at URRC than at RGD in both treatments (Tables 1 and Tables 2). Differences between sites in LRD could also be attributed to the timing of drought, which developed earlier at URRC than at RGD.

Deeper rooting is widely regarded to be an important trait for drought tolerance, since deep roots allow better water acquisition from deep soil layers (Gowda et al., 2011). Greater root vertical distribution can be achieved by increasing depth of nodal roots, which bear many lateral roots and presumably also extract water themselves. At RGD, the percentage of vertical nodal roots at more than 50° increased from 9.9% to 12% under drought stress, and a larger proportion of nodal roots elongated enough to emerge from the baskets (Table 1). In the URRC field experiment, root angles were not measured, but nearly 30% of roots of droughted plants in the URRC rainout shelter had greater than 60° angles, which can be attributed to the sandy soil texture. Additionally, a previous study at the same site indicated total root length at the deep soil layer was promoted by aerobic condition in rainfed lowland (Kato et al., 2013). Kato et al. (2006) indicated that the cultivars ranking with high deep root ratio under irrigated condition resulted similar to that of frequency of higher nodal root growth angles suggesting the nodal root growth angles of rice were associated with the genotypic variation of deep root development. In other cereal crops, deep rooting under progressive drought was attributed to promotion of nodal root elongation in wheat (Ehdaie et al., 2012), deeper root angles in maize (Nakamoto, 1993) and millet (Rostamza et al., 2013), and reduced crown root numbers and lateral root branching in maize (Gao & Lynch, 2016; Zhan et al., 2015). In rice, nodal root angle is controlled in part by *DRO1* (Uga et al., 2013). Using *DRO1* in breeding increases deeper rooting in shallow-rooted rice lines and helps maintain yield under drought stress (Uga et al., 2015, 2013; Wang et al., 2019). Several additional QTL regulating nodal root angle in rice are under investigation (Kitomi et al., 2018).

PCA shows that in almost all environments and conditions, nodal root number per tiller and tiller number together explained the variation in one PC, and root number per tiller was always in the opposite direction to tiller number (Figure 5). The tillering pattern may play a part in genotypic variation in assimilate supply to root growth (Yoshida & Hasegawa, 1982). Innes et al. (1981) suggested that producing fewer unproductive tillers may conserve moisture for the productive tillers and

also produce deep-rooted shoots. Upland rice varieties, which are more drought stress-tolerant, typically have fewer tillers and thicker nodal roots (Gowda et al., 2011). Tiller number was a significant factor in our path analyses for every environment (Figure 6), and varied widely among genotypes at both sites (Tables 1 and Tables 2). One of the donors of the double-haploid parent of the KDML105-CSSL population was an upland Japonica cultivar, while the other parental lines were lowland Indica types (Lanceras et al., 2004), and segregation of the traits from these diverse sources was probably responsible for the contrast in tillering and the variation in root architectural traits.

In our study, a total of eight QTL were identified under well-watered and drought conditions at two field sites and in a rainout shelter. More QTL were identified for root number per tiller than for vertical root distribution or lateral root density (Table 3). Relevant QTL that co-located with root trait QTL identified in this study are presented in Supplemental Table 7. *qRN/T-4.1* on chromosome 4, associated with root number per tiller, is within a larger QTL previously reported by Price et al. (2000) for root number. Three QTL (*qRN/T-1*, *qRN/T-2* and *qRN/T-7*) detected for root number per tiller under drought at URRC overlapped with several previously identified root QTL. The QTL associated with root number per tiller on chromosome 2, *qRN/T-2* was detected in the same region as root number QTL identified by Ray et al. (1996), Hemamalini et al. (2000), and Hemamalini et al. (2000) also reported a QTL related to root number on chromosome 7 which co-located with *qRN/T-7*.

Only one QTL for lateral root density, *qLRD-1*, was detected (Table 3). This QTL co-localized with a previously identified root branching index QTL at the interval marker of RM306-RM23 that is responsible in producing large number of lateral roots per unit axis length in both seminal and adventitious roots (Horii et al., 2006) (Table S6). QTL for percent vertical root distribution (*q%50-90°-1*) identified at well-watered condition in RGD co-located with previously identified QTL for deep root number (B Courtois et al., 2003; Price et al., 2002; Yadav et al., 1997), deep root ratio (Kamoshita et al., 2002a) and maximum root length (Ali et al., 2000, 2000; Champoux et al., 1995; H. G. Zheng et al., 2000; Kamoshita et al., 2002b; Price et al., 2002; Yadav et al., 1997; Zhang et al., 2001). Similarly, *q%50-90°-8* on chromosome 8 overlapped with QTL previously associated with deep root ratio (Yue et al., 2006), deep root weight (Yadav et al., 1997), and maximum root length (Price et al., 2002, 1999; Xu et al., 2004).

The results of PCA and QTL identified strongly support the findings in relation to variations specific to each site. QTL for LRD under stress was found in RGD and PCA shows that LRD, yield and shoot dry weight are in the same PC with the same direction. On the other hand, QTL for RN/T was found in URRC and have the same direction in PC1. Moreover, the variation in PC1 also include improving leaf rolling and leaf drying scores and improved recovery. Wade et al. (2015) studied on yield and rice root growth under various environments and they found the root growth showed sensitivity to environmental conditions. And they suggested that rice response to drought for yield and root growth would be best evaluated within the target environment.

Candidate genes were investigated from 1 Mb upstream and downstream of the significant SNPs. The candidate genes involving root development found lying in the QTL regions are reported in Table S7. *NARROW LEAF 1 (NAL1)* was found in the *qRN/T-4.1* region which encodes a putative trypsin-like serine/cysteine protease. This gene is strongly expressed in root and *nal1* mutant with reduced number of crown roots (Cho et al., 2014). In addition, *NAL1* regulates the expression of *OsPIN1* (Qi et al., 2008) and other genes associated with polar auxin transport (PAT) and *CRL* genes associated with crown root development (Cho et al., 2014). *QHB* is the ortholog of *WUSCHEL RELATED HOMEODOMAIN 5 (WOX5)* in Arabidopsis was found in *q%50-90°-1*, which is specifically expressed in the quiescent center (QC) of the root (Kamiya et al., 2003). Expression of *QHB* was observed in the initiation cells for epidermis, cortex, endodermis, and root cap that surrounds the central cell of root apical meristem (RAM) during radicle and crown root formation. Moreover, overexpression of *QHB* caused abnormal crown root formation. A rice gene called Short postembryonic roots 1 (*OsSPR1*) was located on *qRN/T-1* from URRC under drought stress. Loss of function of *OsSPR1* resulted in defective elongation of all root types, though the defects were more severe in lateral roots and adventitious (nodal) roots (Jia et al., 2011). And *Osspr1* mutant increased H₂O₂ production, suggesting that accumulated H₂O₂ at the root tip elongation zone caused the cell death. Another gene, *OsRPK1*, was found in *qRN/T-7* region from URRC under drought. Zou et al. (2014) found that the *OsRPK1* negatively regulates polar auxin transport in rice and overexpression of this gene suppressed the expression of *OsPIN* genes suggesting that *OsRPK1* plays a role in auxin transport. Under-expressing lines produced more crown roots and tillers compared with wild type. These genes may be useful in breeding programs to improve drought resistance in rice.

Conclusion

Phenotypic variation in root architectural traits was found in the KDML105-CSSL population. Root trait responses to drought depended on environmental factors. Under drought stress, there was an increase in lateral root density in the clay soil at RGD, and an increase in nodal root numbers and decrease in lateral root density in sandy soils of URRC. Specific root architectural traits such as nodal root number per tiller and lateral root density may directly or indirectly contribute to biomass accumulation and yield. QTL were identified from both well-watered and drought stress conditions to explain the variation on root architectural traits in KDML105-CSSL rice population.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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