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Mapping QTLs for seedling root traits in a doubled haploid wheat population under different water regimes

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Abstract A deep and thick root system has a positive effect on wheat yield, particularly in drought environments. A doubled haploid (DH) population of 150 lines derived from the cross Hanxuan 10 × Lumai 14 was used to map QTLs for seedling root characteristics. The DH lines were cultivated in an agarose gel-chamber under well-watered (WW) and water-stressed (WS) regimes. Water stress was simulated by adding mannitol to the agarose gel. The seminal root traits, including maximum root length (MRL), seminal root number, total root length, project root area, root surface area, and seminal root angle were measured after 6 days of seedling development. Grain yields (GY) were measured in a field experiment. A total of 29 QTLs were identified for seedlings cultured under WW regimes, and 23 QTLs under WS regimes. Individual QTL accounted for phenotypic variations ranging from 4.98 to 24.31 %. The QTLs were distributed on 17 chromosomes, except 1D, 4D, 6B and 6D. Seven consistently expressed QTLs were detected for all the traits tested except MRL under both water regimes. The QTLs for root traits were unevenly distributed among chromosomes, and clustered in eight loci on seven chromosomes, showing pleiotropic effects on target traits. One region in the interval *Xgwm644.2–P6901.2* on chromosome 3B contained 9 QTLs affecting most root traits. The present data provide an insight into the genetic basis of seedling root development under different water regimes and may benefit breeding programs using marker-assisted selection (MAS) for root traits.

Keywords *Triticum aestivum* · DH population · Water stress · Drought resistance

Abbreviations

MRL	Maximum root length
SRN	Seminal root number
TRL	Total root length
PRA	Project root area
RSA	Root surface area
SRA	Seminal root angle
GY	Grain yield
WW	Well-watered
WS	Water-stressed

Introduction

Drought is increasingly becoming the most important stress factor limiting wheat (*Triticum aestivum* L.) and

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other crop productivity in rain-fed production systems worldwide. Consequently, developing cultivars with enhanced adaptation to drought and higher yields has become a major objective for many crop improvement programs. A number of morpho-physiological traits associate with the adaptive response of crops to drought (Araus et al. 2003a, b; Reynolds et al. 2007). Among them, root systems are crucial to plants for soil exploration and below-ground resource acquisition, and are closely related to plant adaptation to sub-optimal conditions (Manschadi et al. 2008). Ludlow et al. (1990a) placed higher rooting depth and density in a list of priorities of drought-adaptive traits in crop improvement programs. Price and Courtois (1999) also reported that rice varieties with longer, thicker and bigger root systems showed stronger drought resistance. Other researchers showed that the total length of roots and their distribution in the soil, together with the uptake rate per unit of root length, determine the uptake of water and nutrients (Zhu et al. 2006) as well as overall crop performance (Slafer et al. 2005; Devaiah et al. 2007; Tambussi et al. 2007). O'Toole and Bland (1987) reported that deep and dense root systems could access more soil water for plants, and extensive root systems were positively associated with higher grain yield (GY) in rice under drought stress (Lafitte et al. 2004). Further work indicated that root architecture determined yield under drought conditions; for example, high yielding upland rice varieties with longer root lengths (Steele et al. 2006). Although root traits have vital effects on plant yield under water-stressed (WS) conditions, they are seldom considered as selection criteria for improvement of wheat and other crops because they are difficult to measure. The applications of molecular marker technology and outcomes of quantitative trait locus (QTL) mapping have facilitated a better understanding of the genetic basis of root characteristics and GY. To date, there are few reports about QTLs for root traits in wheat (Hao et al. 2003; Zhou et al. 2005; Landjeva et al. 2008; Shi et al. 2008), rice (Price et al. 2002; Kamoshita et al. 2002; Li et al. 2005) and maize (Hund et al. 2004; Omori and Mano 2007). Furthermore, no report has revealed a genetic correlation between root traits and GY on the basis of molecular analysis.

Seed germination and seedling establishment are considered to be the most critical stages for wheat growth and development, especially under WS conditions. In wheat, both seminal and nodal roots remain functionally active throughout plant life (Araki and Iijima 2001). However, nodal roots may stop growing or their growth may be limited under WS conditions. In contrast, the seminal roots keep growing under WS conditions. In this respect, seminal roots may be more important than nodal roots for sustaining yield (Manske and Vlek 2002), and this was made evident by a maize mutant (*rtcs*) that can grow to maturity and set seeds even though it has only seminal roots (Hetz et al. 1996). Because seedling root architecture expressed at the early stages of crop development determines the growth and functioning of the mature root system later in the season, root traits can be investigated at the seedling stage (Løes and Gahoonia 2004). Many species including wheat have fibrous root systems consisting of extensive masses of thin roots. It is technically difficult and labor-demanding to investigate root architecture on a large number of such plants under field conditions. For this reason, most experiments on root traits were carried out in greenhouses or by using only limited numbers of genotypes in the field (Kara et al. 2000; Manschadi et al. 2006, 2008; Liao et al. 2006). As an alternative to field experiments, monitoring root growth and development of seedlings/plants grown under controlled conditions (e.g., hydroponics, paper rolls, pots, soil columns) provides much less costly ways to investigate genetic variability of root traits (Landi et al. 2002; Tuberosa et al. 2002; Trethowan et al. 2005). Although hydroponics and rolled-germination paper systems are suitable for investigating some root traits (McPhee 2005; Beebe et al. 2006), they are less useful for measuring other traits such as angle of root spread, a useful estimator of the characteristics of the vertical distribution of roots (Oyanagi et al. 1993). So far, reports about seminal root angle are few in wheat. A gel-chamber method described by Bengough et al. (2004) is an effective way to examine root traits; it can be used to investigate root spread angle, which can be preserved perfectly on it, and WS conditions can also be simulated in it. Roots on plants grown in gel-chambers were similar to those from plant grown in the field (Bengough et al. 2004). This method allows researchers to investigate plant root traits very effectively. Although the method has not been widely employed to culture many different types of plant materials for high throughout analysis of root traits, there seems to be no reason for not using it in such a way. Furthermore, no WS regime was reported base on gel-chamber greatly limited the use of gel-chamber.

In the current work 150 lines of a DH population from Hanxuan 10 × Lumai 14 were used for mapping QTLs associated with wheat GY under field conditions and root traits of seedlings grown in a gel-chamber culture system under both WW and WS regimes.

Materials and methods

Materials and cultural conditions

Plant materials

A doubled haploid (DH) population of 150 lines was derived from a cross between Chinese winter wheat (*T. aestivum* L.) cultivars Hanxuan 10 and Lumai 14. The DH population was constructed using anther culture of the F_1 plants (Jing et al. 1999). The parents were initially chosen for their difference in drought tolerance. Female parent Hanxuan 10 is a drought-tolerant cultivar from Shanxi Academy of Agricultural Sciences, released in 1966 and still grown in arid and barren areas. Male parent Lumai 14 is a high-yielding cultivar adapted to abundant water and fertile conditions from Yantai Institute of Agricultural Sciences, Shandong Province, released in 1986 and widely grown during the 1990s in northern China. A genetic linkage map, consisting of 395 marker loci, including 132 AFLP and 263 SSR markers, was established from data on 150 DH lines (DHLs) using MapMaker/Exp 3.0 software (Hao et al. 2003). The map covered 3,904 cM with an average distance of 9.9 cM between adjacent markers. The 395 loci were distributed on 31 linkage groups which belong to all 21 chromosomes with 161, 177, and 57 loci in genomes A, B and D, respectively. The same population was used to map QTLs for a range of agronomic traits (An et al. 2006; Yang et al. 2007a, b; Shi et al. 2008; Wu et al. 2010).

Gel-chamber-based observation system for examining root traits

A gel-chamber-based observation system was constructed as described by (Bengough et al. 2004) with a minor modification. Briefly, two plates of 500 × 200 mm glass were used to establish the culture system. Plastic strips (1 mm thick) were used as spacers around each plate, giving uniform air-gaps on each plate after addition of the gel. Each glass plate was covered with a layer of sterile gel approximately 1 mm deep. Sterilized agar (Sigma Type A; 1 g/100 g water) was poured onto each plate before the two plates were taped together as a sandwich with the agar surfaces inward. Roots were grown within the air gap of approximately 2 mm width between the plates to avoid problems of poor aeration.

Five seeds with equal size from each line were chosen and surface sterilized (10 % sodium hypochlorite for 10 min), then washed 5–6 times using deionized water. Seeds were directly placed on the surface of agar-gel with the embryo pointing vertically downwards. Seeds were approximately 30 mm from the top, with 25 mm spacing between seeds, leaving a 170 mm space to the bottom of the plate. The transparent gel plate was then secured using clips at the corners. Each experimental unit included 15 seedlings grown at 20 °C in a 12 h light photoperiod (400 μmol m^{-2} s^{-1} photosynthetic photon flux density).

The gel-chamber system constructed as described above is a well-watered (WW) system. Added mannitol was used to simulate WS regimes. In order to optimize the concentration of mannitol to induce water-stress on wheat seedlings, the effects of 8 concentrations of mannitol (50, 100, 150, 200, 250, 300, 350 and 400 mM) on the two parental lines were assessed in the gel-chamber-based system in preliminary experiments. A concentration of 150 mM was chosen for the present study; it produced significant inhibition, but did not stop plant growth.

Field experiment for grain yield

Grain yields (GY) were determined in a field experiment conducted on the Experimental Farm of the Institute of Crop Science, Chinese Academy of Agricultural Sciences, Changping (116°13′E; 40°13′N) near Beijing during October 2008 to June 2009. Two water regimes representing WS and WW were applied. WS treatments were represented by the rainfed regime. The rainfall was 174 mm during the growing season. WW treatments were irrigated with 75 mm at the pre-overwintering and flowering stages. The DH lines and parents were planted in four-row plots with a length of 4 m and 30 cm spacing. The field management followed standard agricultural practices. The plots were harvested to determine GY.

Phenotype analysis

Wheat seedlings grown in the gel-chamber for 6 days (when maximum root lengths (MRL) reached the bottom of the gel-chamber) were collected for investigating root traits. The root shapes were digitally imaged using an EPSON 10000XL scanner at 300 dpi resolution. The software ImageJ 1.32 was used to measure the MRL, seminal root number (SRN) and seminal root angle (SRA) from the jpg images recorded by the scanner. Total root length (TRL), project root area (PRA), and root surface area (RSA) were obtained using WinRHIZO (Version 2009a, b, Regent Instruments Ins., Quebec, Canada) (Wang and Zhang 2009). The value of each root trait was represented by the average value of five seedlings; three replications of each line were made.

QTL mapping

The QTL analysis was conducted by composite interval mapping (Zeng 1994) using QTL Cartographer 2.0 (Basten et al. 2001). Model 6 was adopted. Parameters for forward regression analysis were a window size of 10 cM, five control markers, and a 1 cM walk speed. The threshold for a putative QTL was fixed at a LOD value of 2.0. Variance and correlation analyses were conducted using SPSS11.0 for Windows. QTLs were designated according to the rule "QTL + trait + research department + chromosome" (McIntosh et al. 1999).

Results

Phenotypic analysis of the DH population and its parents

Analyses of variance (ANOVA) were conducted for all root trait and GY data from the WW and WS regimes. All traits differed significantly between the parents, Hanxuan 10 and Lumai 14 (Table 1).

As expected, the values of SRN, TRL, PRA, RSA and SRA were larger for Hanxuan 10 than for Lumai 14, whereas the values of MRL and GY were smaller for Hanxuan 10 than in Lumai 14 under the WW regime. The mean value of each trait for all DH lines ranged between the parental values under WW regimes, except for PRA and RSA, which were higher than both parents. Water stress induced reductions in growth parameters of all traits except SRN. In WS conditions, Hanxuan 10 exceeded Lumai 14 for the

Table 1 Phenotypic values of root traits and GY for the DH population and the parents

Trait	Treatment	Hanxuan 10 Mean ± SD	Lumai 14 Mean ± SD	DH population				
				Mean ± SD	Range	Kurt	Skew	h_B^2(%)
MRL (cm)	WW	16.90 ± 0.42	17.60 ± 0.52	16.99 ± 1.22	12.00–19.85	3.16	−1.08	68.70
	WS	10.76 ± 1.34	13.30 ± 2.4	15.17 ± 1.15	10.80–18.13	1.79	−0.81	
SRN	WW	5.00 ± 0.71	3.55 ± 0.83	4.26 ± 0.73	3.00–5.80	−0.91	−0.42	81.07
	WS	5.00 ± 0.50	4.28 ± 0.90	4.23 ± 0.73	3.00–6.00	−0.91	−0.11	
TRL (cm)	WW	70.13 ± 5.21	63.20 ± 9.08	63.46 ± 9.52	32.10–85.86	0.02	−0.02	76.60
	WS	37.04 ± 3.42	38.5 ± 4.47	54.27 ± 8.58	32.90–81.30	0.37	0.13	
PRA (cm^2)	WW	2.20 ± 0.13	2.12 ± 0.26	2.26 ± 0.48	1.35–4.28	1.43	0.95	70.33
	WS	1.65 ± 0.17	1.60 ± 0.20	2.27 ± 0.39	1.48–3.27	−0.06	0.34	
RSA (cm^2)	WW	6.92 ± 0.42	6.69 ± 0.82	7.10 ± 1.52	4.24–13.46	1.43	0.95	70.33
	WS	5.20 ± 0.55	5.03 ± 0.62	7.13 ± 1.19	4.66–10.27	−0.06	0.34	
SRA (°)	WW	99.01 ± 9.41	86.70 ± 6.00	86.87 ± 22.25	33.75–135.34	−0.82	−0.07	74.07
	WS	85.09 ± 9.10	76.89 ± 1.85	80.43 ± 22.97	29.81–129.40	−0.90	−0.07	
GY (kg)	WW	1.69 ± 0.24	2.02 ± 0.28	1.73 ± 0.39	0.66–3.50	2.81	0.90	68.91
	WS	1.64 ± 0.02	1.84 ± 0.13	1.45 ± 0.30	0.48–2.30	0.16	−0.20	

h_B^2 represents the broad sense heritability. *MRL* mean maximum root length, *SRN* seminal root number, *TRL* total root length, *PRA* project root area, *RSA* root surface area, *SRA* seminal root angle, *GY* grain yield, *WW* well-watered regimes, *WS* water-stressed regimes

traits SRN, PRA, RSA and SRA, whereas the values for other traits were smaller or more similar to Hanxuan 10 than to Lumai 14. All traits, except SRA, exhibited transgressive segregation in both directions. The frequency distributions of root traits in the DH population covered wide ranges under both treatments, indicating that the phenotypic data were suitable for QTL mapping. Different root traits had different heritabilities. MRL had the lowest heritability (68.70 %), whereas SRN showed the highest (81.07 %) (Table 1).

Correlations among root traits and grain yield

There were significant correlations among root traits. The correlation coefficients ranged from 0.01 for MRL–SRN to 1.00 for PRA–RSA (Table 2). Significantly positive correlations were found among SRN, TRL, PRA, RSA and SRA with the coefficients ranging from 0.20 ($P < 0.05$) to 1.00 ($P < 0.01$). In addition, MRL was significantly correlated with all root traits except SRN and SRA under both water regimes.

TRL exhibited significantly positive correlations with all other root traits. The correlation coefficients ranged from 0.338 (SRA) to 0.747 (PRA and RSA) under both water regimes. TRL was also significantly correlated with GY (0.195*) under WS. Thus TRL may have affected GY, especially under WS, but the effect was very limited.

SRN was significantly correlated with GY and other root traits except MRL under both water regimes. Although the correlation coefficient with GY was obviously lower than that with other root traits, SRN was the only root trait showing a significantly positive correlation with GY under both water regimes, thus indicating that SRN is more important than other root traits for GY determination.

Identification of QTLs for root traits

A total of 52 additive QTLs were detected for seven traits (Table 3). Among them, 41 QTLs come from Hanxuan 10, whereas 11 come from Lumai 14. Of them, 29 QTLs were identified under the WW regime, and 23 were identified under WS (Fig. 1). Phenotypic variations explained by QTLs varied from 4.98 to 24.31 %. QTLs occurred on all chromosomes except 1D, 4D, 6B and 6D, and 11 QTLs were located on chromosome 3B.

QTLs for MRL

Three QTLs on chromosomes 1B, 5D and 7B showing significant associations with MRL explained from 7.37 to 12.20 % of the phenotypic variation in the WW regime. All favorable alleles increasing phenotypic score come from the parent Hanxuan 10. Under WS, three QTLs were detected on chromosomes 2D, 3A and 5B. Among them, two derived from Lumai 14, explained 32.25 % of the phenotypic variation. There

Table 2 Correlation coefficients between root traits and grain yields of DH lines

Trait	Treatment	MRL	SRN	TRL	PRA	RSA	SRA
SRN	WW	0.010					
	WS	−0.040					
TRL	WW	0.554**	0.667**				
	WS	0.520**	0.589**				
PRA	WW	0.481**	0.484**	0.747**			
	WS	0.308**	0.488**	0.733**			
RSA	WW	0.482**	0.484**	0.747**	1.000**		
	WS	0.308**	0.488**	0.733**	1.000**		
SRA	WW	−0.040	0.573**	0.338**	0.203*	0.203*	
	WS	0.150	0.652**	0.463**	0.320**	0.320**	
GY	WW	−0.100	0.228**	0.080	0.040	0.040	0.030
	WS	0.030	0.252**	0.195*	0.140	0.140	0.150

Significant at * $P = 0.05$; ** $P = 0.01$

Table 3 QTLs for wheat root traits and GY detected in the DH population grown in the gel-chamber

Trait	Treatment	QTL	Interval[a]	Site[b] (cM)	LOD[c]	Additive[d]	H^2 (%)[e]
MRL	WW	*QMRL.cgb-1B*	*CWM140–P8143.282*	0.2	3.29	0.34	7.37
		QMRL.cgb-5D	*Xgwm205.2–Xgwm68*	−2.0	3.13	0.44	12.20
		QMRL.cgb-7B	*CWM466–P1123.2*	−0.3	3.13	0.37	8.49
	WS	*QMRL.cgb-2D*	*WMC453.1–WMC18*	5.2	4.54	−0.41	12.22
		QMRL.cgb-3A	*P3614.280–EST47*	2.5	3.77	0.34	8.08
		QMRL.cgb-5B	*WMC380–Xgwm540*	0.3	5.47	−0.41	11.95
SRN	WW	*QSRN.cgb-2B*	*Xgwm429–Xgwm388*	3.5	2.15	0.20	6.90
		QSRN.cgb-3B	*WMC3–P6934.380*	−5.7	4.65	0.30	14.98
		QSRN.cgb-3D	*Xgwm456–Xgdm8*	10.0	2.15	−0.22	8.55
		QSRN.cgb-5A	*P2470.2–Xgwm154*	−3.0	2.61	0.33	19.82
		QSRN.cgb-7A	*P2071.1–Xgwm260*	1.5	4.31	0.24	9.06
	WS	*QSRN.cgb-2B*	*Xgwm429–Xgwm388*	0.3	3.04	0.22	8.67
		QSRN.cgb-3B	*WMC3–P6934.380*	−1.7	3.91	0.23	9.08
		QSRN.cgb-7A	*WMC9–P5611.3*	4.0	2.89	0.19	6.68
TRL	WW	*QTRL.cgb-1B*	*P3470.2–P4133.1*	−8.0	3.07	−4.06	11.43
		QTRL.cgb-1B	*CWM65–P8222.5*	0.1	7.55	5.40	16.13
		QTRL.cgb-3B	*WMC231–Xgwm284*	−1.2	4.39	3.18	10.43
		QTRL.cgb-3B	*Xgwm644.2–WMC3*	6.1	3.83	3.17	10.42
		QTRL.cgb-4B	*Xgwm149–WMC349*	6.5	2.46	−2.57	6.95
		QTRL.cgb-5D	*Xgwm3–Xgwm43*	12.0	2.12	3.11	10.30
		QTRL.cgb-7D	*Xgwm44–Xgwm121*	8.0	2.99	3.16	10.69
	WS	*QTRL.cgb-1A*	*Xgwm135–CWM516*	0.1	2.78	−2.25	6.25
		QTRL.cgb-3B	*WMC3–P6934.380*	−7.7	4.98	3.25	13.81
		QTRL.cgb-3B	*P3622.4–P2076.1*	−6.4	5.15	3.31	14.23
		QTRL.cgb-5B	*P8143.3–P2454.1*	−0.1	5.22	−2.86	10.90
PRA	WW	*QPRA.cgb-3B*	*Xgwm644.2–WMC3*	−2.6	2.12	0.12	5.43
		QPRA.cgb-4A	*Xgwm601–Xgwm610*	−0.1	3.94	0.15	8.85
		QPRA.cgb-4B	*Xgwm149–WMC349*	−3.9	3.40	0.15	9.01
		QPRA.cgb-7D	*Xgwm44–Xgwm121*	8.0	3.01	0.17	11.90
	WS	*QPRA.cgb-2B*	*WMC441–WMC344*	−0.3	2.86	0.10	6.33
		QPRA.cgb-3B	*Xgwm644.2–WMC3*	−0.6	2.72	0.09	5.97
		QPRA.cgb-5B	*P8143.3–P2454.1*	−0.1	4.80	0.16	16.24
RSA	WW	*QRSA.cgb-3B*	*Xgwm644.2–WMC3*	−2.6	2.12	0.36	5.42
		QRSA.cgb-4A	*Xgwm601–Xgwm610*	−0.1	3.95	0.46	8.88
		QRSA.cgb-4B	*Xgwm149–WMC349*	−3.9	3.40	0.46	8.00
		QRSA.cgb-7D	*Xgwm44–Xgwm121*	8.0	3.02	0.54	11.93
	WS	*QRSA.cgb-2B*	*WMC441–WMC344*	−0.3	2.86	0.31	6.34
		QRSA.cgb-3B	*Xgwm644.2–WMC3*	−0.6	2.72	0.29	5.97
		QRSA.cgb-5B	*P8143.3–P2454.1*	−0.1	4.79	0.50	16.22
SRA	WW	*QSRA.cgb-1A*	*P5522.2–P6934.9*	0.1	2.27	5.13	4.98
		QSRA.cgb-2B	*WMC441–WMC344*	2.0	2.14	5.39	5.39
		QSRA.cgb-3A	*Xcwm48.1– Xcwm 532*	0.2	4.16	7.37	9.42
		QSRA.cgb-7D	*Xgwm44–Xgwm121*	6.0	2.98	7.41	10.46
	WS	*QSRA.cgb-2B*	*WMC474–Xgwm374*	3.0	3.10	7.86	10.66
		QSRA.cgb-2B	*WMC179.2–P6901.2*	4.0	4.15	8.18	11.16
		QSRA.cgb-3B	*WMC3–P6934.3*	−3.7	8.58	11.50	24.31

Table 3 continued

Trait	Treatment	QTL	Interval[a]	Site[b] (cM)	LOD[c]	Additive[d]	H^2 (%)[e]
GY	WW	*QGY.cgb-2A*	*P5644.1–Xgwm122*	6.0	2.17	0.11	6.92
		QGY.cgb-6A	*Xgwm334–WMC297*	2.0	3.71	−0.15	13.36
	WS	*QGY.cgb-1A*	*WMC304–P3156.2*	−6.6	3.13	−0.11	10.81
		QGY.cgb-1B	*P3474.4–CWM548*	−0.9	2.54	0.07	5.50
		QGY.cgb-5A	*Xgwm410–WMC340*	0.2	2.91	−0.10	9.43
		QGY.cgb-6A	*Xgwm334–WMC297*	−2.4	3.86	−0.10	9.76

[a] Interval represents the chromosome region defined by two markers flanking of the QTL

[b] Genetic distance between putative QTL peak value and the nearest flanking marker. Positive values are between the QTL and the left flanking marker, negative values are between the QTL and the right flanking marker

[c] log10 likelihood value

[d] A positive value indicates that the positive alleles are from Hanxuan 10; negative values mean the positive alleles came from Lumai 14

[e] Phenotypic variation explained the QTL

was no common QTL for MRL under both water regimes, suggesting that different genes influence MRL under each water regime.

QTLs for SRN

Five QTLs were located on chromosomes 2B, 3B, 3D, 5A and 7A in the WW regime. Each explained phenotypic variation varying from 6.90 to 19.82 % and in total contributed 59.31 % of the phenotypic variation. Three QTLs were located on chromosomes 2B, 3B and 7A in the WS situation, totally accounting for 24.43 % of the phenotypic variation. Alleles increasing SRN phenotypic score were all contributed by Hanxuan 10, except *QSRN.cgb-3D*, under both water regimes. *QSRN.cgb-2B* and *QSRN.cgb-3B* were detected under both water regimes with positive alleles coming from Hanxuan 10. The total variation explained was 21.88 and 17.75 % in the WW and WS regimes, respectively.

QTLs for TRL

Seven QTLs for TRL were detected in the WW regime, explaining 76.35 % of the phenotypic variation. Four QTLs were detected in the WW regime, explaining 45.19 % of the variation. Individual QTL accounted for variation ranging from 6.25 to 16.13 % under both regimes. Most of the alleles increasing phenotypic score were derived from Hanxuan 10.

QTLs for PRA and RSA

Seven QTLs associated with PRA were identified under the two water treatments. Among them, four were on chromosomes 3B, 4A, 4B and 7D, in the WW regime, with the phenotypic variation ranging from 5.43 to 11.90 %. Three QTLs located on 2B, 3B and 5B were identified under WS, explaining a total 28.54 % of the phenotypic variation. All favorable alleles for PRA were contributed by the drought-tolerant parent Hanxuan 10. The numbers and locations of RSA QTLs co-incided with those for PRA with small differences in additive values and phenotypic variation.

QTLs for SRA

Among the seven QTLs associated with SRA, four were on chromosomes 1A, 2B, 3A and 7D in the WW regime, explaining 30.25 % of the phenotypic variation. Three QTLs located on 2B (2) and 3B were detected under WS conditions, contributing 46.13 % of the variation. *QSRA.cgb-3B* located between *WMC3* and *P6934.3,* had the largest effect (24.31 %) on the phenotype variation, and the positive allele came from Hanxuan 10.

QTLs for GY

Two QTLs controlling GY were located on chromosomes 2A and 6A under WW, accounting for 6.92 %

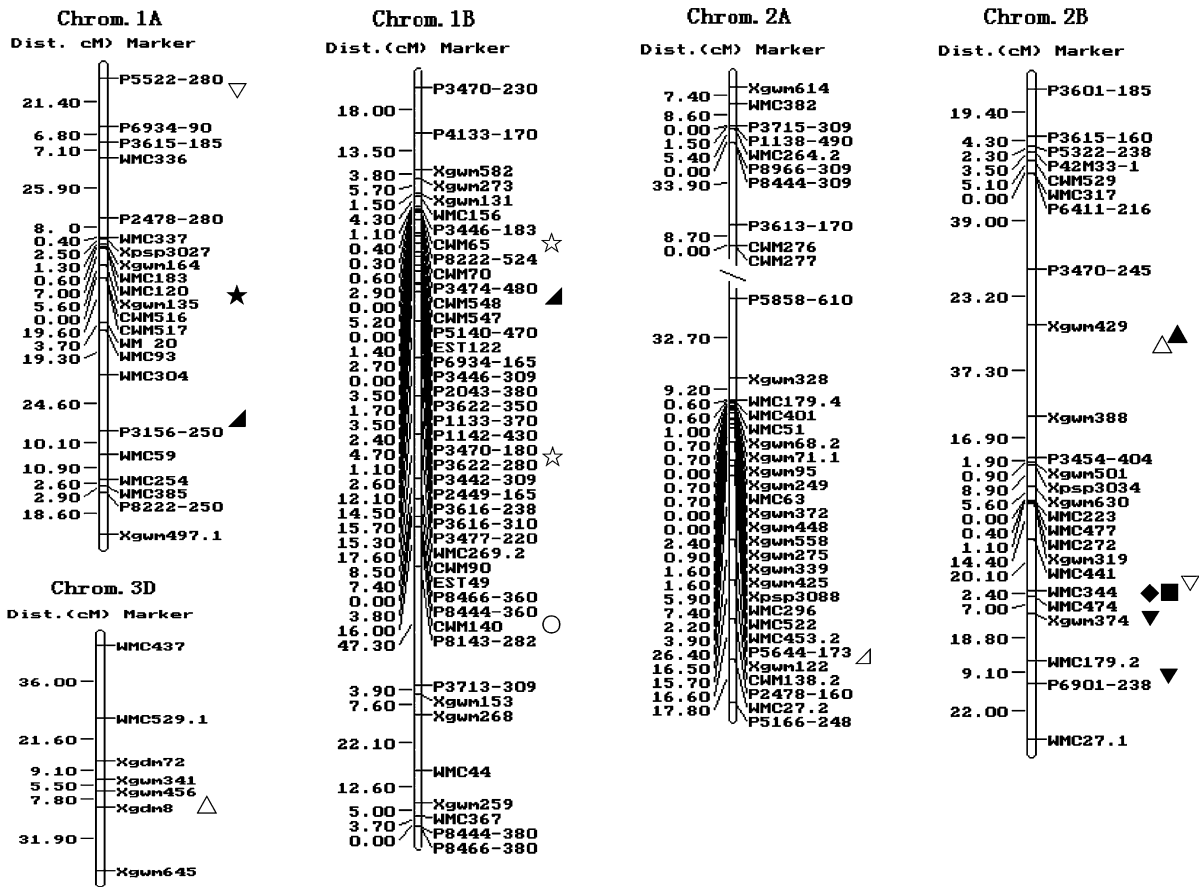

Fig. 1 QTLs for root traits and grain yield in the Hanxuan 10 × Lumai 14 DH lines

and 13.36 % of the phenotypic variation, respectively. Four QTLs, located on chromosomes 1A, 1B, 5A and 6A were detected in WS. All alleles, except *QGY.cgb-2A* and *QGY.cgb-1B*, came from Lumai 14. One common QTL, *QGY.cgb-6A* explained 13.36 % and 9.76 % of the phenotypic variations under WW and WS regimes, respectively. The favorable allele was contributed by the higher yielding parent Lumai 14. The QTL flanking markers *CWM547* on 1B, and *Xgwm122* on 2A detected for GY and/or GY component factors are consistent or adjacent with that detected from the same population grown in multiple environments (Wu et al. 2011, 2012).

Consistently expressed QTLs

Seven QTLs were detected under both treatments (Table 4). We describe them as consistently expressed. For SRN, two consistently expressed QTLs, *QSRN.cgb-2B* and *QSRN.cgb-3B* were identified. They explained 21.88 and 17.75 % of the total phenotypic variation in the WW and WS regimes, respectively.

One QTL for TRL, *QTRL.cgb-3B*, in interval *Xgwm644.2–WMC3–P6934.380*, was consistently expressed in both regimes, with a higher LOD and greater phenotypic variation explained in the WS than the WW regime. Interestingly, consistently expressed QTLs controlling both PRA and RSA were also located in the same chromosome interval as TRL, indicating that this location might have a number of genes governing root development. One consistently expressed QTL affecting SRA was detected between *WMC441* and *Xgwm374* on chromosome 2B. All alleles of consistently expressed QTLs for increasing phenotypic variation of root traits under both water regimes came from Hanxuan 10. One consistently

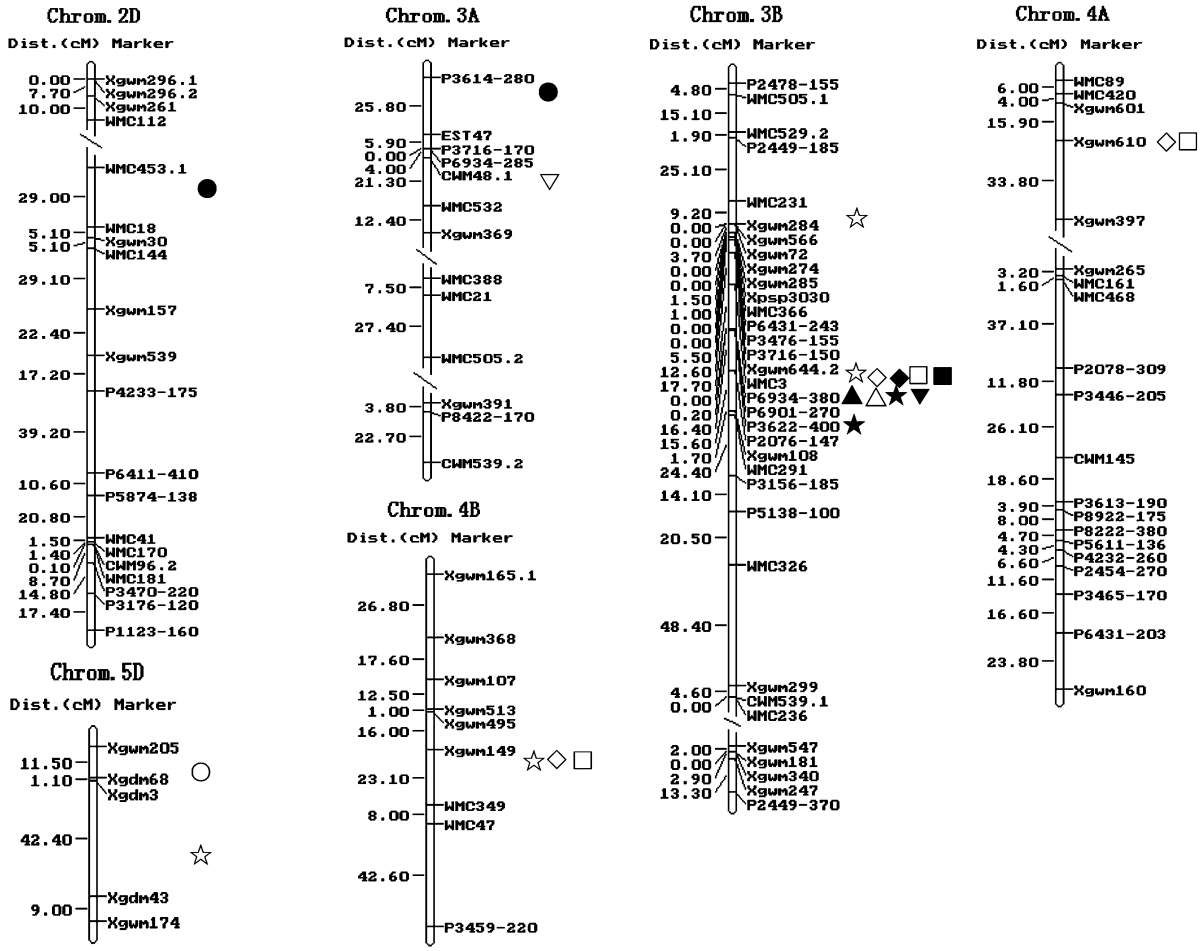

Fig. 1 continued

expressed QTL for GY, *QGY.cgb-6A*, was identified. Unlike other consistently expressed QTLs the positive alleles came from Lumai 14, the higher yielding parent.

Pleiotropic or tightly linked QTLs

The QTLs for the target traits were unevenly distributed across the wheat genome, with 29 QTLs clustered in eight regions on seven chromosomes (Table 5); among them 2B, 3B, 4A, 4B, 5B and 7D. One cluster region *Xgwm644.2–P6934.3* on chromosome 3B included nine QTLs responsible for five root traits (SRN, TRL, PRA, RSA and SRA). All were expressed under both water regimes, except SRA which was only detected under WS.

The other chromosome regions containing multiple QTLs included *WMC441–Xgwm374* on 2B (for PRA, RSA and SRA) and *Xgwm44–Xgwm121* on 7D (for TRL, PRA, RSA and SRA). Apparently, these tightly linked QTLs exhibited pleiotropic effects on wheat root growth and development. On the other hand, multiple QTLs also affected the same trait; for example, regions *Xgwm644.2–P6934.3* on 3B, *Xgwm149–WMC349* on 4B, and *Xgwm44–Xgwm121* on 7D contained QTLs controlling TRL, PRA and RSA under the WW regime, indicating that these regions had important functions in determining root development. The region *Xgwm334–Xgdm36* on chromosome 6A contained two QTLs controlling GY under the both regimes, indicating that this region was important in determining GY.

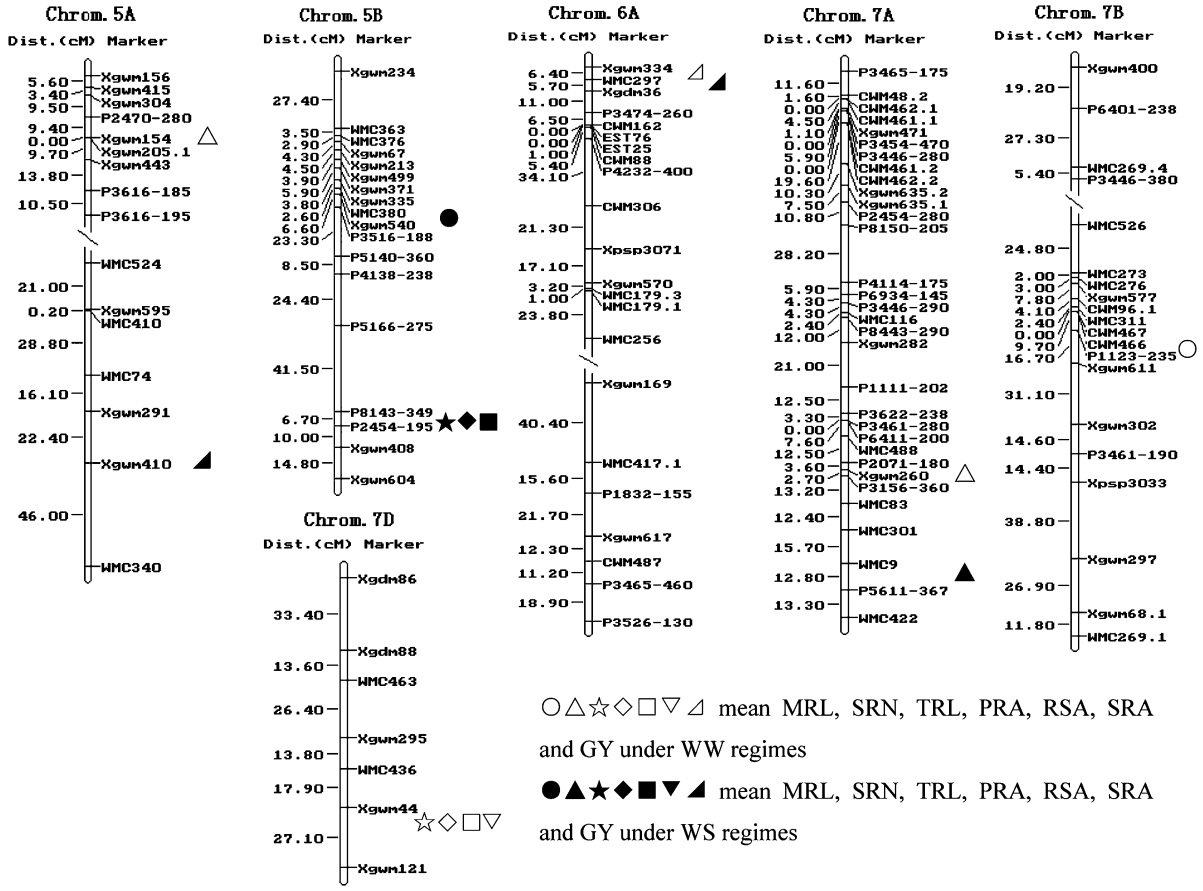

Fig. 1 continued

Discussion

Root systems have several important functions, such as supporting the plant, acquiring water and nutritive elements, and acting as a receptor of environmental changes in the soil including water availability. Under WS condition, plants often develop deep and extensive root systems as an adaptive strategy (Lincoln et al. 1992). Root characteristics, including thickness, length, density and depth, have been associated with drought tolerance in rice (Ekanayake et al. 1985; O'Toole and Bland 1987). Some drought-tolerant genotypes of sorghum have deeper roots (Ludlow et al. 1990b). Kimurto et al. (2005) reported that deeper roots and larger RSA were induced under water stress at the seedling stage in wheat. Additionally, Ito et al. (2006) speculated that lateral root development was accelerated by a moderate soil drying.

It is crucial for drought tolerance improvement in plants to identify the root traits responsible for drought tolerance and to explore the genetic mechanism underlying such characteristics. Because root systems are formed and develop below the soil surface, it is difficult to record root phenotypic data accurately. A gel-chamber-based root culture system was developed as a rapid and non-destructive way to measure root traits on a large-scale.

The gel-chamber is an effective method to culture and investigate root traits

Compared to other root observation methods, the gel-chamber has certain advantages. Firstly, root orientation in a gel-chamber is generally preserved whereas in hydroponics, it is not. Root angle is an important trait affecting water and mineral absorbsion.

Table 4 Consistently expressed QTLs for root traits and grain yield

Trait	Treatment	QTL	Interval[a]	Site[b] (cM)	LOD[c]	Additive[d]	H^2 (%)[e]
SRN	WW	*QSRN.cgb-2B*	*Xgwm429–Xgwm388*	3.5	2.15	0.20	6.90
		QSRN.cgb-3B	*WMC3–P6934.380*	−5.7	4.65	0.30	14.98
	WS	*QSRN.cgb-2B*	*Xgwm429–Xgwm388*	0.3	3.04	0.22	8.67
		QSRN.cgb-3B	*WMC3–P6934.380*	−1.7	3.91	0.23	9.08
TRL	WW	*QTRL.cgb-3B*	*Xgwm644.2–WMC3*	6.1	3.83	3.17	10.42
	WS	*QTRL.cgb-3B*	*WMC3–P6934.380*	−7.7	4.98	3.25	13.81
PRA	WW	*QPRA.cgb-3B*	*Xgwm644.2–WMC3*	−2.6	2.12	0.12	5.43
	WS	*QPRA.cgb-3B*	*Xgwm644.2–WMC3*	−0.6	2.72	0.09	5.97
RSA	WW	*QRSA.cgb-3B*	*Xgwm644.2–WMC3*	−2.6	2.12	0.36	5.42
	WS	*QRSA.cgb-3B*	*Xgwm644.2–WMC3*	−0.6	2.72	0.29	5.97
SRA	WW	*QSRA.cgb-2B*	*WMC441–WMC344*	2.0	2.14	5.39	5.39
	WS	*QSRA.cgb-2B*	*WMC474–Xgwm374*	3.0	3.10	7.86	10.66
GY	WW	*QGY.cgb-6A*	*Xgwm334–WMC297*	2.0	3.71	−0.10	13.36
	WS	*QGY.cgb-6A*	*Xgwm334–WMC297*	−2.4	3.86	−0.09	9.76

[a–e] See footnote to Table 3

Table 5 Pleitropic or tightly linked QTLs for various root traits

Chromosomes	QTL number	Interval	Trait	
			WW	WS
2B	2	*Xgwm429–Xgwm388*	SRN	SRN
2B	4	*WMC441–Xgwm374*	SRA	PRA, RSA, SRA
3B	9	*Xgwm644.2–P6934.3*	SRN, TRL, PRA, RSA	SRN, TRL, PRA, RSA, SRA
4A	2	*Xgwm601–Xgwm610*	PRA, RSA	
4B	3	*Xgwm149–WMC349*	TRL, PRA, RSA	
5B	3	*P8143.3–P2454.1*		TRL, PRA, RSA
6A	2	*Xgwm334–WMC297*	GY	GY
7D	4	*Xgwm44–Xgwm121*	TRL, PRA, RSA, SRA	

According to Bengough et al. (2004) root angle in a gel-chamber was very similar to that in loosely packed soil. Secondly, root growth rate can be measured repeatedly and non-destructively in a gel-chamber, whereas in hydroponics, lifting a root system from the supporting hydroponics solution often damages lateral roots. Thirdly, compared with rhizoboxes, the gel-chamber is non-destructive and no washing is needed for recording root traits. Moreover, the gel-chamber system can be used to perform other experiments. For example, minerals can be added into the gel-chamber to investigate the effect of single or several kinds of minerals to seedling growth and development. One disadvantage is that the system cannot be used to culture plants to maturity. Here, we successfully employed the system to obtain data on wheat seedling root traits from many samples grown under both water regimes, with WS being simulated with the addition of mannitol. Our conclusion was that the system is a promising root culture and observation method for large-scale rapid screening of cereal seedling root characteristics.

Gel-chamber-based culture and mannitol-induced water stress

Mannitol and PEG (polyethylene glycol) are often used to simulate WS regimes for experimental plant

growth (Blum 1989; Gloria et al. 2002), and both may result in osmotic adjustment in addition to imposing WS regimes.

In preliminary experiments, we chose PEG-6000 and Mannitol to simulate WS regimes. However, with PEG added, the agar-gel did not solidify, whereas agar-gel with mannitol concreted well. Consequently, mannitol was chosen to simulate a WS regime in this system. No previous report showed that mannitol could be used to simulate the WS regimes in a gel-chamber, or what concentrations were suitable. The present results demonstrated that mannitol can be used in a gel-chamber to simulate water-stress, and and that acceptable data can be obtained.

Genetic basis of response to water stress in wheat seedlings

The response of plants to water stress is an integration of multiple physiological processes, including plant growth rate, biomass accumulation, balance between water absorption and loss and water accumulation. The processes vary depending on genotypes, timing and severity of water stress. Different environments induce or inhibit different gene expression, a reason why a QTL might show low consistency across different environments. Different QTLs identified under contrasting water regimes indicate that the phenotypic changes in the target traits are controlled by different genetic factors.

In the present study a total a total 52 QTLs for six root traits and GY were detected under two water regimes. Among them, seven consistently expressed QTLs for five of the six traits (except MRL) were clustered or in tightly linked regions under both water regimes (Table 4). Thirty-eight QTLs (73.1 % of the total) were environment-specific. Similar results were presented by Cui et al. (2008) who reported that 77 % of QTLs detected for rice seedling traits were water supply-specific. The environment-specific QTLs detected here indicate that water stress can induce one set of gene expressions and simultaneously inhibit another set.

Our data revealed the following: firstly both parents contributed to increased values in trait phenotypes among the DH lines (Table 3). Secondly, the parent with a lower phenotypic score also contributed positive alleles to DH lines. For example, Hanxuan 10 has a shorter MRL, but it also contributed alleles with positive effects for this trait. Thirdly, QTLs mapped in identical regions might represent a single locus with pleiotropic effects on multiple traits, or could be a group of tightly linked loci. An example of this is the QTL controlling the SRN, TRL, PRA and RSA located on chromosome 3B between *Xgwm644.2* and *P6934.3*. Finally, co-located or tightly linked QTLs may be the genetic basis underlying the phenotypic correlation between the roots traits, especially those detected under the same water treatment.

Co-localization and tight linkage of QTLs governing different root traits

Plant phenotypic expression is affected by both genetic and environmental factors. Our present data shows that some root traits are strongly correlated under WW and WS regimes (Table 2). For example, PRA and RSA were highly correlated under both water treatments. QTLs effecting PRA and RSA were all located between *WMC441* and *Xgwm344* on 2B, *Xgwm644.2–WMC3* on 3B, *Xgwm601–Xgwm610* on 4A, *WMC441–Xgwm349* on 4B, *P8143.3–P2454.1* on 5B and *Xgwm44–Xgwm121* on 7D. Among seven QTL-clustered regions three on chromosomes 2B (2) and 3B affected the same root traits under both water regimes (Table 5), demonstrating that these loci may possess genes consistently expressed under both regimes and that both parents contributed alleles increasing phenotypic value. In addition, QTLs controlling root traits located in three chromosome regions (*Xgwm601–Xgwm610* on 4A, *Xgwm149–WMC349* on 4B and *Xgwm44–Xgwm121* on 7D) were detected only under WW conditions. All of the favorable alleles of these QTLs came from Hanxuan 10. While QTLs for root traits in the interval *P8143.3–P2454.1* on 5B were detected only under WS, such loci may have alleles specifically expressed under WS. Alleles of QTLs on 6A increasing GY came from Lumai 14, the high yielding parent, under both water regimes.

Increasing evidence shows that gene expression is induced by various stresses (Kathiresan et al. 2006). Rabbani et al. (2003) discovered that 62 genes in rice were induced by drought. Similarly, Salekdeh et al. (2002) found that several leaf proteins increased significantly upon drought stress, and contrastingly declined on re-watering. Three genes named *TaSnRK2.7-B*, *TaPP2Aa-B* and *Dreb-B1* were co-located

in the adjacent marker intervals of QTL *QGY.cgb-2A* on chromosome 2A (Zhang et al. 2011), *QMRL.cgb-5B* on chromosome 5B (Wang et al. 2011) and *QTRL.cgb-3B* on chromosome 3B (Wei et al. 2009). These genes are involved in the drought tolerance and/or GY. QTLs detected under WS may represent the expression of genes associated with drought tolerance. QTLs detected under both regimes may represent the consistent expression of genes unaffected by environment. Although the physiological and biochemical functions of those QTLs remain to be addressed further, consistently expressed QTLs would be useful for marker-assisted selection (MAS) for drought tolerance improvement in wheat.

Potential of QTLs for MAS in wheat breeding for drought tolerance

Among all the root traits tested here, only SRN had a significantly positive correlation with GY under both water regimes. The heritability of SRN was highest (81.07 %) among all the root traits showing that it was stable in different water environments. Mac Key (1979) reported a strong correlation between the number of seminal roots and seed size in wheat, although Fritsch (1977) found a weaker relationship. Given that seed size is an important factor affecting GY, the genes controlling SRN might also affect seed size, or maybe the former determines the latter (Tuberosa et al. 2002). Under such conditions, the water volume to support plant growth was determined by the number and water–adsorption capacity of each seminal root. Manschadi et al. (2008) also considered that a large number of seminal roots can make a significant contribution to water uptake of wheat plants. Thus greater numbers of seminal roots allow greater water uptake under WS.

Some studies found that QTLs for closely correlated traits often mapped at or near the same chromosomal region (Hervé et al. 2001; Fracheboud et al. 2002; Tuberosa et al. 2002). Our research is in agreement with this. We found seven clustered regions controlling root traits on chromosomes 2B, 3B, 4A, 4B, 5B and 7D. Among them, a QTL (*QSRN.cgb-2B*) identified in this paper was located within same marker interval as QTL effecting SRN detected by Zhou et al. (2005). A QTL for SRA was located near QTL controlling MRL (Zhou et al. 2005), and another QTL governing SRA was co-located with the PUP QTL between markers *WMC474* and *WMC441* on chromosome 2B (Su et al. 2009). This result was consistent with a report in common bean (*Phaseolus vulgaris* L.) indicating that SRA is a major determinant of root architecture, which can affect topsoil foraging and phosphorous acquisition (Nielsen et al. 1999; Liao et al. 2001; Lynch and Brown 2001). Like Wu et al. (2010) we also found that QTLs for root traits were co-located with those for PH. A chromosome region simultaneously affecting TRL and PH located in the interval *Xgwn273–Xgwm131* on chromosome 1B, and two other chromosome regions located on 3A and 3B between *Xcwm48.1* and *Xcwm532* and *P3622.4* and *P2076*, controlled SRN, TRL, SRA and PH, respectively. The co-location of QTLs for multiple traits could indicate four alternate possibilities: (i) two tightly linked genes modulating the expression of separate traits; (ii) one gene with a single function producing a sequence of causally related events; (iii) one gene with an independent effect on two or more traits; and (iv) two tightly linked genes with effects on the same two or more traits (Lebreton et al. 1995). To understand them in greater detail, fine mapping using larger populations of segregating materials and greater numbers of markers focused to the region of interest will be required (Tuberosa et al. 2002).

Consistently expressed QTLs for multiple traits detected across different environments may be helpful for MAS for target traits in breeding programs and also for theoretical studies. Nine QTLs were clustered in the interval *Xgwm644.2–P6934.3* on chromosome 3B, including those affecting most seminal root traits under both water regimes. Thus, this chromosome region may contain major genes responsible for seminal root development, and the corresponding QTLs are potential targets for wheat improvement by MAS to enhance drought tolerance and/or GY in wheat.

Conclusions

In this work, we explored the use of a gel-chamber to culture wheat seedlings and to measure root traits using mannitol to simulate WS conditions. In all, 52 QTLs, each explaining 4.9–24.31 % of the phenotypic variations, were identified on 17 chromosomes under two water treatments. Most of the QTLs were environment-specific. Seven consistently expressed

QTLs were detected for six of the seven traits examined (except MRL). The QTLs for seminal root traits were unevenly distributed among chromosomes, but were clustered in eight loci on seven chromosomes. These loci may contain pleiotropic genes affecting root development. The present data provide an insight into the genetic basis of seedling root development under different water regimes and could benefit molecular breeding by MAS.

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