

Full Length Research Paper

Quantitative trait loci analysis for some root traits in Bread Wheat (*triticum aestivum* L.)

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In India, large areas of wheat cultivation suffer with water-stress leading to poor yield, which may be improved through genetic manipulation of plant architecture, particularly involving the root morphology. The root system plays a key role in water and nutrient absorption from the soil, but has not received due attention of geneticists in the past due to the difficulties associated with phenotyping of this trait. During the present study, we dissected the genetic architecture of four root traits through QTL analysis using a RIL mapping population derived from the cross Chinese Spring × Rye Selection. Eight QTLs located on six chromosomes were identified, which included two suggestive QTLs (one each for root length and root dry weight), and six significant QTLs, which included one QTL for root number, four QTLs for root volume and one QTL for root dry weight. A major QTL (*QRv.ccsu-4A.1*) for root volume, detected at a LOD score of 6.5, explained ~30% phenotypic variation in root volume. The remaining five minor QTL each explained 8.82% (*QRv.ccsu-2D.1* for root volume) to 15.93% (*QRdw.ccsu-2A.1* for root dry weight) of the phenotypic variation. SSR markers *Xgwm89* and *Xgwm610* flanking the major QTL *QRv.ccsu-4A.1* may be used for marker-assisted selection for higher root volume for improvement of water absorption efficiency of wheat grown in limited-water conditions.

Key words: *Triticum aestivum*, Chinese spring, rye selection, RIL, root traits, QTL analysis, marker-assisted selection, SSR markers.

INTRODUCTION

Wheat is one of three most important cereal food crops of the world. Globally, India ranks first in terms of area (29.50 mha) under wheat cultivation and ranks second after China in terms of production (93.9. mt in 2012), which was approximately 12% of the total world's wheat production (<http://www.thebioenergysite.com/articles/418/world-agricultural-production-july-30-2012>). Wheat production in India, like many other food crops, is constrained due to a variety of diseases, and due to abiotic stresses like heat and drought (Gupta et al., 2010). It is estimated that 80% wheat in India is cultivated under irrigated conditions and the remaining 20% is grown under rainfed environments (Reynolds et al., 1999). Even under irrigated conditions,

~66% wheat receives only partial (1-2) irrigation (Joshi et al., 2007). Therefore, there is an urgent need to breed wheat varieties that may give higher yield under low-soil moisture conditions. In the past, progress in this direction in India has been rather slow. However, the variety C306 bred in 1969 is still widely grown and is used as a standard check cultivar under drought conditions.

Empirical breeding in the past has not proved of much help in improving grain yield under water stress due to high genotype × environment interaction and low heritability of grain yield (Richards et al., 2008). Therefore, a trait-based approach involving shoot-traits contributing to increased crop water use, transpiration efficiency, stomatal conductance and increased harvest index have been suggested as traits for use in wheat breeding programmes (Reynolds et al., 1999, Richards et al., 2008). However, the root-traits, which make-up nearly half of the total plant biomass and are critical for absorption of water and nutrients from the soil have received little attention due to the difficulties associated

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with effective phenotyping of these traits in the field (Hurd 1976, Manschadi 2006, Richards et al., 2007, Petrarulo et al., 2009). However, an array of methods have been used to study variation in root traits in crop plants (O'Toole and Bland 1983, Gregory et al., 2009) but most of these methods have been developed for controlled conditions. For example, these include phenotyping in hydroponics (O'Brien 1979), in agar (Sanguineti et al., 2007, Manschadi et al., 2008), in soil using clear boxes (Hurd 1968, Liao et al., 2006), through wax barriers (Botwright Acuna et al., 2007) and in pots or columns of soil (Sharma et al., 2009). However, variability of seedling/young plant root traits in wheat has been observed following above methods but the observed variability is not correlated with the variability of root system traits of field grown plants (McDonald et al., 2012, Atta et al., 2013). A recent study showed also genetic variability for root length, root diameter and root length density in a modest set of 15 field grown wheat genotypes (Atta et al., 2013).

However, in view of the key role, which the roots play in water absorption, the genetic dissection of root traits should prove helpful in better understanding of the genetic control of tolerance to water stress and thus should also help in the development of strategies for breeding improved root architecture for higher grain yield under water stress. The genetics of most of the traits associated with improved performance under water-stress is complex (Richards et al., 2007, Rebetzke et al., 2008, Yang et al., 2007), and root architecture is no exception. Further, available evidence suggests that a number of loci control different seedling root traits in wheat (Petrarulo et al., 2009, Zhuo-Kun et al., 2010, Hamada et al. 2012, Christopher et al. 2013, Zhang et al. 2013). During the present study, we followed an approach for phenotyping of root traits that mimicked the field conditions to a large extent and identified genomic regions (QTL) involved in shaping four different root traits recorded at plant maturity in wheat. A mapping population (RIL) of bread wheat derived from the cross Chinese Spring (CS) × Rye Selection 111(RS) was utilized for this purpose.

MATERIALS AND METHODS

Materials

Mapping population: A mapping population of bread wheat comprising 87 recombinant inbred lines (RILs) was used for the present study. The population was derived from the cross Chinese Spring (CS) × Rye Selection 111 (RS) at PAU, Ludhiana and was kindly made available to us by Dr. H. S. Dhaliwal earlier at PAU, Ludhiana; now at Eternal University, Baru Sahib, Sirmour, H.P.

Genetic map: A framework linkage map of the CS × RS mapping population prepared earlier using SSR, AFLP,

and SAMPL markers in our laboratory was used during the present study (Mir et al., 2012). The framework linkage map contained 294 (194 SSR + 86 AFLP + 14 SAMPL) loci, which were distributed on all the 21 different chromosomes, covering a map length of 5211.8 cM, with an average chromosome length of 248.2 cM (range = 129.3 to 297.5 cM).

Methods

Experimental layout: A modified pot culture method using polythene bags, was standardized and used during the present study. Single plants of each of the 87 RILs of the CS × RS population along with the two parental genotypes were planted in separate polythene bags of 20 × 30 cm each containing 3Kg mixture of top field soil and compost manure in 4:1 ratio. The polythene bags were arranged in randomized block design with two replicates and the plants were raised in a net-house at the Research Farm of the Department of Genetics and Plant Breeding, Ch. Charan Singh University, Meerut. The plants were watered with Hoagland's solution as per the requirements to raise healthy plants.

Recording of data: At the time of crop maturity, data on whole roots of individual plants raised in polythene bags were recovered by giving an incision on one side of the bag with the help of a scalpel followed by removing the soil around the roots by repeated dipping of the plant roots in a water tank until the soil was completely removed. The recovered roots were air dried and the data on each of the 87 RILs and the two parental genotypes were recorded on the following four traits: (i) The root length, measured in cm from the base of the plant to the tip of the longest root; (ii) the dry weight of roots (g), weighed with the help of an electronic weighing balance; (iii) root volume (cm³), measured by the water displacement method and (iv) root number, determined by counting the total number of seminal and adventitious roots.

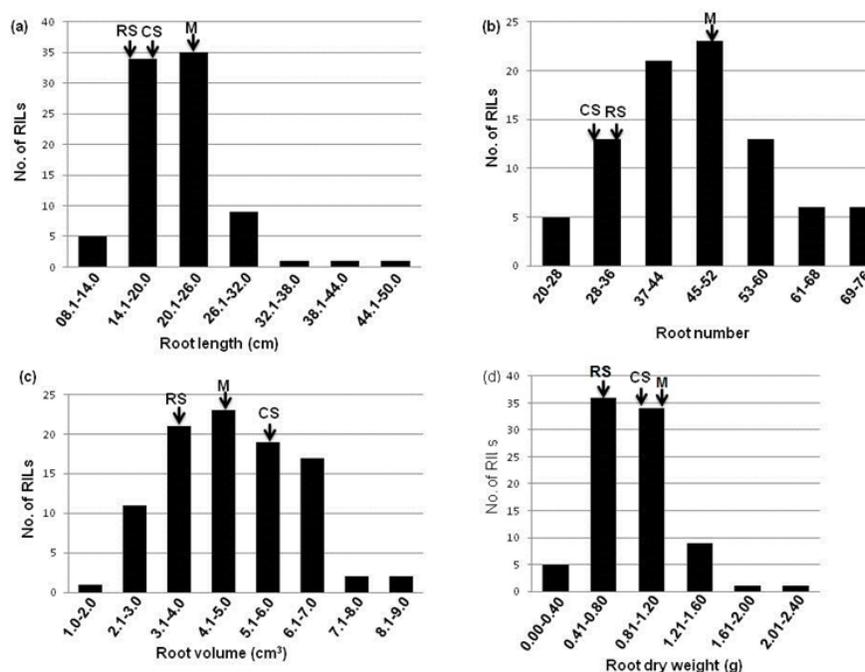
STATISTICAL ANALYSIS

The mean, range and coefficient of variation (CV%) for all the four root traits were determined following Panse and Sukhamate (1985). The histograms were prepared using Microsoft Excel.

QTL analysis: Single-locus QTL analysis for each trait was carried out following inclusive composite interval mapping (ICIM) using Ici Mapping V2.0 (Li et al., 2007). A LOD score of 2.5 was used for suggesting the presence of a significant QTL. A QTL detected below LOD score of 2.5 was treated as suggestive. A peak of the LR (Likelihood ratio) in the linkage map was taken as position of a QTL. Two or more QTL detected with overlapping confidence intervals (also called as support

Table 1. The mean, range values and coefficient of variation in percent (CV%) for the four different root traits of the two parental genotypes and RILs of the CS × RS mapping population of wheat.

Trait	Parental genotype		RIL population	
	Chinese Spring	Rye Selection	Mean (range)	CV(%)
	Mean (range)	Mean (range)		
Root length (cm)	18.00 (16.00-20.00)	18.65 (18.50-18.80)	20.64 (11.70-46.50)	27.04
Root number	39.00 (36.00-42.00)	41.00 (29.00-53.00)	46.90 (23.66-76.66)	26.45
Root volume (cm ³)	6.00 (5.00-7.00)	4.00 (3.00-5.00)	4.68 (2.00-9.00)	29.73
Root dry weight (g)	0.98 (0.68-1.28)	0.40 (0.21-0.65)	0.83 (0.21-2.30)	41.65

**Figure 1.** Histograms showing distribution of (a) root length, (b) root number, (c) root volume and (d) root dry weight of RILs of Chinese Spring X Rye Selection 111 mapping population of wheat. RS: Rye selection, CS: Chinese Spring, M: Overall mean value of RILs.

intervals) were treated as one QTL. The relative contribution of a genetic component (R^2/h^2) was calculated as the proportion of the phenotypic variation explained (PVE).

RESULTS

Means and correlations (parental genotypes and RILs)

Mean and range values of the two parental genotypes

and the RILs for four root traits are given in Table 1. The data indicated a narrow range for all the four root traits among the individual plants of the two parental genotypes. The mean values of root length and root number of the two parental genotypes did not differ very much, though the mean values of the remaining two traits differed significantly. Rye Selection had longer and more number of roots, while Chinese Spring had higher root volume and more root dry weight.

Relative to the two parental genotypes, a wide variation for different root traits, which ranged from 11.70 to 46.50 (cm) for root length and 0.21 to 2.30 (g) for root dry



Figure 2. A representative picture showing variation in root architecture of the two parental genotypes and eight RILs of the Chinese Spring X Rye Selection 111 mapping population of wheat. 1: Chinese Spring, 2: Rye Selection; 3-10 eight RILs.

Table 2. Simple correlation coefficients among four root traits in Chinese Spring × Rye Selection 111 RIL mapping population of wheat.

Traits	Root number	Root volume (cm ³)	Root dry weight (g)
Root length (cm)	0.94**	0.96 **	0.90*
Root number	-	0.97 **	0.86*
Root volume (cm ³)	-	-	0.90*

** Significant at 1% level

weight was noticed among the RILs (Table 1, Figure.1 and 2). The overall mean values of the RILs for root length, root number and root dry weight exceeded the mean values of the two parental genotypes while the overall mean value of the RILs for root volume was intermediate between the two parental genotypes (Table 1 and Figure 1).

The values for all the four root traits of individual RILs showed a good fit to a normal distribution, and transgressed the mean values of the respective traits of both the parental genotypes (Figure 1). The values of coefficient of variation (%) for each of the four traits were high and ranged from 26.45% (root number) to 41.65% (root dry weight). Pearson's correlation coefficients among the four root traits of the RILs were positive and significant (Table 2). The magnitude of correlation coefficients among the four root traits was noticeably high and ranged from 0.86 (between root number and root dry weight) to 0.96 (between root number and root volume).

Composite interval mapping

A total of eight QTLs located on six different chromosomes at LOD scores ranging from 2.2 to 6.5

were detected for all the four traits (Table 3). These included one QTL each for the root length and root number, four QTLs for root volume and two QTLs for root dry weight. Two QTLs, one each for root length (*QRl.ccsu-2B1*) and root dry weight (*QRDw.ccsu-2A.2*), detected at a LOD scores of <2.5, were suggestive and the remaining six QTLs detected at LOD scores of >2.5 were considered as significant. Seven out of the eight QTLs for the different root traits were minor and individual QTL explained 8.82% (*QRv.ccsu-2D.1* for root volume) to 15.93% (*QRdw.ccsu-2A.1* for root dry weight) of the phenotypic variation in the root traits. One of the four QTLs for root volume, located on chromosome 4A (*QRv.ccsu-4A.1*) and detected with a LOD score of 6.5, was a major QTL explaining nearly 30% phenotypic variation in root volume (Table 3 and Figure 3).

DISCUSSION

Roots play a key role in nutrient and water absorption from the soil and are very critical for high grain yield by providing adaptation to water stress (Hurd 1968, 1974,

Table 3. QTL analysis for four different root traits in wheat using QTL Ici Mapping.

Trait/QTL	Chromo-some	Flanking markers	Position (cM)	a	LOD	R ² (%)
Root length						
<i>QRl.ccsu-2B.1</i>	2B	E35M4711 -E35M4710	62	1.82	2.2	10.80
Root number						
<i>QRn.ccsu-2A.1</i>	2A	E35M4734- S7M472	252	-4.13	2.5	10.84
Root volume						
<i>QRv.ccsu-1A.1</i>	1A	E36M5911- E36M5912	295	0.49	2.6	8.91
<i>QRv.ccsu-1B.1</i>	1B	E35M4722 -E35M4719	110	0.46	2.8	8.90
<i>QRv.ccsu-2D.1</i>	2D	Xgwm455 -Xbarc124	36	0.41	2.8	8.82
<i>QRv.ccsu-4A.1</i>	4A	Xgwm89 -Xgwm610	10	-0.78	6.5	29.95
Root dry weight						
<i>QRdw.ccsu-2A.1</i>	2A	E35M4737 - E35M4738	208	0.13	3.5	15.93
<i>QRdw.ccsu-2A.2</i>	2A	E35M4734- S7M472	252	-0.11	2.4	10.60

*Closest marker to the QTL is shown in bold letters.

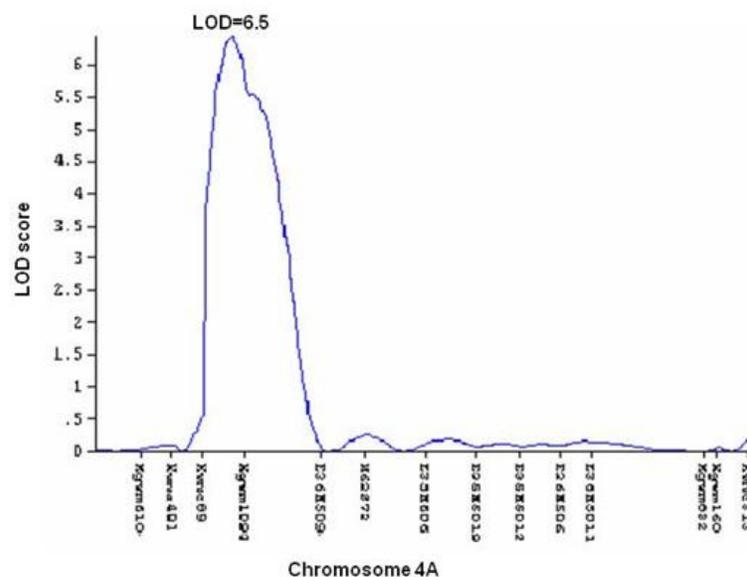


Figure 3. A QTL plot of a major QTL for root volume on wheat chromosome 4A obtained using inclusive composite interval mapping (ICIM). Marker designations are given on the x-axis. The LOD values are given on the y-axis.

O'Brian 1979, Manske and Vlek 2002, Richards and Passioura 1989, Nakmoto and Oyanagi 1994, Siddique et al., 1990, Sinclair and Mukhow 2001, Manchandi et al., 2006, Reynolds et al., 2007). Genotypic differences in root architecture traits and their functional implications for water uptake and increased yields under water-limited

environments have been reported in several crops including wheat (O'Toole and Bland 1987, Manschadi et al., 2008, Wasson et al., 2012). However, only a limited number of studies have been conducted for understanding the genetic control of root architecture traits in wheat; these studies mainly focused on seedling

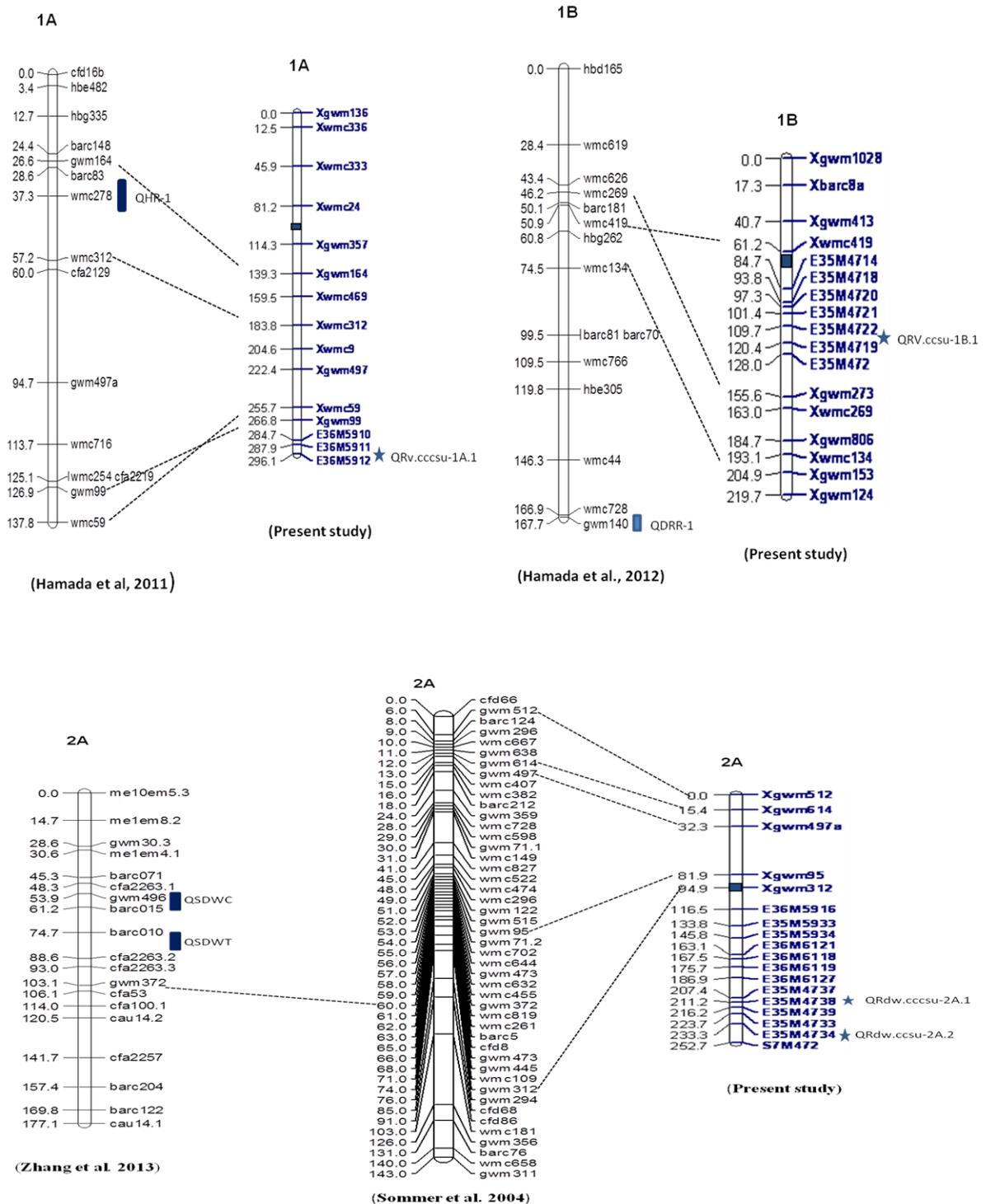


Figure 4. A comparison of the map positions of QTLs for root traits detected during the present study with the QTLs earlier reported on wheat chromosomes 1A (Hamada et al.2011) and 1B(Hamada et al.2012) and 2A (Zhang et al.2013).

root traits (Petrarulo et al. 2009, Zhuo-Kun et al.,2010, Hamada et al.,2012, Christopher et al. 2013, Zhang et

al.,2013). However, a lack of correlation between the root traits of the seedlings or young plants raised in controlled

conditions with root system traits of field grown plants is well known (McDonald et al., 2012, Atta et al., 2013). Therefore, the present study on root system traits carried out on mature wheat plants under conditions that mimic the field environment, makes it a unique study for QTL analysis with a potential of direct application of the important findings in wheat breeding.

In comparison to the two parental genotypes, large genetic variation was noticed among the RILs comprising the mapping population for all the four root traits, namely root length, root number, root volume and root dry weight. This suggested that RILs segregated for genes/QTLs for all the four root traits each showing high coefficient of variability (CV%) suggesting that the two parental genotypes differed for the QTLs controlling each of the four root traits studied during the present study. Further, all the four root traits of the RILs displayed normal distribution that was slightly skewed in case of root length and root dry weight (Figure 1). This suggested continuous quantitative nature of the traits and a high level of genetic variability in the RIL populations, which is in agreement with earlier studies (Hurd 1974, Petrarulo et al., 2009, Zhuo-Kun et al., 2010, Hamada et al., 2012, Christopher et al., 2013, Zhang et al., 2013). Transgressive segregation for all the four root traits suggested that the positive and negative alleles for each of the four traits are distributed in the two parental genotypes of the mapping population.

The QTL for a large number of seedling root traits have been reported on the all 21 chromosomes of wheat (Petrarulo et al., 2009, Zhuo-Kun et al., 2010, Hamada et al. 2012, Christopher et al. 2013, Zhang et al., 2013). The eight QTL reported on six different chromosomes (1A, 2A, 1B, 2B, 2D and 4A) during the present study (Table 3) differ from the QTLs for seedling root traits reported in earlier studies involving durum and bread wheat (Petrarulo et al., 2009, Zhuo-Kun et al., 2010, Hamada et al., 2012, Christopher et al., 2013, Zhang et al., 2013), although some of the seedling root traits like seminal root angle are treated as 'proxy' for root length of the mature wheat plants (for details see Wasson et al., 2012). Out of the eight QTLs that were identified during the present study, four QTLs were such, which were located on chromosomes 1A, 1B and 2A that are known to harbour QTLs for seedling root angle in response of hydrotropism, deep root ratio and seedling dry weight under controlled and treated conditions (Hamada et al. 2011, Zhang et al., 2013). These included two QTLs each for root volume (chromosomes 1A and 1B) and root dry weight (chromosome 2A). A comparison of the map positions of the above four QTLs for root volume and root dry weight with the map positions of QTLs for root angle in response of hydrotropism, deep root ratio and seedling dry weight under controlled and treated conditions reported earlier is shown in Figure 4. It is clear from the above comparison that the QTLs reported during the present study and those reported earlier by Hamada et al., (2011)

and Zhang et al., (2013) have different map positions and thus represent different sets of QTLs. The map positions of the remaining four QTLs also differed from those reported earlier (Petrarulo et al., 2009, Zhuo-Kun et al., 2010, Hamada et al., 2012, Christopher et al., 2013, Zhang et al., 2013), although a direct comparison like the above could not be made due lack of common markers between the maps prepared during the present study and those used for QTL analysis in earlier studies. The differences in the map positions of the QTL observed in different studies may be attributed to the study of different root traits at different development stages and also to the differences in the genetic make-up of the plant material used in different studies. Though the separate QTLs for individual traits indicated independent genetic control for each of the four traits. The high and significant positive correlations among the four root traits during the present study suggested causal relationship among the traits, which may be of significance for improvement of root architecture in wheat.

A major QTL for root volume (*QRv.ccsu-4A.1* with 30% PVC) that was detected on chromosome 4A (flanked by SSR markers *Xgwm89* and *Xgwm610*) is an important contribution of the present study. This QTL is apparently different from the QTLs for seedling root length and root dry weight earlier reported on chromosome 4A (Zhang et al., 2013), and the markers flanking this QTL may be used for indirect marker-assisted selection for improvement in root volume in wheat. The positive and highly significant correlation of the root volume with the remaining three root traits shall be helpful in improvement of these traits through positive indirect correlated response to the selection for high root volume. In the past, total root mass and root depth, respectively, were shown to be associated with carbon isotope discrimination ($\Delta^{13}\text{C}$) and canopy temperature depression (CTD) in wheat (Araus et al., 2003, Lopez and Reynolds 2010, Wasson et al., 2012). Therefore, $\Delta^{13}\text{C}$ and CTD may be tried as 'surrogates' for the study of genetic potential for efficient water-uptake under water-deficit environments with a view to improve grain yield of wheat under drought stress.

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