ISSN 1479-2621

Plant Genetic Resources: Characterization and Utilization (2020) **18**(3); 130–142
doi:10.1017/S1479262120000192

Dissection of quantitative trait loci for root characters and day length sensitivity in SynOpDH wheat (*Triticum aestivum* L.) bi-parental mapping population

Harun Bektas*†, Christopher Earl Hohn*‡ and John Giles Waines

Department of Botany and Plant Sciences, The University of California at Riverside, Riverside, CA 92521, USA

Received 25 February 2020; Accepted 8 July 2020 – First published online 3 August 2020

Abstract

The genetics of the root system is still not dissected for wheat and lack of knowledge prohibits the use of marker-assisted selection in breeding. To understand the genetic mechanism of root development, Synthetic W7984 × Opata M85 doubled-haploid (SynOpDH) mapping population was evaluated for root and shoot characteristics in PVC tubes until maturity. Two major quantitative trait loci (QTLs) for total root biomass were detected on homoeologous chromosomes 2A and 2D with logarithm of the odds scores between 6.25–10.9 and 11.8–20.86, and total phenotypic effects between 12.7–17.7 and 26.6–40.04% in 2013 and 2014, respectively. There was a strong correlation between days to anthesis and root and shoot biomass accumulation (0.50–0.81). The QTL for biomass traits on chromosome 2D co-locates with QTL for days to anthesis. The effect of extended vegetative growth, caused by photoperiod sensitivity (*Ppd*) genes, on biomass accumulation was always hypothesized, this is the first study to genetically support this theory.

Keywords: *Aegilops tauschii*, Ppd-D1, QTL, root biomass, SynOpDH, wheat

Introduction

Even though the root system is essential to plant growth, historically roots have not been studied in as much detail as the above-ground parts in plants. Currently, the necessity to study root systems is widely recognized (Lynch, 2007; Herder *et al*., 2010). Also, methodological progress in various fields has improved our ability to visualize, quantify and conceptualize root architecture along with its relationship to plant productivity (Kuijken *et al*., 2015; Wasaya *et al*., 2018). Knowledge of the genetic basis of root architectural and morphological traits in crop species is limited (Lynch and Brown, 2012; Jung and McCough, 2013). Thus, novel research is needed to address this gap (Manschadi *et al*., 2006). Dissection of root traits using quantitative trait locus (QTL) analyses may provide insight into the heritability of such traits and make a marker-assisted selection in plant breeding possible with new markers.

Here, the Synthetic W7984 × Opata M85 doubled haploid (SynOpDH) standard mapping population in bread wheat (*Triticum aestivum* L.) was selected due to its diverse genetic background (Sorrells *et al*., 2011). The original reference population of Synthetic W7984 × Opata M85 (ITMI) recombinant inbred lines (RILs) has been studied extensively for many traits including abiotic stress tolerance. Significant differences reported (Mujeeb-Kazi *et al*., 1996; Landjeva *et al*., 2008; Sorrells *et al*., 2011) for drought tolerance between the two parents and on the ITMI population encouraged us to identify genome regions that may be responsible for the differences in root system architecture and development.

Root systems of field crops have been studied since the pioneering work of Weaver and Bruner (1926) with many

*Corresponding author. E-mail: bektasharun@gmail.com
†Present Address: Department of Agricultural Biotechnology, Siirt University, Siirt 56100, Turkey.
‡ Present Address: KAYAgene LLC, Salinas, CA, USA.

root system traits being evaluated (Richards and Passioura, 1981, 1989; Sharma *et al*., 2011). More recently with the advantage of genetic mapping, several studies have been performed on QTL associated with root system traits. These studies were performed with many different screening methods to understand genetics, morphology and anatomy of the root system, including but not limited to gel observation chambers, clear pots, 2D and 3D imaging, soil columns, PVC tubes, field core samples and shovelomics (Weave and Bruner, 1926; Oyanagi, 1994; Bengough *et al*., 2004; Ehdaie and Waines, 2006; Trachsel *et al*., 2011; Topp *et al*., 2013; Richard *et al*., 2015). These studies derived important characteristics such as increased nodal root number, xylem vessel diameter, long root hairs, seedling root vigour, vigorous and deep root system, root weight, root length (RL) density, root angle and high hydraulic resistance (Richards and Passioura, 1981; Lynch, 2007).

Climate change and yield losses force plant breeders to redesign breeding schemes. Priorities are shifting to drought/heat tolerance, local adaptability and resource allocation (Lynch, 2007; Herder *et al*., 2010). Plants with deep and dense root systems, which have the potential for higher soil exploration to access stored water in deeper soil zones, have better stress tolerance under drought conditions (Passioura, 1983; Ehdaie *et al*., 2003; Manschadi *et al*., 2006; Bengough *et al*., 2011).

Here, we aimed to evaluate biomass allocation and phenology interactions. Our study aimed to dissect genotypic variation for root and shoot biomass (SM) allocation, grain yield (GY) and important phenological traits in the SynOpDH population under glasshouse conditions and to identify genome regions associated with these traits.

Materials and methods

Seed samples of a set of DH lines from the SynOpDH mapping population (*T. aestivum* L.) were provided by Dr Mark Sorrells, Department of Plant Breeding and Genetics, Cornell University, Ithaca, NY. This population consists of 215 DH lines generated from the F1 hybrid of Synthetic W7984 with cv. Opata M85. Synthetic W7984 is a man-made amphiploid derived from the durum wheat line, 'Altar 84' (*Triticum turgidum* subsp. *durum* (Desf.) Husn), crossed with the accession (219) 'CIGM86.940' of *Aegilops tauschii* Coss. (Nelson *et al*., 1995). From the entire set of DH lines in the SynOpDH population, 147 lines and parental lines were selected for the experiments – the same set of 147 lines genotyped by Poland *et al*. (2012).

Seeds of similar size were sterilized with 1% sodium hypochlorite solution, rinsed with distilled water before germination. According to vernalization data from Sorrells *et al*. (2011), lines with vernalization requirement were planted in flats with sand and vernalized for 10 weeks at 2–5°C. Other seeds without a vernalization requirement were germinated 5 d before transplanting into tubes. It was aimed to match average seedling sizes between vernalized and unvernalized seedlings. From the set of seedlings for each genotype, seedlings of similar size were transplanted into PVC tubes of 1 m long and 10 cm diameter filled with 10.5 kg #30-grade silica sand with a bulk density of 1.42 g ml^{-1} and 24% field capacity (w/w) in polyethylene tubular inner sleeves (Sharma *et al*., 2009) on 20 February 2013 and 15 January 2014. Sand-filled tubes were brought to the water holding capacity by generous watering for two consecutive days prior to planting. One seedling per PVC tube with three replications (randomized complete blocks design) in each season was tested. Plants were grown under natural photoperiod in a temperature-controlled glasshouse (20–30°C and 50–90% relative humidity). Plants in PVC tubes were irrigated daily with half-strength Hoagland's nutrient solution (1000 ppm) (Hoagland and Arnon, 1950), 100 ml in early growth periods and 250 ml in later periods to avoid drought stress. Two small holes were made at the bottom of each plastic bag for proper drainage.

After the plants were grown until maturity (GS92), spikes and shoots were harvested separately and dried in a hot air oven at 65°C for 72 h. The plastic sleeves were taken out of the PVC tubes and cut lengthwise. Roots were washed out of the sand carefully and their total length was measured. Deep roots and shallow roots were separated at 30 cm depth from the soil level according to previous observations and packed separately for air drying in the glasshouse followed by a hot air oven for 72h at 65°C. To evaluate phenological traits for each plant, days from transplanting into tubes to booting (DTB-GS41), to heading (DTH-GS51), to anthesis (DTA-GS61) and to maturity (DTM-GS92) were recorded (Zadoks *et al*., 1974), and plant height (PH), number of tillers (NT), number of fertile tillers (FT), number of spikes (NS), flag leaf length (FLL) and flag leaf width (FLW) were measured prior to harvest. Shoot biomass (SM), shallow root weight (SRW), deep root weight (DRW), total root biomass (RM), total plant biomass (PM), GY, 1000 grain weight (1000gW), harvest index 1 (HI1; GY divided by above-ground total biomass), harvest index 2 (HI2; GY divided by PM including roots), root/shoot (R/S) ratio and RL per plant were collected after harvest (Ehdaie *et al*., 2010; Gonzalez-Paleo and Ravetta, 2012).

Statistical analysis

Statistical analyses were performed using the Statistix software (Analytical Software; Tallahassee, FL, USA). The normality of data distribution was tested by Pearson

https://doi.org/10.1017/S1479262120000192 Published online by Cambridge University Press

probability plots. Analysis of variance (ANOVA) (Steel *et al.*, 1997) was performed to evaluate the main phenotypic effect of genotype, year and genotype × year interactions for all traits (online Supplementary Table S1). Genotypes were replicated three times each year and averages of three replicates were calculated in order to obtain means for each genotype in each year.

Heritability (H2) within and between years was calculated as H2 = VG/VP, where VG is the genetic variance and VP is the phenotypic variance, by using ANOVA function of the software package ICIMapping by composite interval mapping (Li *et al.*, 2008).

Significant main effects for genotype and the year were observed for all traits ($P < 0.01$), except for the FT. The magnitude of the genotype × year interaction was significant across all traits except DRW, PH, 1000gW and R/S ratio. Therefore, the data for experiments conducted in 2013 and 2014 were analysed separately and compared later for ratings of genotypes, histogram distributions and QTL validation.

Genetic mapping

The SynOpDH population is a standard population mapped multiple times. Two genotyping-by-sequencing (GBS) (Elshire *et al.*, 2011) based maps by Poland *et al.* (2012) and Saintenac *et al.* (2013) were used for linkage and QTL mapping. A total of 1485 GBS single nucleotide polymorphism (SNP) markers were placed in 21 linkage groups with a total of 3243.53 cM map length by using the marker data of Poland *et al.* (2012). Similarly, Saintenac *et al.* (2013) mapped 2740 gene associated SNP markers from the 9 K iSelect SNP assay (Cavanagh *et al.*, 2013). The genetic linkage map of Poland *et al.* (2012) was used for QTL mapping and marker data from Saintenac *et al.* (2013) were used to create a second linkage map for validation of *Ppd-D1* gene. The parental line Opata M85 is spring wheat with a day-length insensitivity allele (Ppd-D1a) and Synthetic W7984 carries a day-length sensitivity allele (Ppd-D1b) (http://www.wheatpedigree.net/sort/show/46697; Sorrells *et al.*, 2011).

Linkage mapping was done using the software package JoinMAP (Van Ooijen, 2006). The mean phenotypic value of three replications in each year was used to detect QTL by the software package ICIMapping by composite interval mapping (Li *et al.*, 2008). Logarithm of the odds (LOD) score of 3.45 was derived as a threshold based on Van Ooijen (1999). LOD score of 2.5 was also tested to catch more marker × trait associations. However, those associations were not called as QTL, unless the same loci were observed over 2 years with 2.5 or higher LOD score. Kosambi function and Maximum likelihood algorithm were used for mapping. QTL analysis was performed separately for each year and phenotypic means for each trait from the second year's data were used to validate the QTL found in the first year. Simple correlation analysis (Pearson) was performed to evaluate interactions between all traits separately for each year's mean data.

Results

Analysis of variance (ANOVA) was performed to determine the genotypic variation for each trait measured in the experiment. Histograms for all traits were prepared and most distributions were normal while some were skewed to right or left (online Supplementary Fig. S1). Parental lines Synthetic W7984 and Opata M85 were significantly different for RM, SRW, DRW, NS per plant, seed/spike (S/S), PH, RL and days to heading (DTH) in both years. Even though line distribution for both years was mostly similar, the mean values for synthetic and Opata M85 parental lines were contrasting for some traits over the years. We do not have a clear explanation for the contrasting values at this moment except it may be due to seasonal changes. There were no consistent differences between parents for SM, GY, FT, NT, days to booting (DTB), DTH, days to anthesis (DTA), 1000gW, HI1, HI2, R/S ratio and PM over 2 years. However, strong transgressive segregation and highly significant differences were observed within the progeny. For most traits, the range of variation among progeny was well outside of the range of parents (Table 1).

The mean values for biomass accumulated in 2014 were higher than in 2013. Mean values of RM ranged from 0.61 to 8.57 g per plant in 2013 and 1.59 to 13.1 g per plant in 2014, respectively. Means of SM ranged from 8.8 to 62.5 g per plant in 2013 and 25.7 to 98.8 g per plant in 2014, respectively. Shallow root weights ranged from 0.61 to 7.51 g in 2013 and from 1.59 to 11.57 g per plant in 2014. Means for DRW were between 0 and 2.10 g in 2013 and between 0 and 1.95 g per plant in 2014. The phenotypic range of PH was between 60.7 and 99 cm in 2013 and between 51.1 and 137.9 cm in 2014. Mean values for GY ranged from 1.6 to 23.4 g per plant in 2013 and 8.9 to 39.5 g per plant in 2014. The average DTA was 59 and 71.8 d for 2013 and 2014, respectively, while ranges for the same trait were between 40.3 and 103.7 d in 2013 and between 48.7 and 103 d in 2014 (Table 1).

Significant positive correlations were observed, when RM on one hand and SM, NT, RL, DTA and DRW on the other hand. Additionally, SM was positively correlated with GY, DRW, NT, RL and DTA. Grain yield was positively correlated with RL, whereas HI1 had a slightly negative correlation with RM, SRW and NT (Table 2).

Significant associations were detected over 15 linkage groups for 14 different traits based on QTL analysis. Even though 41 marker × trait associations in 2013 and 27 in

https://doi.org/10.1017/S1479262120000192 Published online by Cambridge University Press

Table 1. Mean phenotypic values for parents and 147 progeny of the SynOpDH bread wheat population; minimum and maximum values and standard deviations, *F* test and *P* values for RM, SRW, DRW, SM, GY, number of seeds (NSd), S/S, FT, NT, PH, RL, DTB, DTH, DTA, 1000 gW, HI1, HI2 (GY/PM), R/S ratio and PM in 1 m tubes under well-watered conditions

2013								
Trait	Synthetic W7984	Opata M85	Progeny lines-range	Progeny lines-mean	St. Dev.	*F* test	*P* values	H2
RM*	2.597	3.297	0.610–8.573	3.474	1.78	4.72	0.000	0.71
SRW*	2.843	4.227	0.610–7.517	2.944	1.45	5.42	0.000	0.76
DRW*	0.280	0.583	0.000–2.107	0.530	0.52	2.00	0.000	0.41
SM	23.910	24.620	8.817–62.530	33.483	13.41	9.49	0.000	0.82
GY	6.797	6.103	1.627–23.483	10.729	5.89	6.24	0.000	0.77
NS*	185.333	127.333	42.000–704.333	268.701	164.68	8.25	0.000	0.86
S/S*	20.577	11.356	3.817–46.939	19.178	10.16	6.72	0.000	0.83
FT	11.000	11.333	6.000–23.667	14.101	4.32	4.47	0.000	0.76
NT	12.333	11.333	6.000–29.333	14.726	4.74	4.57	0.000	0.76
PH*	65.000	87.000	60.667–99.000	79.024	8.46	4.61	0.000	0.77
RL*	62.667	94.667	28.333–105.000	81.394	22.26	2.28	0.000	0.54
DTB	90.000	34.000	27.333–90.000	46.941	15.40	30.38	0.000	0.95
DTH	97.000	42.667	35.000–97.000	52.553	14.70	3.17	0.000	0.67
DTA	103.667	46.333	40.300–103.667	58.993	14.69	27.75	0.000	0.94
1000 gW	35.720	48.172	0.000–58.636	40.180	8.31	1.02	0.448	0.00
HI1	0.298	0.254	0.054–0.498	0.325	0.12	3.26	0.000	0.67
HI2	0.263	0.213	0.047–0.456	0.291	0.11	3.91	0.000	0.74
R/S	0.109	0.134	0.025–0.359	0.117	4.67	1.00	0.498	0.00
PM	27.033	29.430	10.127–66.847	36.958	14.56	9.70	0.000	0.83
Trait				2014.				
RM*	5.160	4.893	1.597–13.127	5.435	3.06	5.09	0.000	0.78
SRW*	4.867	3.940	1.597–11.977	4.663	2.64	5.11	0.000	0.76
DRW*	0.293	0.953	0.000–1.983	0.773	0.71	2.74	0.000	0.31
SM	63.437	51.257	25.757–98.847	59.507	19.14	4.01	0.000	0.78
GY	20.013	29.090	8.963–39.527	24.667	8.76	1.99	0.000	0.60
NS*	579.000	762.667	159.660–922.666	540.158	196.83	3.34	0.000	0.72
S/S*	42.062	44.806	10.718–84.320	40.531	18.12	2.15	0.000	0.59
FT	14.667	17.000	7.666–21.666	14.127	3.93	4.55	0.000	0.57
NT	18.667	17.667	8.333–27.333	16.322	4.91	4.91	0.000	0.64
PH*	74.333	53.933	51.100–137.900	76.0337	17.63	3.28	0.000	0.40
RL*	56.667	73.000	27.000–100.000	78.794	25.07	4.01	0.000	0.67
DTB	68.333	48.000	35.333–90.000	58.803	15.42	16.58	0.000	0.95
DTH	75.333	56.000	42.000–96.667	65.849	14.98	6.17	0.000	0.95
DTA	82.000	61.333	48.667–103.000	71.809	15.38	14.23	0.000	0.93
1000gW	37.825	38.009	31.645–93.573	46.305	9.30	1.26	0.029	0.52
HI1	0.323	0.571	0.144–0.629	0.4232	0.10	3.02	0.000	0.72
HI2	0.298	0.521	0.127–0.584	0.3905	0.10	3.20	0.000	0.73
R/S	0.0813	0.0954	0.0407–0.165	0.0910	0.034	0.97	0.568	0.58
PM	68.597	56.150	1.597–13.127	64.942	21.51	4.27	0.000	0.94

H2: broad sense heritability. *$p < 0.05$.

https://doi.org/10.1017/S1479262120000192 Published online by Cambridge University Press

Table 2. Overall means for each line from 2013 and 2014 were used separately for Pearson correlation analysis

2013	RM	SRW	DRW	SM	GY	FT	NT	PH	RL	DTA
RM	1.0000									
P value	0.0000									
SRW	0.9695	1.0000								
	0.0000	0.0000								
DRW	0.7198	0.5275	1.0000							
	0.0000	0.0000	0.0000							
SM	0.6376	0.5934	0.5288	1.0000						
	0.0000	0.0000	0.0000	0.0000						
GY	0.1788	0.1768	0.1189	0.7511	1.0000					
	0.0291	0.0310	0.1487	0.0000	0.0000					
FT	0.4138	0.3919	0.3241	0.6145	0.4099	1.0000				
	0.0000	0.0000	0.0001	0.0000	0.0000	0.0000				
NT	0.5426	0.5184	0.4121	0.6038	0.2928	0.9467	1.0000			
	0.0000	0.0000	0.0000	0.0000	0.0003	0.0000	0.0000			
PH	0.1772	0.1815	0.1002	0.3141	0.2231	−0.0263	−0.0371	1.0000		
	0.0306	0.0268	0.2242	0.0001	0.0062	0.7505	0.6537	0.0000		
RL	0.4818	0.4193	0.4819	0.6036	0.4139	0.4570	0.4390	0.1039	1.0000	
	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.2073	0.0000	
DTA	0.5513	0.5749	0.2824	0.7290	0.4240	0.3650	0.4264	0.2689	0.3064	1.0000
	0.0000	0.0000	0.0005	0.0000	0.0000	0.0000	0.0000	0.0009	0.0001	0.0000
HI1	−0.2915	−0.3317	−0.0711	0.0605	0.5858	−0.0861	−0.1953	−0.0133	−0.0226	−0.2511
	0.0003	0.0000	0.3891	0.4638	0.0000	0.2967	0.0170	0.8724	0.7844	0.0020
2014	RM	SRM	DRM	SM	GY	FT	NT	PH	RL	DTA
RM	1.0000									
P value	0.0000									
SRW	0.9911	1.0000								
	0.0000	0.0000								
DRW	0.7969	0.7092	1.0000							
	0.0000	0.0000	0.0000							
SM	0.8163	0.8041	0.6724	1.0000						
	0.0000	0.0000	0.0000	0.0000						
GY	0.2780	0.2674	0.2576	0.6718	1.0000					
	0.0006	0.0010	0.0015	0.0000	0.0000					
FT	0.1430	0.1286	0.1721	0.2886	0.3375	1.0000				

	0.0819	0.1180	0.0358	0.0004	0.0000	0.0000							
NT	0.4136	0.4068	0.3428	0.4755	0.2318	0.7405	1.0000						
	0.0000	0.0000	0.0000	0.0000	0.0044	0.0000	0.0000						
PH	0.3964	0.3939	0.3114	0.5560	0.2996	−0.0217	0.1136	1.0000					
	0.0000	0.0000	0.0001	0.0000	0.0002	0.7931	0.1679	0.0000					
RL	0.5089	0.4460	0.6695	0.5823	0.5059	0.2462	0.3045	0.2942	1.0000				
	0.0000	0.0000	0.0000	0.0000	0.0000	0.0025	0.0002	0.0003	0.0000				
DTA	0.8431	0.8589	0.5660	0.7908	0.2477	0.0480	0.3445	0.5284	0.2689	1.0000			
	0.0000	0.0000	0.0000	0.0000	0.0023	0.5609	0.0000	0.0000	0.0009	0.0000			
HI1	−0. 6673	−0.6661	−0.5103	−0.4360	0.3495	−0.0088	−0.3057	−0.3627	−0.0975	−0.6741			
	0.0000	0.0000	0.0000	0.0000	0.0000	0.9154	0.0001	0.0000	0.2368	0.0000			

P values are given below each correlation.

2014 were detected, only 14 of those were validated in the second year (Table 3).

The same segment on chromosome 2A was associated with biomass (DRW, SRW, RM and SM) and phenology (DTA) related traits (Fig. 1a). An apparently homoeologous locus on chromosome 2D was associated with biomass traits (DRW, SRW, RM and SM), phenology (DTA), and other traits (RL, FLW and GY) in both years (Fig. 1b). A locus on chromosome 4D affected FT and was detected in both years (Fig. 1-c). The region on chromosome 2D is in the general area of the Ppd-D1 locus on chromosome 2D, affecting day length sensitivity (Fig. 2). Genetic locations of peak points for the QTL for DTA and biomass related traits (SM, RM, DRW and SRW) were within 1 cM distance on chromosome 2D. Additional minor marker × trait associations are listed in online Supplementary Table S3. But they were not called as QTL due to low LOD scores and/or only seen at 1 year.

Discussion

A wheat root ideotype may have deep and dense seminal roots in order to capture water for high plant water status, narrow xylem vessel diameters (or thinner roots) for high hydraulic resistance, long root hairs and extensive lateral root development for maximum nutrient acquisition (Passioura, 1983). These features would increase the plant's chances of surviving an entire season with minimum stress limitations. Therefore, screening germplasm accessions for variation in root architecture is necessary to identify and perhaps breed wheat lines with some of the above-mentioned root characters.

Any given study evaluating crops in controlled conditions needs field trials as a validation. However, field evaluation of mapping populations for mature root characteristics in a replicated trial is still not feasible. Also, phenotypic data gained from field evaluations have lower resolution than controlled experiments given the current technical limitations on root studies. Therefore, experiments were conducted in a glasshouse in PVC tubes. Evaluation of 147 progeny is not an optimal number (>500 is suggested), due to the possibility of the Beavis effect (Beavis, 1994); thus, the results obtained in this study need further validation with larger population sizes.

The present study aimed to dissect QTL affecting the below-ground traits of bread wheat at maturity in a standard mapping population and to look for the associations of these traits with the above-ground characteristics and phenological traits. Root studies on mature plants are limited and this study aimed to add some steps to understanding mature wheat root architecture and its genetic background. The below-ground traits or the root system architecture can be measured/expressed in a number of

https://doi.org/10.1017/S1479262120000192 Published online by Cambridge University Press

Table 3. QTL associated with GY, SM, RM, SRW, DRW, FT, PH, RL, DTA and FLW in the SynOpDH population

Trait	Year	Chromosome	Position (cM)	Left marker	Right marker	LOD[a]	PVE (%)[b]	Additive[c]
GY	2013	2D	66.230	SynopGBS579	SynopGBS1212	8.3815	22.7431	2.4269
	2014		69.230	SynopGBS1310	SynopGBS745	7.6586	19.2896	3.0240
SM	2013	2A	44.000	SynopGBS374	SynopGBS262	11.8271	15.9259	−4.8331
	2014		43.000	SynopGBS374	SynopGBS262	10.5461	12.6847	−6.0381
	2013	2D	68.230	SynopGBS579	SynopGBS1212	28.7604	49.7337	8.5153
	2014		68.230	SynopGBS579	SynopGBS1212	29.5029	47.0760	11.6047
RM	2013	2A	42.000	SynopGBS1017	SynopGBS374	6.2478	12.7480	−0.5337
	2014		42.000	SynopGBS1017	SynopGBS374	10.9396	17.7488	−1.1143
	2013	2D	68.230	SynopGBS579	SynopGBS1212	11.8589	26.6052	0.7685
	2014		68.230	SynopGBS579	SynopGBS1212	20.8598	40.0480	1.6684
SRW	2013	2A	41.000	SynopGBS1017	SynopGBS374	6.6197	12.6267	−0.4415
	2014		42.000	SynopGBS1017	SynopGBS374	11.4227	18.3967	−0.9861
	2013	2D	68.230	SynopGBS579	SynopGBS1212	12.0590	24.7044	0.6161
	2014		68.230	SynopGBS579	SynopGBS1212	21.0773	40.0207	1.4497
DRW[d]	2013	2A	46.000	SynopGBS374	SynopGBS262	3.1739	7.2611	−0.0994
	2014		43.000	SynopGBS374	SynopGBS262	2.9768	6.8181	−0.1250
	2013	2D	62.230	SynopGBS579	SynopGBS1212	6.7513	17.0202	0.1518
	2014		69.230	SynopGBS1310	SynopGBS745	7.7114	17.9760	0.2025
FT	2013	4D	0.000	SynopGBS838	SynopGBS570	4.3443	8.5731	−1.0700
	2014		0.000	SynopGBS838	SynopGBS570	3.4662	8.4491	−0.8708
RL	2013	2D	68.230	SynopGBS579	SynopGBS1212	7.6124	16.6847	6.6057
	2014		63.230	SynopGBS579	SynopGBS1212	5.3770	14.0827	7.3716
DTA	2013	2A	33.000	SynopGBS855	SynopGBS1016	13.5656	18.1694	−5.9840
	2014		41.000	SynopGBS1017	SynopGBS374	19.9053	27.2447	−7.7978
	2013	2D	67.230	SynopGBS579	SynopGBS1212	25.7259	40.4835	8.9389
	2014		68.230	SynopGBS579	SynopGBS1212	27.8183	42.9904	9.7529
FLW	2013	2D	71.230	SynopGBS745	SynopGBS250	7.3270	16.4576	0.0817
	2014		69.230	SynopGBS1310	SynopGBS745	13.3987	29.3358	0.1702

Plants were grown in 1 m PVC tubes under well-watered conditions until maturity for two seasons. Peak positions (cM) with the highest LOD score, left and right markers, the LOD scores, percent phenotypic effects and additive effects.
[a]LOD score of 3.45 was used for the declaration of QTL.
[b]Phenotypic variation explained by QTL.
[c]Additive effect of QTL.
[d]LOD threshold value of 2.5 was used for the QTL declaration.

ways. Perhaps the most accurate, but technically the most challenging, would be to count the numbers of nodal and/or seminal roots to determine their weights and lengths individually, and as classes. Such approaches are common at the seedling stage. However, at maturity, the root system of wheat is very dense, and it would be extremely difficult to separate individual roots, or even classes of roots. For this reason, in this study, the RM and the weights of deep and shallow roots were measured.

The SynOpDH population was selected for its unique characteristics. Even if the parent's Synthetic W7984 and Opata M85 did not differ for some of the traits, the wide genetic background of the population almost guarantees segregation in the progeny. Additionally, the grandparent, accession (219) 'CIGM86.940' of *A. tauschii* was specifically selected for genetic improvement in bread wheat by Mujeeb-Kazi *et al.* (1996).

Phenotypic differences between parents are not a prerequisite for segregation in the progeny. As we observed here, both parents are spring type, but there are more than 30 lines that segregate for vernalization genes in the progeny (Sorrells *et al.*, 2011). And this vernalization process added more complications to the experimental system. Since the study was planned to run until maturity, we had to

https://doi.org/10.1017/S1479262120000192 Published online by Cambridge University Press

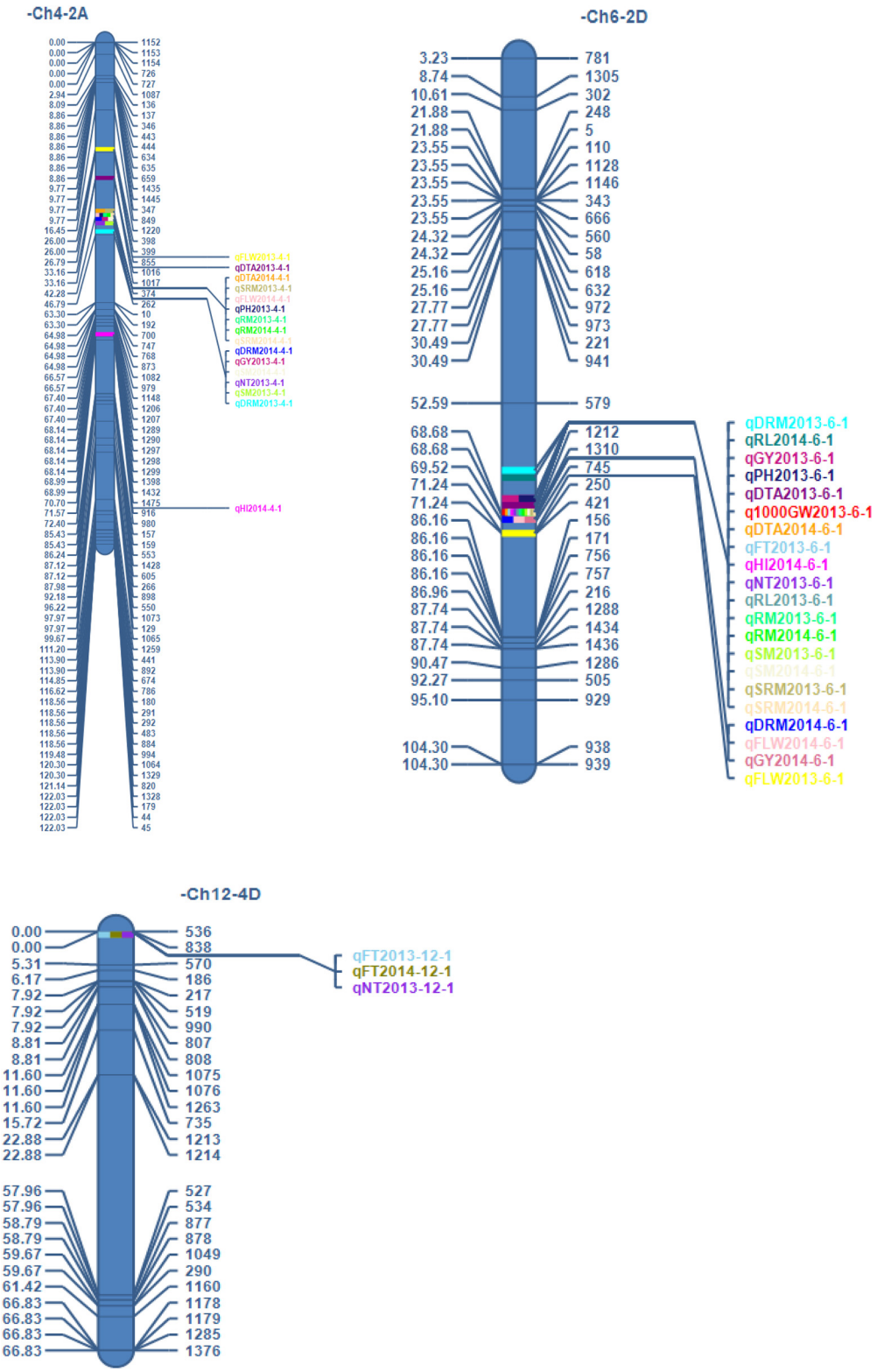

Fig. 1. Ch4-2A: location of QTL on bread wheat chromosomes 2A for DRM/DRW, SRM/SRW, RM, SM and DTA with the linkage map from Poland *et al*. (2012). Ch6-2D: location of QTL on bread wheat chromosomes 2D for DRM/DRW, SRM/SRW, RM, SM, DTA, RL, FLW and GY with the linkage map from Poland *et al*. (2012). Ch12-4D: location of QTL on bread wheat chromosomes 4D for the FT with the linkage map from Poland *et al*. (2012). Marker names, marker positions and LOD scores are presented on the linkage map. The loci that only found 1 year, are not called as QTL.

https://doi.org/10.1017/S1479262120000192 Published online by Cambridge University Press

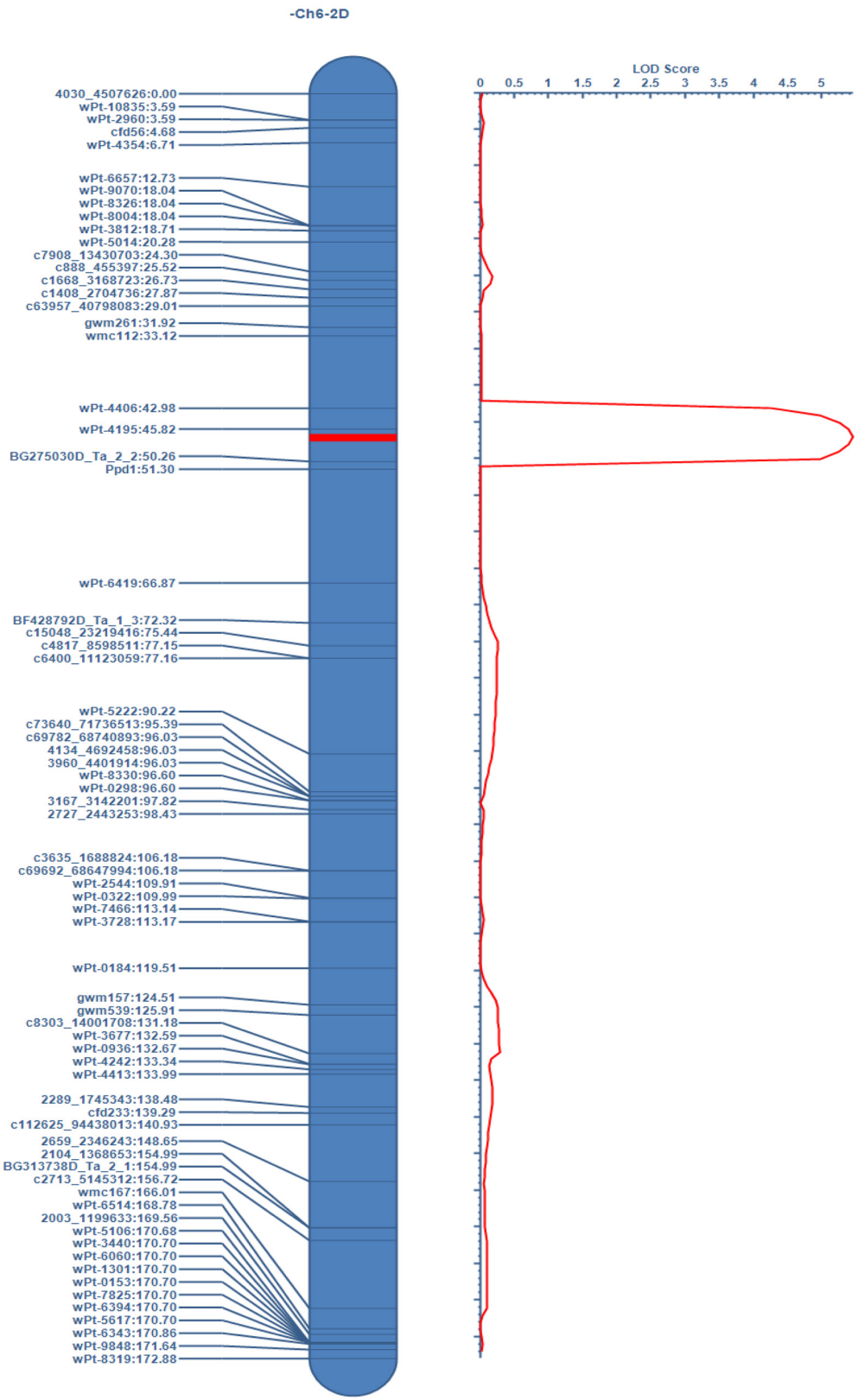

Fig. 2. High-resolution linkage map from Saintenac *et al*. (2013) for the QTLs listed in Figure S2b (RM, SM, SRW, DRW) on chromosome 2D of bread wheat. Marker names, locations and LOD scores are presented on the linkage map. An additional marker between the peak point of the QTL and the *Ppd-D1* gene is located.

https://doi.org/10.1017/S1479262120000192 Published online by Cambridge University Press

vernalize some lines but not others. We do not know if vernalization itself, and all the manual handling associated with it, has any impact on root characteristics, but we are unable to design and execute an experiment to test it. When QTL analysis was performed with and without the vernalized lines, the same QTLs were found and LOD scores were similar (Table 3 and online Supplementary Table S2). So, vernalization did not have any significant effect on QTL detection. Nevertheless, all the above factors and the unique genetic structure made SynOpDH population a well-defined set of lines for our study of the root system and phenological traits for QTL mapping.

Phenotypic values for most above and below ground traits were in a significant positive correlation with DTA. The two loci on homoeologous group 2 chromosomes were responsible for 6.81–7.26% (2A) and 17.02–17.97% (2D) of the phenotypic variation for DRW in 2013 and 2014, respectively. This effect was statistically significant given that the trait is multigenic. There are no previous reports of QTLs for DRW at maturity, shared results between our study and previous studies. Many environmental factors affect the growth rate of above-ground plant parts, and it would be unreasonable to assume they do not affect root development, especially when the root system is capable of plastic responses to environmental cues. Therefore, the results collected at the seedling stage, in experiments of short duration, may not follow the same trends in the later stages of development. There is still no clear picture of the entire lifecycle of the root system and factors affecting it. However, to understand the progress root development we need to evaluate it at every stage and up to maturity. We do know that during the grain filling period major changes take place in a wheat plant with regard to resource allocation and remobilization, and it is sensible to assume that this also involves the root system (Radville *et al*., 2016; Hu *et al*., 2018). In this sense, our measurements were taken at maturity to complement the picture created at the seedling stage. However, the same SynOpDH population now must be studied at earlier stages of development to establish any correlations between seedlings and mature plant root systems.

One major effect of QTL on chromosome 2D was responsible for 24.7 and 40.02% of the phenotypic variation of the SRW in 2013 and 2014, respectively. The same locus on 2D co-located with DRW and RM as well as SM (Fig. 1b). These results indicate that lines with larger RM had well-distributed DRW and SRW through the soil profile. We are not aware of any report of SRW QTL at maturity except our previous publication with a different RIL (Iran #49 × Yecora Rojo) population (Ehdaie *et al*., 2016). We identified a locus on chromosome 2D affecting RM and SRW in that study. Shallow root weight becomes important in certain nutrient deficiencies since the number of nodal roots increases total soil volume exploration. Long nodal roots and root hairs are indicators of a large shallow root system. Shallow root weight can be used as an easy-to-measure parameter to detect genotypic variation in germplasm to prevent nutrient deficiencies. Breeding extensively shallow-rooted cultivars for nutrient-deficient conditions and better uptake of non-mobile nutrients may help save yield losses (Lynch, 2013; York *et al*., 2013). A wheat ideotype with narrow root diameters, long-haired and wide-angled roots for better nutrient uptake is suggested (Lynch, 2013). Therefore, knowing the limitations of target regions is important to make the right decisions in breeding targets. Breeders need to choose either a relatively large shallow root system to prevent nutrient deficiencies or a deep and dense root system to prevent water stress/drought (Asseng *et al*., 1998). A major part of the carbon consumed by the root system goes to nodal root development. It is suggested that reduced shallow-nodal root size and increased deep-seminal root size may reduce the carbon cost of roots and increase GY significantly (Watt *et al*., 2013). This approach may be applicable in high-fertilizer input conditions or soils without any mineral deficiency.

Two QTLs on chromosomes 2A and 2D explained 12.75–17.75% (2A) and 26.60–40.04% (2D) of the total phenotypic variation for RM in 2013 and 2014, respectively (Table 3). Our findings were in agreement with Bai *et al*. (2013) and Ehdaie *et al*. (2016) who reported QTL affecting seminal root biomass on chromosome 2D, and Sanguineti *et al*. (2007) who reported a QTL on chromosome 2A. Other studies reported RM (root dry weight) QTL mostly for the seedling stage (Sanguineti *et al*., 2007; Sharma *et al*., 2011; Bai *et al*., 2013; Zhang *et al*., 2014). Plants with deep and dense root systems, which have the potential to access water stored in deeper soil zones, have better stress tolerance and less nitrogen leaching (Passioura, 1983; Ehdaie *et al*., 2003; Bengough *et al*., 2011). Two of the major characteristics of green revolution wheat were day length insensitivity and semi-dwarfing. This provided a wide adaptation of cultivars to diverse environments. Our study implies that the two characteristics might have also had an indirect effect on root vigour. First, semi-dwarfing genes reduced PH and tillering in order to increase GY and HI, but also limited the carbon allocated to the above and/or below ground biomass accumulation. Second, day length insensitivity reduced the stay green period of plants by allowing intermediate and spring types to grow in any part of the world with a shorter vegetative period, allowing less time for root and shoot growth. Even though these efforts helped to increase GY and HI under optimum growth conditions, reduced carbon flow to roots and shoots reduced total biomass thus resulting in shallow, small rooted cultivars with limited drought tolerance.

The locus on chromosome 2D for root characteristics was located near the known major locus for the photoperiod sensitive response, Ppd-D1b on chromosome 2D

https://doi.org/10.1017/S1479262120000192 Published online by Cambridge University Press

(Fig. 2). The question asked here is: are the changes observed in root characteristics a pleiotropic effect of the photoperiod response or are there a separate locus/loci controlling root characters in the vicinity of Ppd-D1 locus? To get more marker density in this region, a different linkage map with a marker for the Ppd-D1 locus was used (Saintenac *et al.*, 2013). In the new map, there was one additional marker between the *Ppd-D1* gene and the most likely location of the root biomass QTL. Moreover, with the new map, the linkage block was 9 cM instead of 16 cM of the previous linkage map. On the new linkage map, the *Ppd* gene is located just outside of the linkage block (Fig. 2). As a result, the location of QTL was more accurate with the new map. Genetic maps with much higher resolution and larger populations are needed to fine map the QTL and to validate its phenotypic effect. There may be an interaction between *Ppd* genes and root biomass but to evaluate it properly, sets of isogenic lines, developed specifically for this purpose, are needed.

Day length sensitivity genes (*Ppd*) have a major effect on plant phenology. Here, we observed a significant effect of the Ppd-D1b allele. Opata M85 is spring wheat with day-length insensitivity allele Ppd-D1a, while Synthetic W7984 carries Ppd-D1b (http://www.wheatpedigree.net/sort/show/46697; Sorrells *et al.*, 2011). The Ppd-D1b allele of Synthetic W7984 causes day length sensitivity (longer vegetative growth), while the Ppd-D1a allele from the Opata M85 is day length insensitive.

We located the same locus on chromosome 2D with a 16.68 and 14.08% phenotypic effect on RL in 2013 and 2014, respectively. We did not find any previous study reporting QTL for RL on 2D, not surprisingly given that most previous studies reported RL at the seedling stage. However, three other associated regions that we located in only one year were on chromosomes 3B, 2D and 7D and they were in agreement with Li *et al.* (2011), Liu *et al.* (2013) and Bai *et al.* (2013). Since we found the effects of the above loci only in one year with relatively low LOD scores, we are not including them as validated QTL (online Supplementary Table S3). However, these marker × trait associations are worth further evaluation.

SM was also associated with the same loci on 2A with 12.68–15.92%, and on 2D with 47.07–49.73% total phenotypic effects in 2013 and 2014, respectively. Li *et al.* (2010) reported QTL for SM on 2D and 5D. Other SM QTL were reported for seedling on chromosomes 1D, 2A, 2B, 4A, 4B, 5D, 6B, 6D (Zhang *et al.*, 2014), 4D, 5A (Bai *et al.*, 2013) and 1B (Sanguineti *et al.*, 2007; Petrarulo *et al.*, 2015). SM is an important parameter of vigorous growth habit. The extensive shoot development of some cultivars is of significant interest for farmers of remote regions, due to straw being used as animal feed (Morgounov *et al.*, 2016).

A major QTL on chromosome 2D was responsible for 22.7 and 19.2% of the phenotypic variation in GY in 2013 and 2014, respectively. Additionally, GY and most biomass traits were positively correlated (0.27–0.83). The vigorous growth of the above and/or below ground biomass seems associated with increased GY, at least in the conditions of our experiments. As previously reported by Worland (1996) an allele of the *Ppd* gene may affect the vegetative period by 4–8 d, and the 63 and 54 d of the range observed on phenology suggests multiple allelic variabilities (Ppd-A1, B1 and D1 alleles). The extended vegetative growth allows more carbon allocation for stem elongation and deep rooting (Worland, 1996).

Conclusions

In the present study, we evaluated root and SM traits as well as GY-related traits at maturity for SynOpDH doubled haploid mapping population. Two major QTLs were detected on chromosomes 2A and 2D explaining major phenotypic variation for root and SM traits as well as GY. These QTLs were closely located with the day length sensitivity alleles of the *Ppd-D1* gene.

The QTL reported here require further validation. Finding QTL that increases root biomass, root density and RL may provide useful candidate lines for marker-assisted breeding. Targeting root ideotypes including deep rooting for water deficit conditions and a large shallow root system for nutrient deficiencies, which are needed for changing environmental conditions, may be feasible and easier with the benefit of marker-assisted selection.

Supplementary material

The supplementary material for this article can be found at https://doi.org/10.1017/S1479262120000192.

Acknowledgements

The authors are grateful to Dr Adam J. Lukaszewski, University of California, Riverside for discussions and critical edits on manuscript preparation. This work was supported by the University of California, Riverside, Botanic Gardens, The California Agricultural Experiment Station and a doctoral fellowship of the Turkish Republic Ministry of National Education to Harun Bektas.

References

Asseng S, Ritchie JT, Smucker AJM and Robertson MJ (1998) Root growth and water uptake during water deficit and recovering in wheat. *Plant and Soil* 201: 265–273.

Bai C, Liang Y and Hawkesford MJ (2013) Identification of QTLs associated with seedling root traits and their correlation with plant height in wheat. *Journal of Experimental Botany* 64: 1745–1753.

Beavis WD (1994) The power and deceit of QTL experiments: lessons from comparative QTL studies. In Proceedings of the

49th Annual Corn & Sorghum Industry Research Conference. American Seed Trade Association, Washington, DC, pp. 250–266.

Bengough AG, Gordon DC, Al-Menaie H, Ellis RP, Allan D, Keith R, Thomas WT and Forster BP (2004) Gel observation chamber for rapid screening of root traits in cereal seedlings. *Plant and Soil* 262: 63–70.

Bengough AG, McKenzie BM, Hallett PD and Valentine TA (2011) Root elongation, water stress, and mechanical impedance: a review of limiting stresses and beneficial root tip traits. *Journal of Experimental Botany* 62: 59–68.

Cavanagh CR, Chao S, Wang S, Huang BE, Stephen S, Kiani S, Forrest K, Saintenac C, Brown-Guedira GL, Akhunova A and See D (2013) Genome-wide comparative diversity uncovers multiple targets of selection for improvement in hexaploid wheat landraces and cultivars. *Proceedings of the National Academy of Sciences* 110: 8057–8062.

Ehdaie B and Waines JG (2006) Determination of a chromosome segment influencing rooting ability in wheat-rye 1BS-1RS recombinant lines. *Journal of Genetics & Breeding* 60: 71–76.

Ehdaie B, Whitkus RW and Waines JG (2003) Root biomass, water-use efficiency, and performance of wheat–rye translocations of chromosomes 1 and 2 in spring bread wheat 'Pavon'. *Crop Science* 43: 710–717.

Ehdaie B, Merhaut DJ, Ahmadian S, Hoops AC, Khuong T, Layne AP and Waines JG (2010) Root system size influences water-nutrient uptake and nitrate leaching potential in wheat. *Journal of Agronomy and Crop Science* 196: 455–466.

Ehdaie B, Mohammadi S, Nouraein M, Bektas H and Waines J (2016) Erratum to: QTLs for root traits at mid-tillering and for root and shoot traits at maturity in a RIL population of spring bread wheat grown under well-watered conditions. *Euphytica* 211: 17–39.

Elshire RJ, Glaubitz JC, Sun Q, Poland JA, Kawamoto K, Buckler ES and Mitchell SE (2011) A robust, simple genotyping-by-sequencing (GBS) approach for high diversity species. *PLoS ONE* 6: e19379.

Gonzalez-Paleo L and Ravetta DA (2012) Allocation patterns and phenology in wild and selected accessions of annual and perennial Physaria (*Lesquerella*. Brassicaceae). *Euphytica* 186: 289–302.

Herder GD, Van Isterdael G, Beeckman T and De Smet I (2010) The roots of a new green revolution. *Trends in Plant Science* 15: 600–607.

Hoagland DR and Arnon DI (1950) The water-culture method for growing plants without soil. Circular. California Agricultural Experiment Station, 347(2nd edit).

Hu T, Sørensen P, Wahlström EM, Chirinda N, Sharif B, Li X and Olesen JE (2018) Root biomass in cereals, catch crops and weeds can be reliably estimated without considering aboveground biomass. *Agriculture Ecosystems & Environment* 251: 141–148.

Jung JKH and McCouch S (2013) Getting to the roots of it: genetic and hormonal control of root architecture. *Frontiers in Plant Science* 4: 186.

Kuijken RCP, van Eeuwijk FA, Marcelis LFM and Bouwmeester HJ (2015) Root phenotyping: from component trait in the lab to breeding. *Journal of Experimental Botany* 66: 5389–5401.

Landjeva S, Neumann K, Lohwasser U and Börner A (2008) Molecular mapping of genomic regions associated with wheat seedling growth under osmotic stress. *Biologia Plantarum* 52: 259–266.

Li H, Ribaut JM, Li Z and Wang J (2008) Inclusive composite interval mapping (ICIM) for digenic epistasis of quantitative traits in biparental populations. *Theoretical and Applied Genetics* 116: 243–260.

Li Z, Peng T, Xie Q, Han S and Tian J (2010) Mapping of QTL for tiller number at different stages of growth in wheat using double haploid and immortalized F_2 populations. *Journal of Genetics* 89: 409.

Li P, Chen J, Wu P, Zhang J, Chu C, See D, Brown-Guedira G, Zemetra R and Souza E (2011) Quantitative trait loci analysis for the effect of Rht-B1 dwarfing gene on coleoptile length and seedling root length and number of bread wheat. *Crop Science* 51: 2561–2568.

Liu X, Li R, Chang X and Jing R (2013) Mapping QTLs for seedling root traits in a doubled haploid wheat population under different water regimes. *Euphytica* 189: 51–66.

Lynch JP (2007) Roots of the second green revolution. *Australian Journal of Botany* 55: 493–512. http://dx.doi:10.1071/bt06118.

Lynch JP (2013) Steep, cheap and deep: an ideotype to optimize water and N acquisition by maize root systems. *Annals of Botany* 112: 347–357.

Lynch JP and Brown KM (2012) New roots for agriculture: exploiting the root phenome. *Philosophical Transactions of the Royal Society B-Biological Sciences* 367: 1598–1604, doi: 10.1098/rstb.2011.0243.

Manschadi AM, Christopher J, de Voil P and Hammer GL (2006) The role of root architectural traits in adaptation of wheat to water-limited environments. *Functional Plant Biology* 33: 823–837.

Morgounov A, Keser M, Kan M, Küçükçongar M, Özdemir F, Gummadov N, Muminjanov H, Zuev E and Qualset CO (2016) Wheat landraces currently grown in Turkey: distribution, diversity, and use. *Crop Science* 56: 3112–3124.

Mujeeb-Kazi A, Rosas V and Roldan S (1996) Conservation of the genetic variation of *Triticum tauschii* (Coss.) Schmalh. (*Aegilops squarrosa* auct. non L.) in synthetic hexaploid wheats (*T. turgidum* L. s. lat. × *T. tauschii*; $2n = 6 \times = 42$, AABBDD) and its potential utilization for wheat improvement. *Genetic Resources and Crop Evolution* 43: 129–134.

Nelson JC, Deynze AE, Sorrells ME, Autrique E, Lu YH, Negre S, Bernard M and Leroy P (1995) Molecular mapping of wheat. homoeologous group 3. *Genome* 38: 525–533.

Oyanagi A (1994) Gravitropic response growth angle and vertical distribution of roots of wheat (*Triticum aestivum* L.). *Plant and Soil* 165: 323–326.

Passioura JB (1983) Roots and drought resistance. In *Developments in Agricultural and Managed Forest Ecology,* vol. 12, Elsevier, pp. 265–280. https://doi.org/10.1016/B978-0-444-42214-9.50025-9.

Petrarulo M, Marone D, Ferragonio P, Cattivelli L, Rubiales D, De Vita P and Mastrangelo AM (2015) Genetic analysis of root morphological traits in wheat. *Molecular Genetics and Genomics* 290: 785–806.

Poland JA, Brown PJ, Sorrells ME and Jannink JL (2012) Development of high-density genetic maps for barley and wheat using a novel two-enzyme genotyping-by-sequencing approach. *PLoS ONE* 7: e32253.

Radville L, McCormack ML, Post E and Eissenstat DM (2016) Root phenology in a changing climate. *Journal of Experimental Botany* 67: 3617–3628.

Richard CA, Hickey LT, Fletcher S, Jennings R, Chenu K and Christopher JT (2015) High-throughput phenotyping of seminal root traits in wheat. *Plant Methods* 11: 13.

Richards RA and Passioura JB (1981) Seminal root morphology and water use of wheat II. genetic variation 1. *Crop Science* 21: 253–255.

Richards RA and Passioura JB (1989) A breeding program to reduce the diameter of the major xylem vessel in the seminal roots of wheat and its effect on grain yield in rain-fed environments. *Australian Journal of Agricultural Research* 40: 943–950.

Saintenac C, Jiang D, Wang S and Akhunov E (2013) Sequence-based mapping of the polyploid wheat genome. *G3: Genes, Genomes, Genetics* 3: 1105–1114.

Sanguineti MC, Li S, Maccaferri M, Corneti S, Rotondo F, Chiari T and Tuberosa R (2007) Genetic dissection of seminal root architecture in elite durum wheat germplasm. *Annals of Applied Biology* 151: 291–305.

Sharma S, Bhat PR, Ehdaie B, Close J, Lukaszewski AJ and Waines JG (2009) Integrated genetic map and genetic analysis of a region associated with root traits on the short arm of rye chromosome 1 in bread wheat. *Theoretical and Applied Genetics* 119: 783–793.

Sharma S, Xu S, Ehdaie B, Hoops A, Close TJ, Lukaszewski AJ and Waines JG (2011) Dissection of QTL effects for root traits using a chromosome arm-specific mapping population in bread wheat. *Theoretical and Applied Genetics* 122: 759–769.

Sorrells ME, Gustafson JP, Somers D, Chao S, Benscher D, Guedira-Brown G, Huttner E, Kilian A, McGuire PE, Ross K and Tanaka J (2011) Reconstruction of the Synthetic W7984 × Opata M85 wheat reference population. *Genome* 54: 875–882.

Steel RGD, Torrie JH and Dickey DA (1997) *Principles and Procedures of Statistics: A Biometrical Approach*. New York: McGraw-Hill.

Topp CN, Iyer-Pascuzzi AS, Anderson JT, Lee CR, Zurek PR, Symonova O, Zheng Y, Bucksch A, Mileyko Y, Galkovskyi T and Moore BT (2013) 3D Phenotyping and quantitative trait locus mapping identify core regions of the rice genome controlling root architecture. *Proceedings of the National Academy of Sciences* 110: E1695–E1704.

Trachsel S, Kaeppler SM, Brown KM and Lynch JP (2011) Shovelomics: high throughput phenotyping of maize (*Zea mays* L.) root architecture in the field. *Plant and Soil* 341: 75–87.

Van Ooijen JW (1999) LOD Significance thresholds for QTL analysis in experimental populations of diploid species. *Heredity* 83: 613–624.

Van Ooijen JW (2006) JoinMap® 4, Software for the calculation of genetic linkage maps in experimental populations. Kyazma BV, Wageningen, 33(10.1371).

Wasaya A, Zhang X, Fang Q and Yan Z (2018) Root phenotyping for drought tolerance: a review. *Agronomy* 8: 241.

Watt M, Wasson A, Chochois V, Eshel A and Beeckman T (2013) Root-based solutions to increasing crop productivity. In: Eshel A and Beeckman T (eds) *Plant Roots: The Hidden Half*. New York, NY: CRC Press, pp. 21–21.

Weaver JE and Bruner WE (1926). *Root Development of Field Crops*. New York: McGraw-Hill.

Worland AJ (1996) The influence of flowering time genes on environmental adaptability in European wheats. *Euphytica* 89: 49–57.

York LM, Nord EA and Lynch JP (2013) Integration of root phenes for soil resource acquisition. *Frontiers in Plant Science* 4: 355. doi: 10.3389/fpls.2013.00355.

Zadoks JC, Chang TT and Konzak CF (1974) A decimal code for the growth stages of cereals. *Weed Research* 14: 415–421.

Zhang H, Cui F and Wang H (2014) Detection of quantitative trait loci (QTLs) for seedling traits and drought tolerance in wheat using three related recombinant inbred line (RIL) populations. *Euphytica* 196: 313–330.