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Genome-Wide Linkage Mapping of Quantitative Trait Loci for Late-Season Physiological and Agronomic Traits in Spring Wheat under Irrigated Conditions

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Abstract: Many late-season physiological traits affect grain yield in wheat, either directly or indirectly. However, information on the genetic control of yield-related traits is still limited. In this study, we aimed to identify quantitative trait loci (QTL) for canopy temperature and chlorophyll content index during anthesis (CTa and CCIa, respectively), the mid grain-filling stage (CTg1 and CCIg1, respectively), and the late grain-filling stage (CTg2 and CCIg2, respectively) as well as for plant height (PH), thousand kernels weight (TKW), and grain yield (GY) using genome-wide linkage mapping. To this end, a double haploid population derived from a cross between two high yielding wheat cultivars, UI Platinum and SY Capstone, was phenotyped in four irrigated environments and genotyped using the wheat 90K iSelect platform and simple sequence repeats. The genotypic data were used to construct a high-density genetic map of 43 linkage groups (LGs) with a total length of 3594.0 cm and a marker density of 0.37 cm. A total of 116 QTL for all nine traits was detected on 33 LGs, spreading to all wheat chromosomes, except for Chr. 7D. Of these, six QTL (*CTa.ui-4B.1*, *Q.CTg1.ui-5B-2.1*, *Q.CTg2.ui-6B.1*, *Q.PH.ui-6A-2.1*, *Q.TKW.ui-2D-1*, and *Q.GY.ui-6B*) were consistently detected in more than three irrigated environments, called as stable QTL. Additionally, we identified 26 QTL clusters for more than two traits, of which the top four were located on Chromosomes 4A-1, 1B-1, 5B-2, and 2D-1. Overall, the stable QTL significantly related with grain yield, QTL clusters, and linked molecular markers identified in this study, may be useful in marker-assisted selection in early generation and early growth stage for grain yield improvement.

Keywords: linkage mapping; QTL; 90K SNP; canopy temperature; chlorophyll content index; plant height; grain yield

1. Introduction

Wheat (*Triticum aestivum* L.) is one of the most important food crops worldwide [1] since it is a valuable source of carbohydrates and protein suitable for human consumption [2]. However, wheat production is negatively affected by the gradual reduction of arable land area due to climate change as well as biotic and abiotic stresses [3–6]. Therefore, further improvement in grain yield (GY) is necessary to meet the current and future demand.

Canopy temperature (CT) or CT depression and chlorophyll content index (CCI) or SPAD value of leaf chlorophyll content are important physiological traits significantly associated with GY in wheat [7–11]. CT is considered an indicator of the transpiration level, whereas the chlorophyll content of flag leaf is

used for the indirect estimation of photosynthesis capacity [12]. A high chlorophyll content in the flag leaf during post-anthesis positively affects yield stability by extending photosynthesis under a wide range of conditions [13]. Agronomic traits, such as plant height (PH) and thousand kernels weight (TKW), are also closely related to GY [8,11]. Therefore, it would be useful to elucidate the genetic control of late-season physiological traits that are closely related to GY in order to further improve wheat yield.

Molecular techniques have accelerated progress in plant breeding programs [14]. Of these, quantitative trait locus (QTL) mapping that is carried out to detect potential chromosome regions associated with important traits using molecular markers [15] has been proved to be an effective way to understand the genetic architecture of physiological and yield-related traits in crops [16]. In wheat, QTL mapping has been extensively conducted for PH, TKW, and GY [1,9,11,17–24] as well as for CT (or CT depression) and CCI (or SPAD), since these two traits are significantly correlated with GY and its components [9–11]. Some QTL for CT (or CT depression) and CCI (or SPAD) have been identified during anthesis or at 10 d (days) post-anthesis using different mapping populations and considered as potential tools for improving wheat yield under different stress environments [7,9–11,21,25–27]. QTL for CT during the vegetative and grain-filling stages have been identified on Chromosomes (Chr.) 1B, 2B, 3B, and 7A across different environments, whereas one QTL for CT during the vegetative stage has been identified on Chr. 4A [28]. Previous study reported QTL for CT during the vegetative (25 d after emergence) and grain-filling stages on Chr. 3A, 3BS, 3BL, 5B, and 7A under irrigated, heat, and drought conditions [21]. QTL for CT depression during anthesis have been mapped on Chr. 2AL, 3BL, 4BS, 5BS, and 6BL, whereas QTL for CT depression at 10 d post-anthesis on Chr. 4AS, 4BS, and 5BS [10]. QTL for SPAD at 0 d, 7 d, and 14 d post-anthesis have been detected on Chr. 1A, 1B, 1D, 2B, 3B, 4D, 6B, and 7B under unstressed conditions [29]; on Chr. 1A, 2B, 3A, 4A, 4D, 5B, and 6A at 0 d, 7 d, and 14 d post-anthesis under high-light stress conditions [7]; on Chr. 3D and 7A at the seeding stage under salt stress conditions [26]; on Chr. 7A during anthesis under different nitrogen and water conditions [25]; and on Chr. 1B and on 1A, 1D, 3A, 3B, and 5A under heat and drought conditions [28]. Previous study reported QTL for SPAD during anthesis on Chr. 2AS, 2AL (2), 2DS, 2DL, 3AS, 4AL, 4DS, 5AS, and 5AL, and at 10 d post-anthesis on Chr. 2AL (2), 2BS, 2D, 5AL, 5BL, 6AS, and 7A [11].

However, only a few QTL for CT and CCI have been reported during the late growth stages under irrigated conditions. Additionally, most studies used a limited number of markers and resulted in QTL with relatively large genetic distances, which are not appropriate for marker-assisted selection (MAS). The high-density single nucleotide polymorphism (SNP) technology is an efficient tool for QTL detection, since it allows the construction of high-density linkage maps [30,31]. SNP makers are co-dominant, abundant, and evenly distributed along the genome [32,33]. In wheat, the 9 K and 90 K iSelect SNP arrays have been successfully applied for the QTL mapping of yield and yield-related traits [10,11,23,31,34,35].

Here, we aimed to identify QTL for CT and CCI during anthesis, the early grain-filling stage, and the middle grain-filling stage as well as for PH, TKW, and GY in a double haploid (DH) population that phenotyped under irrigated conditions and genotyped using genome-wide high-density SNP markers combined with simple sequence repeats (SSRs).

2. Materials and Methods

2.1. Plant Materials and Field Experiments

In this study, we used a mapping population, consisting of 110 doubled haploid (DH) lines that derived from a cross between two spring wheat cultivars, UI Platinum and SY Capstone. The former cultivar (PI 672533) was developed by the Idaho Agricultural Experimental Station and released in 2014 [36], whereas the latter was developed by Syngenta Cereals and released in 2011 [37]. The DH lines were created from F_1 under service from Heartland Plant Innovation using wheat by maize hybridization [38].

Four trials were performed in Aberdeen, Idaho, USA (42.96° N, 112.83° W; elevation 1342 m) in the 2014/2015 and 2015/2016 cropping seasons under irrigated conditions (AB15E1, AB15E2, AB15E3, and AB16E4). A detailed description of all environments is provided in Table 1. The precipitation of four trails during the growing season was 217.4 mm, 217.4 mm, 217.4 mm, and 249.0 mm, respectively,

and irrigation was applied from May to July with a total amount of 362.7 mm, 373.4 mm, 384.0 mm and 453.4 mm, respectively, making total moisture 580.1 mm, 590.8 mm, 601.4 mm and 702.4 mm, using aluminum sprinkler pipes. In AB15E1, and AB15E2, 120 entries were arranged in an augmented design. 120 replicated DH lines were assigned at random to four blocks, while two parents as checks were replicated, being randomly assigned to plots within each of the four blocks, therefore, each sub-block comprised 28 un-replicated DH lines and the two cultivar checks. In AB15E3 and AB16E4, the DH and parental lines were arranged in a randomized complete block design with two replications. Each plot included seven rows (3.0 m in length, 1.5 m in width, 0.25 m in row spacing). The sowing density was 0.48 million seeds per ha at each trial. Fertilization and weeding were applied, when necessary, to achieve the optimal cultivation conditions. A wheat border was planted to minimize the edge effect in each trial.

Table 1. Rainfall and irrigation (mm) during the two wheat-growing seasons for the 4 trials.

Trials	Sowing Date	September–March	April		May		June		July		August		Total
		R	R	IRR	R	IRR	R	IRR	R	IRR	R	IRR	
15ABE1	20 March 2015	92.4	2.5	42.7	83.6	53.3	19.8	181.4	19.1	85.3	-	/	580.1
15ABE2	26 March 2015	92.4	2.5	42.7	83.6	53.3	19.8	181.4	19.1	96.0	-	/	590.8
15ABE3	1 April 2015	92.4	2.5	42.7	83.6	53.3	19.8	192.0	19.1	96.0	-	/	601.4
16ABE4	8 April 2016	165.4	43.2	/	36.8	74.7	0.8	218.7	2.8	160.0	0	/	702.4

15ABE1, 15ABE2, 15ABE3: trial 1, 2 and 3 in Aberdeen in 2015, respectively; 16ABE4, trial 4 in Aberdeen in 2016; R, rainfall; IRR, irrigation water; -, not included; /, no irrigation.

2.2. Phenotypic Evaluation

CT, CCI, PH, TKW, and GY were recorded in all four environments in two seasons (AB15E1, AB15E2, AB15E3, and AB16E4). CT (°C) was measured using an infrared thermometer (IRtec MicroRay HVAC; Langhorne, PA) from noon to 2:00 PM on clear and non-windy days. The CCI of flag leaves was measured from five randomly selected fertile plants using a portable chlorophyll content meter (CCM-200; Opti-Sciences, Hudson, NH, USA). CT and CCI were measured during anthesis (Feekes 10.5.2; CTa and CCIa, respectively), the mid grain-filling stage (Feekes 11.1; CTg1 and CCIg1, respectively), and the late grain-filling stages (Feekes 11.2; CTg2 and CCIg2, respectively) using the Feekes growth scale [39].

PH (cm) was measured from the soil surface to the tip of the spike (awns excluded) at the maturity stage (Feekes 11.3–11.4) [39]. Plots were harvested by a Wintersteiger Classic small plot combine (Wintersteiger; Salt Lake City, UT, USA) equipped with a Harvest Master weighing system (Juniper Systems; Logan, UT, USA). After harvest, GY was determined as grain weight extrapolated at the 12% moisture content and expressed in t ha^{-1}. TKW (g) was recorded using the single-kernel characteristics system (SKCS 4100; Perten Instruments, Springfield, IL, USA).

2.3. Phenotypic Data Analysis

Phenotypic data analysis, including mean, genotype variance (δ_g^2), error variance (δ_e^2), correlation analysis between parameters, and broad-sense heritability (H_B^2), was conducted using JMP 8.0 (SAS Institute, Cary, NC, USA). The adjusted means of each trait measured in AB15E1 and AB15E2 were estimated for block differences which were measured by the cultivar checks [40]. The analysis of variance was performed with PROC GLM, in which genotypes were treated as fixed effects and environments and the interaction of genotypes and environments and blocks nested in environments were all treated as random effects [40]. The inverse of the variance of the individual environments were treated as weights. H_B^2 was estimated in all environments as follows:

$$H_B^2 = \sigma_g^2 / \left(\sigma_g^2 + \sigma_{ge}^2 / r + \sigma_\varepsilon^2 / er \right),$$

where δ_g^2 is the genetic variance, σ_{ge}^2 is the genetic × environment interaction variance, δ_ε^2 is the error variance, r is the replicates per environment, and e is the number of environments.

2.4. SNP Genotyping and Molecular Marker Analysis

Total genomic DNA was extracted from young leaves of the DH and parental lines using the method as described by [41]. DNA concentration was estimated using a Nanodrop ND-1000 Spectrophotometer (Nanodrop; Wilmington, DE, USA) and then, adjusted to 80 ng μL^{-1} for SNP assays and molecular marker analysis.

The DH and parental lines were genotyped at the USDA-ARS Small Grains Genotyping Laboratory, Fargo, ND, USA, using the Illumina 90 K iSelect SNP array [31]. Genotype calling and SNP clustering were conducted using GenomeStudio 2011 with the polyploid clustering V1-0 (Illumina, San Diego, CA, USA). SNP names were designated as "IWB" followed by an index number.

A total of 300 SSRs was selected for genotyping the parental lines as described by [42]. Molecular markers for dwarfing genes (*Rht-B1b* and *Rht-D1b*) were used for confirming the association with PH [43,44].

2.5. Linkage Map Construction and QTL Analysis

SNP markers were filtered for monomorphism, high frequency of missing values (≥10%), or segregation distortion (≥0.35). The genetic linkage map was constructed using JMP Genomics 8.0 (SAS Institute) as described by [45] and [46]. The initial number of linkage groups (LGs) was identified using interactive hierarchical clustering and K-means clustering (automated radius K-means) by reducing the number of markers in the recombination and LG function. Markers were ordered on each LG using the Kosambi mapping function and the accelerated map order optimization algorithm in the linkage map order function. LGs were split when the genetic distance between adjacent markers was higher than 35 cm by default.

QTL analysis was performed for each trait within and across four environments by composite interval mapping (CIM) using JMP Genomics 8.0 [46]. CIM was used to find QTL with an expectation maximization (EM) algorithm threshold of 2.5. Genetic distance between markers was calculated in cm. The contribution of SY and UI toward higher trait values was indicated by positive and negative signs of the estimates for additive QTL effects, respectively. The proportion of phenotypic variation (R^2) for each QTL was determined by the square of the partial correlation coefficient.

The final map was constructed using the linkage map viewer function of JMP Genomics, and LGs were assigned to chromosomes based on the 90 K consensus map as described by [31]. Each linkage map was named according to the wheat chromosome followed by a number. A QTL was characterized as stable when it was identified in at least three or four environments.

3. Results

3.1. Phenotypic Evaluation

The analysis of variance showed that the effect of genotype was significant for all traits across environments, except for CTa and CTg1(across 15ABE3 and 16ABE4) ($p < 0.05$), whereas the effect of environment and that of genotype by environment were significant for CTa, CTg2, CCIa, CCIg2 and GY across 15ABE1 and 15ABE2 as well as CCIg2, TKW and GY across 15ABE3 and 16ABE4 ($p < 0.05$) (Table 2). The phenotypic performance of DH and parental lines indicated that UI and SY were significantly different for CCI and TKW in all the environments (Table S1); UI had markedly higher TKW, whereas SY had higher CCIa, CCIg1, and CCIg2. The mean for most traits of DH lines was near to the mid-parental value. The range of variation for each trait of DH lines showed transgressive segregation in both directions across the environments, demonstrating that positive alleles were present from both parental lines. All traits showed continuous frequency distribution within and across the environments, indicating that they were under polygenic control (Figure S1). The $H_B{}^2$ was the highest for TKW (0.81 across 15ABE1 and 15ABE2, 0.72 across 15ABE3 and 16ABE4) and PH (0.77 across 15ABE1 and 15ABE2, 0.75 across 15ABE3 and 16ABE4), indicating that both traits were stable and mainly affected by the genotype, whereas the $H_B{}^2$ was the lowest for CTa, CTg1, and CTg2, suggesting that they were greatly affected by the environment.

Table 2. Analysis of variance (ANOVA) and broad-sense heritability ($H_B{}^2$) for the traits measured in four environments (110 doubled haploid (DH) lines and two cultivar checks in 15ABE1 and 15ABE2, two replications in 15ABE3 and 16ABE4).

SV	DF	MS		Across 15ABE1 and 15ABE2		DF	MS		Across 15ABE3 and 16ABE4	
		15ABE1	15ABE2	DF	MS		15ABE3	16ABE4	DF	MS
CTa										
Block/Replication	3	0.08	0.36				0.79	163.57 ****		
Genotype (G)	111	2.07 *	0.52	111	1.54 ***		0.46	1.12	109	0.91
Environment (E)				1	4.46 **				1	4531.88 ****
G × E				111	1.31 **				109	0.67
Error	3	0.09	0.51	12	0.26		0.56	1.27	220	1.65
$H_B{}^2$					0.52					0.38
CTg1										
Block/Replication	3	1.98 *	0.20				6.56 ****	79.32 ****		
Genotype (G)	111	1.89 *	0.15	111	1.84 *		0.60	2.51	109	1.70
Environment (E)				1	1.16				1	0.57
G × E				111	1.98 *				109	1.41
Error	3	0.15	0.06	12	0.60		0.50	2.38	220	1.81
$H_B{}^2$					0.45					0.42
CTg2										
Block/Replication	3	4.58	0.01				0.08	57.53 ****		
Genotype (G)	111	7.13	0.21	111	6.56 **		0.44	1.76 *	109	1.32 *
Environment (E)				1	967.59 ****				1	23.60 ****
G × E				111	6.14 **				109	0.89
Error	3	1.21	0.09	12	1.47		0.36	1.16	220	1.01
$H_B{}^2$					0.49					0.49
CCIa										
Block/Replication	3	5.31 *	1.92				6.19	78.00 *		
Genotype (G)	111	30.45 **	19.18 *	111	27.36 ****		18.16 **	28.15 ***	109	32.93 ****
Environment (E)				1	340.08 ****				1	2.11
G × E				111	23.74 ****				109	13.38
Error	3	0.43	1.05	12	2.18		11.52	14.89	220	13.47
$H_B{}^2$					0.52					0.62
CCIg1										
Block/Replication	3	8.44	2.81				2.86	61.16		
Genotype (G)	111	36.31	26.20	111	38.21 ***		37.24 *	41.32 ****	109	56.37 ****

Table 2. Cont.

SV	DF	MS		Across 15ABE1 and 15ABE2		DF	MS		Across 15ABE3 and 16ABE4	
		15ABE1	15ABE2	DF	MS		15ABE3	16ABE4	DF	MS
Environment (E)				1	16.47				1	1600.20 ****
G × E				111	25.31 **				109	22.19
Error	3	10.34	4.40	12	6.50		24.65	17.07	220	20.96
H_B^2					0.57					0.63
CCIg2										
Block/Replication	3	3.79	6.41				22.66	54.80		
Genotype (G)	111	27.06	23.56	111	31.39 **		25.43 ***	39.86 ****	109	45.84 ****
Environment (E)				1	127.22 ***				1	453.71 ****
G × E				111	20.42 *				109	19.46 *
Error	3	12.25	4.69	12	6.79		13.72	16.05	220	15.10
H_B^2					0.57					0.63
PH										
Block/Replication	3	1.38	2.61				708.13 ****	3.07		
Genotype (G)	111	22.31	27.57	111	43.20 ***		42.56 ****	55.95 ****	109	81.12 ****
Environment (E)				1	0.02				1	6763.57 ****
G × E				111	9.51				109	17.39
Error	3	18.38	4.65	12	6.75		16.30	14.94	220	18.71
H_B^2					0.77					0.75
TKW										
Block/Replication	3	4.07	2.11				47.48 **	38.89 *		
Genotype (G)	111	13.74	9.87	111	21.21 ***		18.79 ****	19.60 ****	109	29.85 ****
Environment (E)				1	7.44				1	2480.45 ****
G × E				111	3.05				109	8.53 *
Error	3	5.64	3.28	12	3.78		4.97	6.23	220	5.95
H_B^2					0.81					0.72
GY										
Block/Replication	3	0.20	0.13				5.06 ****	1.80		
Genotype (G)	111	0.40	0.53	111	0.71 **		0.72 ****	1.59 ****	109	1.67 ****
Environment (E)				1	66.28 ****				1	6.16 ***
G × E				111	0.32 *				109	0.64 **
Error	3	0.11	0.08	12	0.13		0.26	0.55	220	0.43
H_B^2					0.65					0.66

15ABE1, 15ABE2, 15ABE3: trial 1, 2 and 3 in Aberdeen in 2015, respectively; 16ABE4, trial 4 in Aberdeen in 2016; SV, Source of variation; DF, degree of freedom; MS, Mean square, CTa, CTg1, CTg2, canopy temperature during anthesis, mid- and late grain-filling stage, respectively; CCIa, CCIg1, CCIg2, chlorophyll content index during anthesis, mid- and late grain-filling stage, respectively; PH, plant height; TKW, thousand kernels weight; GY, grain yield; **, $p < 0.01$; **, $p < 0.01$; ***, $p < 0.001$; ****, $p < 0.0001$.

3.2. Correlation between Traits

Pearson's correlation between traits was analyzed across environments (Table 3). CTa, CTg1, and CTg2 were significantly negatively correlated with GY (r = −0.72–−0.89, $p < 0.0001$), whereas CCIa, PH, and TKW were significantly positively correlated with GY (r = 0.45–0.87, $p < 0.001$). CTa, CTg1, and CTg2 were significantly negatively correlated with CCIa, PH, and TKW (r = −0.30–−0.77, $p < 0.01$), whereas CCIa was significantly positively correlated with PH and TKW (r = 0.33–0.37, $p < 0.0001$). PH was significantly positively correlated with TKW (r = 0.71, $p < 0.0001$). Significant positive correlations were also found between CTa, CTg1, and CTg2 (r = 0.50–0.83, $p < 0.0001$) as well as between CCIa, CCIg1, and CCIg2 (r = 0.33–0.65, $p < 0.0001$).

Table 3. Pearson's correlations between phenotypic traits measured in DH population from UI Platinum/SY Capstone over four environments.

	CTa	CTg1	CTg2	CCIa	CCIg1	CCIg2	PH	TKW
CTg1	0.50 ****							
CTg2	0.61 ****	0.83 ****						
CCIa	−0.30 **	−0.34 **	−0.44 ****					
CCIg1	0.24 *	0.11	0.08	0.33 ****				
CCIg2	0.02	−0.05	−0.13	0.60 ****	0.65 ****			
PH	−0.77 ****	−0.60 ****	−0.71 ****	0.37 ****	−0.11 *	0.09		
TKW	−0.71 ****	−0.55 ****	−0.62 ****	0.33 ****	−0.12 *	0.05	0.71 ****	
GY	−0.72 ****	−0.72 ****	−0.89 ****	0.45 ****	−0.06	0.14 **	0.87 ****	0.71 ****

CTa, CTg1, CTg2, canopy temperature during anthesis, mid- and late grain-filling stage, respectively; CCIa, CCIg1, CCIg2, chlorophyll content index during anthesis, mid- and late grain-filling stage, respectively; PH, plant height; TKW, thousand kernels weight; GY, grain yield; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$; ****, $p < 0.0001$.

3.3. Marker Analysis and Construction of LGs

Of 81,587 SNPs on the 90 K iSelect SNP array and 300 selected SSRs, only 9687 SNP marker and 44 SSRs were polymorphic between the parental lines and used for the construction of the linkage map. Both parental lines carried *Ppd-D1a* and *Rht-D1b*, but not *Rht-B1b*.

We identified 43 LGs that represented all the 21 chromosomes of wheat (Table S2). Chr. 1A, 5A, 4B, 6B, and 7B were represented by one LG each; Chr. 2A, 4A, 6A, 1B, 3B, 5B, 1D, 2D, 3D, 4D, and 7D by two LGs each; Chr. 3A, 7A, 5D, and 6D by three LGs each; and Chr. 2B by four LGs (Table S2). The linkage map had a total length of 3633.19 cm, whereas each LG had an average length of 173.01 cm, ranging from 54.61 cm (Chr. 1D) to 261.51 cm (Chr. 5A). The average number of markers on each chromosome was 463.5, ranging from 15 on Chr. 3D to 1125 on Chr. 6A. Although markers on Chr. 1D, 3D, 4D, and 7D were low in number, they had a good distribution. The average marker density was 0.37 cm, ranging from 0.19 (Chr. 6A) to 5.56 (Chr. 3D). The map of A genome included 4320 markers (44.4%) and had a total length of 1420.51 cm with an average marker density of 0.33 cm; the map of B genome included 4367 markers (44.9%) and had a total length of 1571.15 cm with an average marker density of 0.36 cm; and the map of D genome included 1046 markers (10.7%) and had a total length of 641.53 cm with an average marker density of 0.61cm. The D genome had the lowest marker coverage, suggesting that more markers were polymorphic in the A and B genomes. Of 9687 SNPs, only 357 were newly mapped (Table S3).

3.4. QTL Detection for Physiological and Agronomic Traits

After further optimization, 1002 SNP makers and 30 SSRs were used for QTL detection. We identified 116 QTL for all traits within and across environments; 71 QTL for CT and CCI, and 45 QTL for PH, TKW, and GY (Tables 4 and 5 and Table S4; Figure 1).

Table 4. Quantitative trait locus (QTL) detected for canopy temperature in the DH population of UI Platinum/SY Capstone.

Traits	Trial	QTL [a]	Peak Marker	LG	Position [b]	Marker Interval	LOD [c]	Add [d]	R^2 [e]
CTa	15ABE1	Q.CTa.ui-2A-2	IWB21598	2A-2	11.05	IWB3678–IWB21598	2.5	0.30	9.8
		Q.CTa.ui-6B	IWB10604	6B	3.64	IWB75959–IWB10604	5.8	−0.48	21.6
	15ABE2	Q.CTa.ui-2B-2.1	IWB21394	2B-2	8.2	IWB21394–IWB67534	5.5	0.77	20.4

Table 4. *Cont.*

Traits	Trial	QTL [a]	Peak Marker	LG	Position [b]	Marker Interval	LOD [c]	Add [d]	R^2 [e]
		Q.CTa.ui-2B-2.2	IWB594	2B-2	44.63	IWB11092–IWB594	2.5	−0.51	10.0
		Q.CTa.ui-2B-3	IWB35482	2B-3	63.36	IWB35482–IWB74377	2.7	0.40	10.3
		Q.CTa.ui-4B.1	*IWB10190*	*4B*	*29.65*	*IWB20226–IWB57507*	*4.0*	*−0.48*	*15.5*
		Q.CTa.ui-5B-2	IWB626	5B-2	42.9	IWB36579–IWB18101	5.8	−0.62	21.7
	15ABE3	Q.CTa.ui-2B-3	IWB35482	2B-3	55.36	IWB35482–IWB74377	3.0	0.29	11.6
		Q.CTa.ui-4B.1	*IWB10190*	*4B*	*29.65*	*IWB20226–IWB57507*	*3.3*	*−0.44*	*12.8*
	16ABE4	Q.CTa.ui-3B-1	IWB10973	3B-1	82.18	IWB21837–IWB10973	2.6	0.62	10.4
		Q.CTa.ui-4B.1	*IWB10190*	*4B*	*29.65*	*IWB20226–IWB57507*	*2.6*	*−0.41*	*11.2*
		Q.CTa.ui-4B.2	IWB59992	4B	84.48	IWB27326–IWB21502	2.8	−0.64	11.0
	Average [f]	Q.CTa.ui-1A	IWB36144	1A	66.72	IWB21167–IWB36144	2.5	0.23	10.1
		Q.CTa.ui-4B.1	*IWB10190*	*4B*	*29.65*	*IWB20226–IWB57507*	*3.8*	*−0.47*	*14.6*
CTg1	15ABE1	Q.CTg1.ui-5A.2	IWB65470	5A	14.26	IWB65470–IWB13571	3.4	−1.47	13.3
		Q.CTg1.ui-3D-1	IWB63148	3D-1	45.53	IWB63148 -IWB51532	2.8	1.18	11.3
	15ABE2	Q.CTg1.ui-6A-2	IWB12439	6A-2	88.2	IWB12439–IWB13795	2.5	0.20	9.8
		Q.CTg1.ui-2B-4	Barc13	2B-4	26	Barc13–IWB22058	2.8	0.26	11.1
		Q.CTg1.ui-5B-2.1	*IWB80334*	*5B-2*	*10.96*	*IWB80334–IWB29709*	*3.1*	*−0.24*	*12.3*
		Q.CTg1.ui-5B-2.2	IWB19921	5B-2	20.97	IWB36033–IWB19921	3.3	−0.24	12.8
	15ABE3	Q.CTg1.ui-7A-3	IWB49784	7A-3	52.99	IWB25307–IWB34223	4.7	0.41	17.8
		Q.CTg1.ui-1B-1	IWB58775	1B-1	128	IWB10780–IWB58775	2.9	−0.31	13.6
		Q.CTg1.ui-2B-3	IWB18944	2B-3	22	IWB18944–Wmc149	2.6	−0.34	10.2
		Q.CTg1.ui-5B-2.1	*IWB80334*	*5B-2*	*10.96*	*IWB80334–IWB29709*	*2.8*	*−0.23*	*11.1*
	16ABE4	*Q.CTg1.ui-5B-2.1*	*IWB80334*	*5B-2*	*10.96*	*IWB80334–IWB29709*	*2.6*	*−0.35*	*10.4*
		Q.CTg1.ui-6B	IWB10604	6B	3.64	IWB75959–IWB10604	2.9	−0.67	11.5
	Average [f]	Q.CTg1.ui-3B-1	IWB8756	3B-1	1.82	IWB11545–IWB63436	3.8	−0.37	14.8
		Q.CTg1.ui-5B-2.1	*IWB80334*	*5B-2*	*10.96*	*IWB80334–IWB29709*	*2.6*	*−0.35*	*10.2*
		Q.CTg1.ui-5B-2.3	IWB36579	5B-2	41.08	IWB36579–IWB18101	4.2	0.49	16.2
CTg2	15ABE1	Q.CTg2.ui-1B-1	IWB58775	1B-1	128	IWB10780–IWB58775	3.5	6.69	13.6
		Q.CTg2.ui-6B.1	*IWB10400*	*6B*	*88.11*	*IWB65137–IWB10400*	*3.8*	*2.32*	*14.5*
		Q.CTg2.ui-5D-1	IWB79949	5D-1	0	IWB79949–IWB4139	3.7	−2.28	14.5
	15ABE2	Q.CTg2.ui-2B-2	Barc18	2B-2	21.88	IWB22675–IWB11319	3.9	0.30	15.1
		Q.CTg2.ui-4B.1	IWB10190	4B	29.65	IWB20226–IWB57507	3.2	−0.27	12.4
		Q.CTg2.ui-5B-2	IWB29709	5B-2	13.69	IWB80334–IWB29709	3.3	−0.29	13.0
	15ABE3	Q.CTg2.ui-3A-1	IWB33546	3A-1	2	IWB33546–IWB14315	2.5	0.26	9.8
		Q.CTg2.ui-6B.1	*IWB10400*	*6B*	*88.11*	*IWB65137–IWB10400*	*2.9*	*1.47*	*10.2*
		Q.CTg2.ui-2D-1	cfd73	2D-1	108.19	cfd73–IWB1093	3.1	0.29	12.1
	16ABE4	*Q.CTg2.ui-6B.1*	*IWB10400*	*6B*	*88.11*	*IWB65137–IWB10400*	*2.6*	*1.08*	*10.4*
		Q.CTg2.ui-6B.2	IWB75959	6B	0	IWB75959–IWB10604	5.2	−0.76	19.7
	Average [f]	Q.CTg2.ui-1A	IWB36377	1A	33.94	IWB36377–IWB21518	4.0	−0.61	15.3
		Q.CTg2.ui-7A-1	IWB46359	7A-1	48.95	IWB25077–IWB46359	2.6	−0.49	10.3
		Q.CTg2.ui-6B.1	*IWB10400*	*6B*	*88.11*	*IWB65137–IWB10400*	*2.6*	*0.47*	*10.3*
		Q.CTg2.ui-2D-2	IWB11455	2D-2	20.15	IWB12523–IWB11455	2.8	−0.52	11.1

15ABE1, 15ABE2, 15ABE3: trial 1, 2 and 3 in Aberdeen in 2015, respectively; 16ABE4, trial 4 in Aberdeen in 2016. [a] CTa, CTg1, CTg2, canopy temperature during anthesis, mid- and late grain-filling stage, respectively; ui, university of Idaho. Different QTL on the same linkage group was indicated with 1 and 2 after the period following the linkage group. [b] Position of QTL located on linkage group, as CM distance from the top of each linkage group. [c] An LOD threshold of 2.5 was used for declaration of QTL. [d] Positive "additive effect" indicated effect from SY Capstone, negative "additive effect" indicated effect from UI Platinum. [e] Percentage of phenotypic variation explained by the QTL. [f] Average data across the four environments was used. LG, linkage group. Italic and bold showed the stable QTL for traits.

For CTa, 10 QTL were detected on Chr. 1A, 2A-2, 2B-2, 2B-3, 3B-1, 4B, 5B-2, and 6B, explaining 9.8–21.7% of the phenotypic variation across environments (Tables 4 and S4; Figure 1). Two QTL on Chr. 2B-3 between *IWB35482* and *IWB74377* at 55.36–63.62 cm and on Chr. 4B between *IWB20226* and *IWB57507* at 27.83–30.56 cm were found in two (15ABE2 and 15ABE3) and four environments (15ABE2, 15ABE3, 16ABE4 and Average environment), respectively, explaining 10.3%–11.6% and 11.2%–14.6% of the phenotypic variation, respectively.

For CTg1, 12 QTL were detected on Chr. 5A, 6A-2, 7A-3, 1B-1, 2B-3, 2B-4, 3B-1, 5B-2, 6B, and 3D-1, explaining 9.8%–17.8% of the phenotypic variation across environments (Tables 4 and S4; Figure 1). A stable QTL on Chr. 5B-2 tightly linked to *IWB80334* at 10.96–13.69 cm was found in four environments (15ABE2, 15ABE3, 16ABE4 and Average environment), explaining 10.2%–12.3% of the phenotypic variation.

For CTg2, 12 QTL were detected on Chr. 1A, 3A-1, 7A-1, 1B-1, 2B-2, 4B, 5B-2, 6B, 2D-1, 2D-2, and 5D-1, explaining 9.8%–19.7% of the phenotypic variation across environments (Tables 4 and S4; Figure 1). A QTL on Chr. 6B between *IWB65137* and *IWB10400* at 87.2–88.11 cm was stable in four environments (15ABE1, 15ABE3, 16ABE4 and Average environment), explaining 10.2%–14.5% of the phenotypic variation.

For CCIa, 15 QTL were detected on the homologous chromosome groups 2 and 6 as well as on Chr. 3A-1, 3A-2, 4A-1, 5A, 7A-2, 7B, 3D-1, 3D-2, and 4D-1, explaining 9.9%–19.2% of the phenotypic

variation across environments (Tables 5 and S4; Figure 1). Three QTL on Chr. 3A-2, 7A-2, and 3D-2 were found in two environments, each explaining 11.6%–19.1% of the phenotypic variation.

For CCIg1, nine QTL were detected on Chr. 3A-2, 4A-1, 5A, 1D-1, 1D-2, 2D-1, and 2B-2, explaining 11.0%–31.3% of the phenotypic variation across environments (Tables 5 and S4; Figure 1). A QTL on Chr. 5A between *IWB14149* and *IWB10765* at 91.35–93.17 cm was found in four environments (15ABE2, 15ABE3, 16ABE4 and Average environment), explaining 15.2%–30.6% of the phenotypic variation. Additionally, two QTL on Chr. 3A-2 between *IWB*17683 and *IWB*13444 at 51.17–52.08 cm and on Chr. 2D-1 between *IWB*15442 and *IWB*60397 at 133.01–134.83 cm were found in two environments, explaining 11.9%–12.2% and 11.8%–20.6% of the phenotypic variation, respectively.

Table 5. QTL detected for chlorophyll content index in the DH population of UI Platinum/SY Capstone.

Traits	Trial	QTL [a]	Peak Marker	LG	Position [b]	Marker Interval	LOD [c]	Add [d]	R^2 [e]
CCIa	15ABE1	Q.CCIa.ui-3D-1	IWB45650	3D-1	18	IWB45650–Wms3	2.6	−3.44	10.3
	15ABE2	Q.CCIa.ui-3A-2	IWB10063	3A-2	87.62	IWB11450–IWB10063	3.9	2.99	15.1
		Q.CCIa.ui-7B	IWB6754	7B	233.72	IWB25433–IWB6754	4.1	−3.23	15.9
		Q.CCIa.ui-3D-2	IWB9674	3D-2	16.91	IWB9674–IWB71478	3.0	3.23	11.9
		Q.CCIa.ui-4D-1	IWB8050	4D-1	45.41	IWB14984–IWB8050	2.9	−2.60	11.4
		Q.CCIa.ui-6D-3	IWB13767	6D-3	0.91	IWB13767–IWB46507	2.5	2.42	10.0
	15ABE3	Q.CCIa.ui-4A-1	IWB12946	4A-1	78.95	IWB37346–IWB10035	3.6	1.89	13.9
		Q.CCIa.ui-7A-2	IWB12020	7A-2	81.58	IWB39758–IWB12020	4.1	−1.45	15.9
		Q.CCIa.ui-2D-1	IWB15442	2D-1	133.01	IWB15442–IWB60397	3.4	1.86	13.4
	16ABE4	Q.CCIa.ui-2A-1	IWB10499	2A-1	12.87	IWB10836–IWB29812	3.2	3.26	12.5
		Q.CCIa.ui-3A-1	IWB33546	3A-1	2	IWB33546–IWB14315	2.8	−2.20	11.2
		Q.CCIa.ui-5A	IWB21197	5A	165.38	IWB21197–IWB35869	2.9	2.16	11.4
		Q.CCIa.ui-6A-2	IWB19789	6A-2	70.82	IWB22680–IWB19789	3.3	−2.31	13.0
	Average [f]	Q.CCIa.ui-3A-2	IWB10063	3A-2	87.62	IWB11450–IWB10063	2.9	1.20	11.6
		Q.CCIa.ui-7A-2	IWB12020	7A-2	81.58	IWB39758–IWB12020	5.1	−1.71	19.1
		Q.CCIa.ui-2B-3	IWB18944	2B-3	22	IWB18944–Wmc149	2.5	−1.28	9.9
		Q.CCIa.ui-6B	IWB58083	6B	68.05	IWB52064–IWB58083	5.1	1.66	19.2
		Q.CCIa.ui-3D-2	IWB9674	3D-2	4.91	IWB9674–IWB71478	3.9	1.54	15.1
CCIg1	15ABE1	Q.CCIg1.ui-2B-2.1	IWB67534	2B-2	10.93	IWB67534–IWB13631	4.2	9.26	16.3
		Q.CCIg1.ui-2B-2.2	Barc18	2B-2	21.88	IWB22675–IWB11319	3.2	−6.80	12.5
		Q.CCIg1.ui-2D-1	IWB15442	2D-1	133.01	IWB15442–IWB60397	3.0	3.68	11.8
	15ABE2	Q.CCIg1.ui-4A-1	IWB12946	4A-1	78.95	IWB37346–IWB10035	2.8	2.73	11.1
		Q.CCIg1.ui-5A.1	*IWB14149*	*5A*	*91.35*	*IWB14149–IWB10765*	*3.9*	*3.09*	*15.2*
		Q.CCIg1.ui-5A.2	IWB35869	5A	166.29	IWB21197–IWB17983	9.0	−5.45	31.3
	15ABE3	Q.CCIg1.ui-3A-2	IWB17683	3A-2	51.17	IWB17683–IWB13444	3.1	−2.70	12.2
		Q.CCIg1.ui-5A.1	*IWB14149*	*5A*	*91.35*	*IWB14149–IWB10765*	*4.7*	*3.36*	*17.8*
		Q.CCIg1.ui-2D-1	IWB15442	2D-1	133.01	IWB15442–IWB60397	4.7	3.02	18.0
	16ABE4	Q.CCIg1.ui-3A-2	IWB17683	3A-2	51.17	IWB17683–IWB13444	3.0	−2.20	11.9
		Q.CCIg1.ui-5A.1	*IWB14149*	*5A*	*91.35*	*IWB14149–IWB10765*	*8.7*	*5.21*	*30.6*
		Q.CCIg1.ui-1D-2	IWB65713	1D-2	0	IWB65713–IWB55046	3.6	2.42	14.1
	Average [f]	*Q.CCIg1.ui-5A.1*	*IWB14149*	*5A*	*91.35*	*IWB14149–IWB10765*	*5.9*	*5.34*	*21.8*
		Q.CCIg1.ui-1D-1	IWB42629	1D-1	19.94	IWB42629–IWB80211	2.8	−1.64	11.0
		Q.CCIg1.ui-2D-1	IWB15442	2D-1	133.01	IWB15442–IWB60397	5.5	2.22	20.6
CCIg2	15ABE1	Q.CCIg2.ui-1B-1	IWB58775	1B-1	128	IWB10780–IWB58775	3.0	3.08	11.7
		Q.CCIg2.ui-6D-3	IWB46507	6D-3	0	IWB46507–IWB13767	2.9	−3.07	11.3
	15ABE2	Q.CCIg2.ui-4A-1	IWB12946	4A-1	78.95	IWB37346–IWB10035	3.0	2.74	11.7
		Q.CCIg2.ui-5A.1	IWB11865	5A	167.2	IWB21197–IWB17983	6.6	−4.33	24.1
		Q.CCIg2.ui-1B-2.1	IWB27496	1B-2	38.81	IWB5753–IWB27496	3.1	4.99	12.2
		Q.CCIg2.ui-1B-2.2	IWB21945	1B-2	53.38	IWB21945–IWB14060	2.7	−4.33	10.7
		Q.CCIg2.ui-3B-1	IWB5790	3B-1	50.52	IWB5790–IWB10800	3.5	−3.12	13.7
	15ABE3	Q.CCIg2.ui-1A	IWB12695	1A	157.15	IWB11395–IWB13624	6.6	2.93	24.1
		Q.CCIg2.ui-5B-2	IWB5882	5B-2	43.81	IWB36579–IWB18101	3.7	2.17	14.3
		Q.CCIg2.ui-2D-1	IWB15442	2D-1	133.01	IWB15442–IWB60397	6.9	2.98	25.2
	16ABE4	Q.CCIg2.ui-3A-2	IWB29612	3A-2	100.63	IWB29612–IWB63761	2.6	−2.14	10.2
		Q.CCIg2.ui-5A.1	IWB11865	5A	167.2	IWB21197–IWB17983	3.9	−3.73	14.9
		Q.CCIg2.ui-5A.2	IWB14149	5A	91.35	IWB14149–IWB10765	6.2	4.58	22.7
		Q.CCIg2.ui-7A-3	IWB27037	7A-3	0	IWB27037–IWB65210	4.0	−2.70	15.5
	Average [f]	Q.CCIg2.ui-1A	IWB13624	1A	158.79	IWB44568–IWB13624	2.7	1.38	10.6
		Q.CCIg2.ui-3B-1	IWB5790	3B-1	50.52	IWB5790–IWB10800	3.8	−1.59	14.6

15ABE1, 15ABE2, 15ABE3: trial 1, 2 and 3 in Aberdeen in 2015, respectively; 16ABE4, trial 4 in Aberdeen in 2016. [a] CCIa, CCIg1, CCIg2, chlorophyll content index during anthesis, mid- and late grain-filling stage, respectively; ui, university of Idaho. Different QTL on the same linkage group was indicated with 1 and 2 after the period following the linkage group. [b] Position of QTL located on linkage group, as CM distance from the top of each linkage group. [c] A LOD threshold of 2.5 was used for declaration of QTL. [d] Positive "additive effect" indicated effect from SY Capstone, negative "additive effect" indicated effect from UI Platinum. [e] Percentage of phenotypic variation explained by the QTL. [f] Average data across the four environments was used. LG, linkage group. Italic and bold showed the stable QTL for traits.

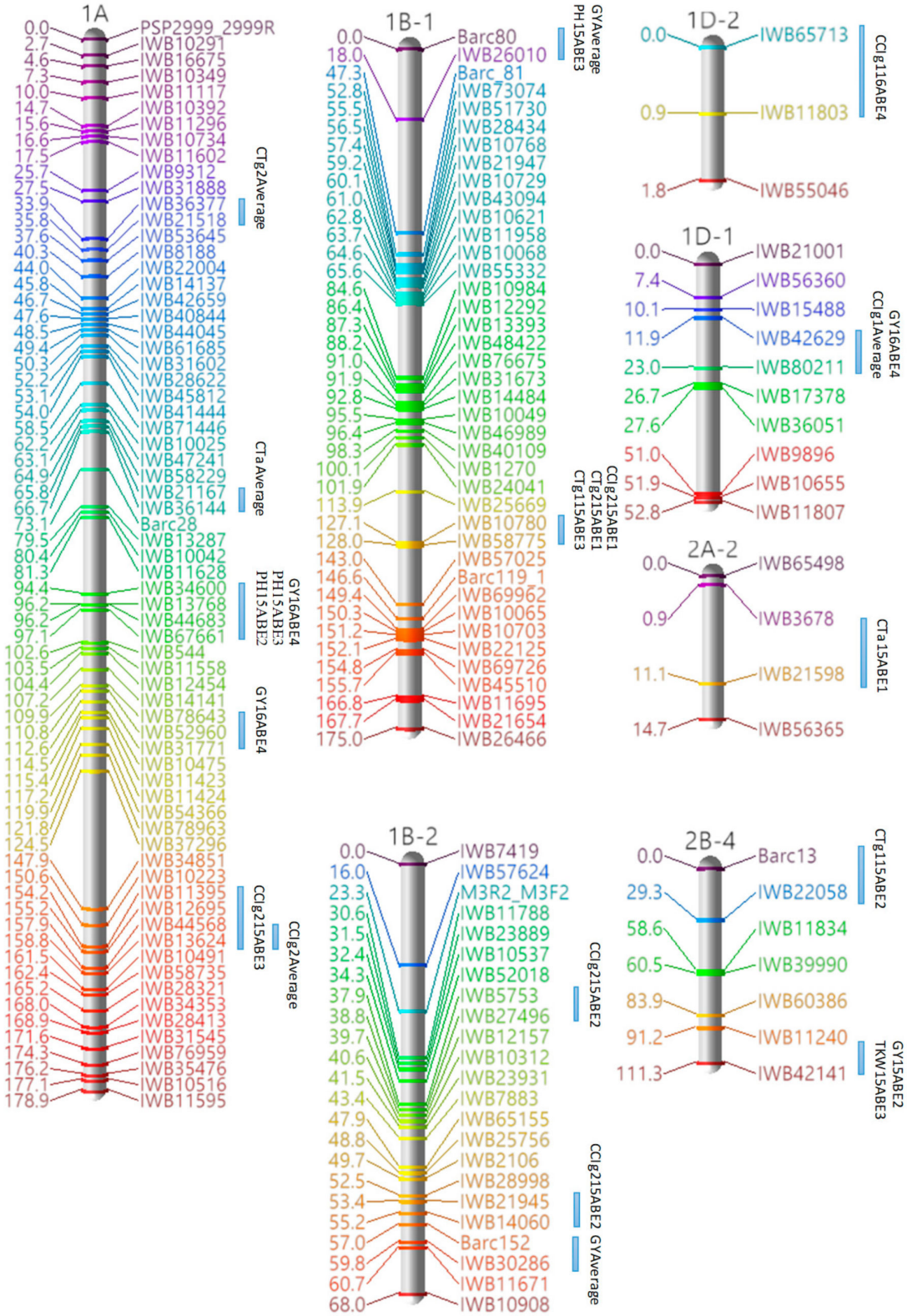
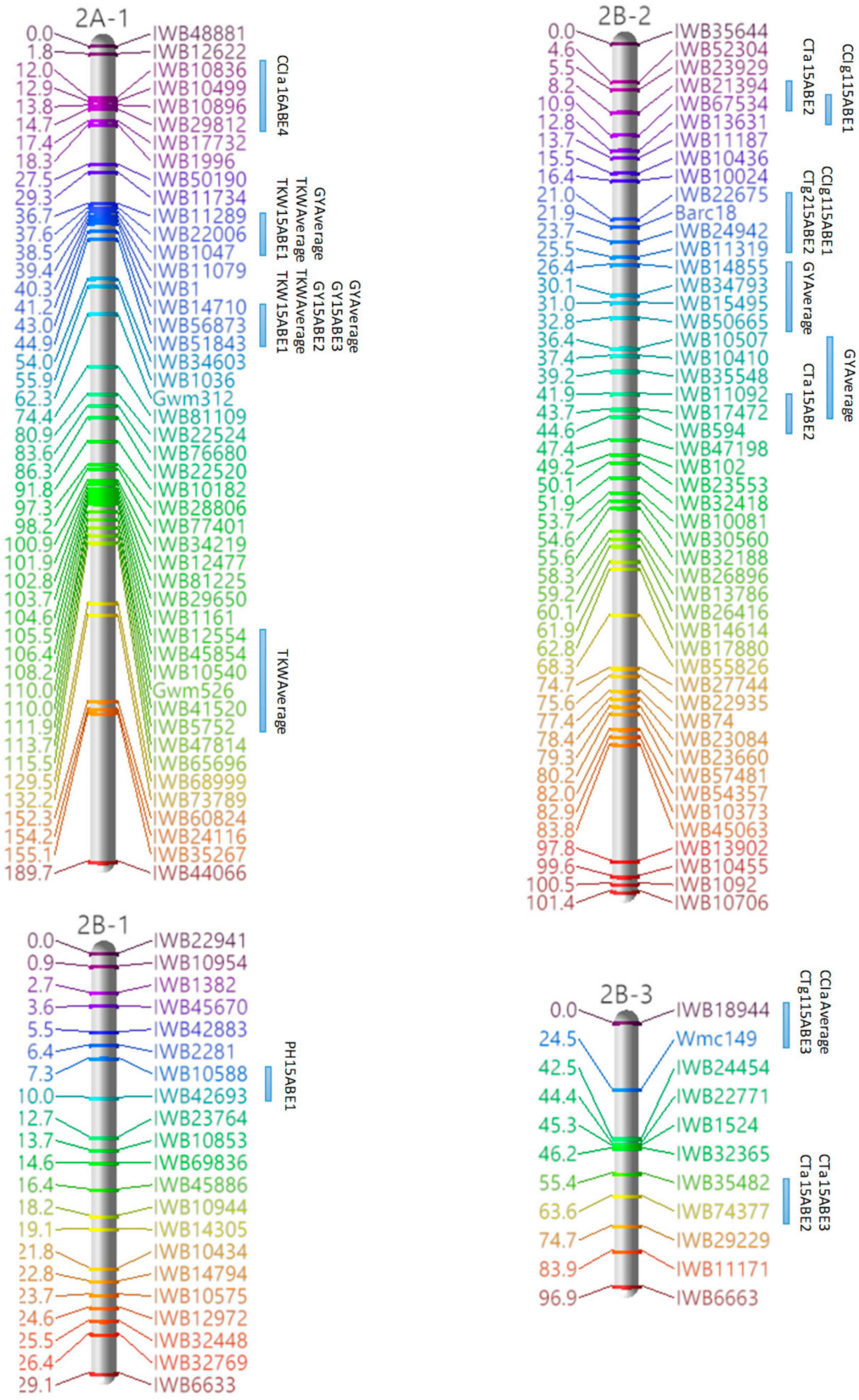


Figure 1. *Cont.*



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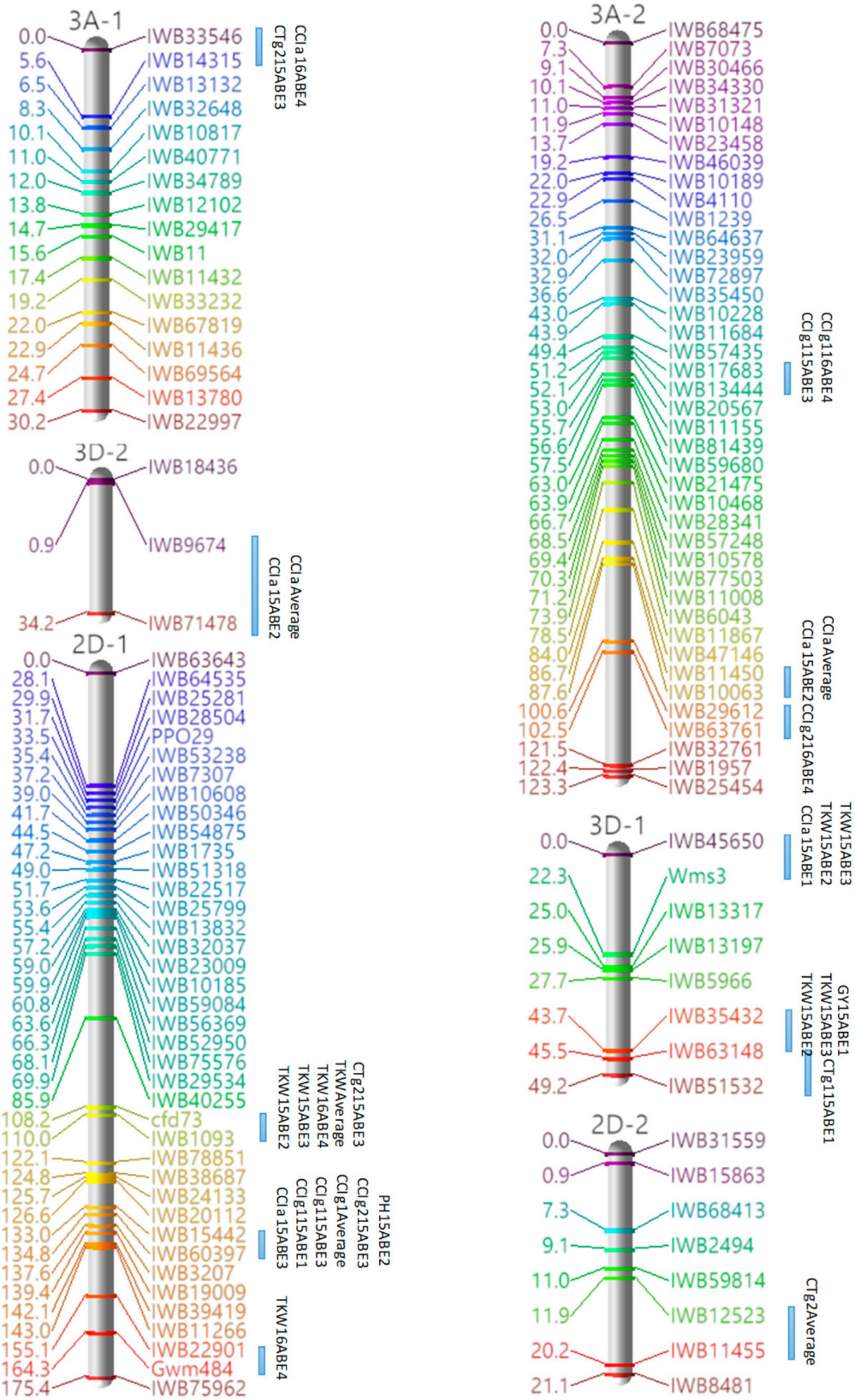

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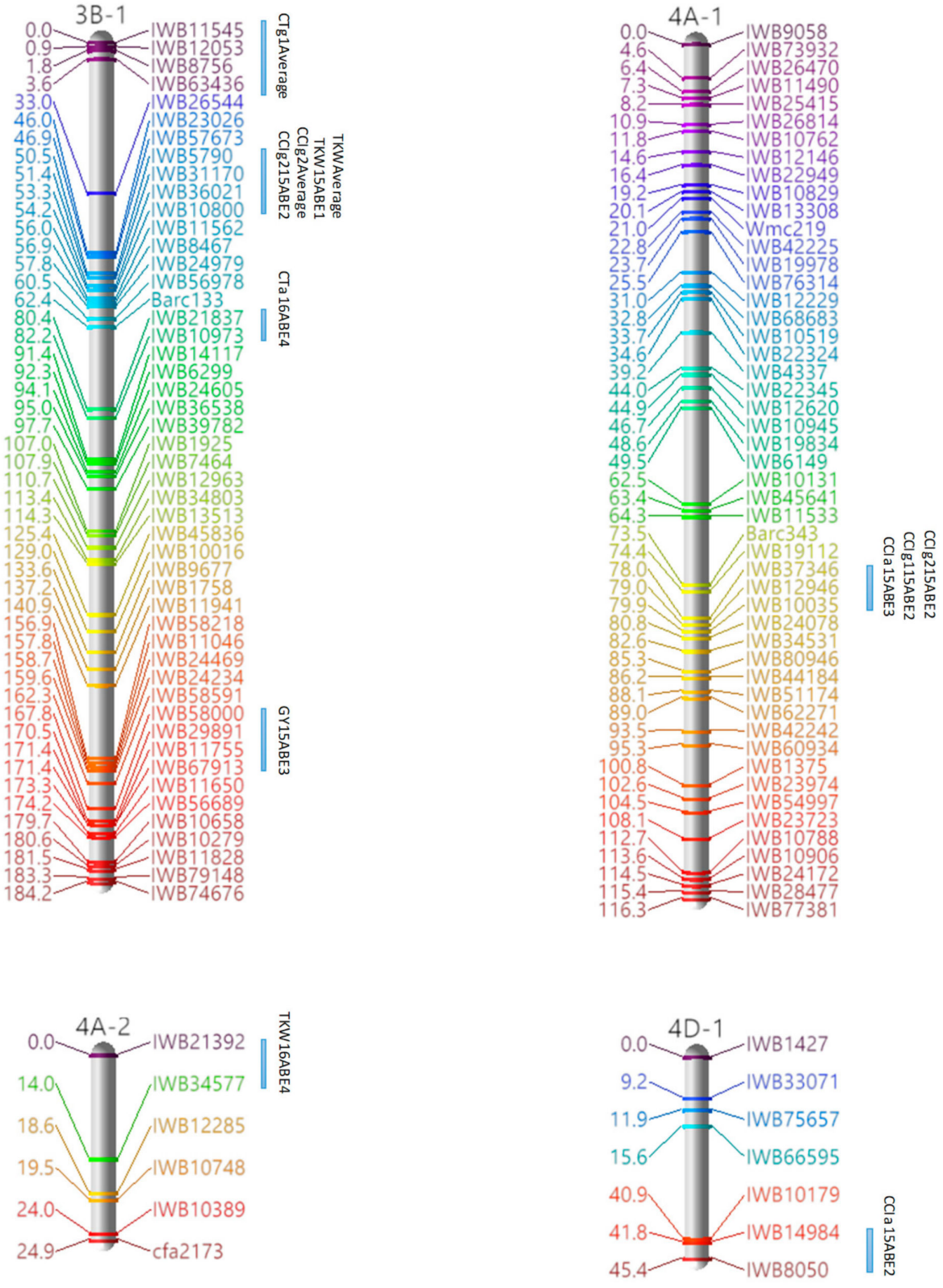

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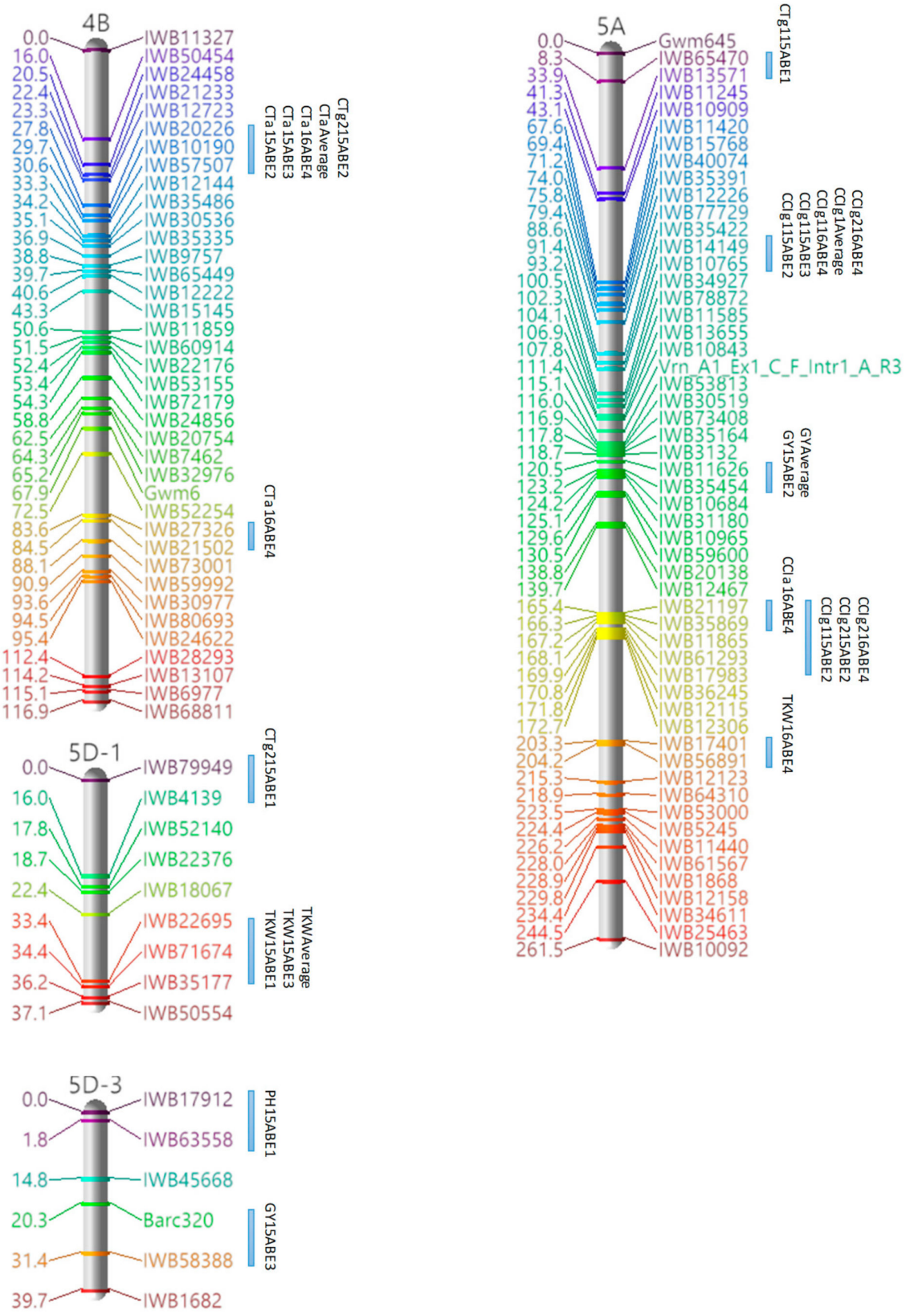

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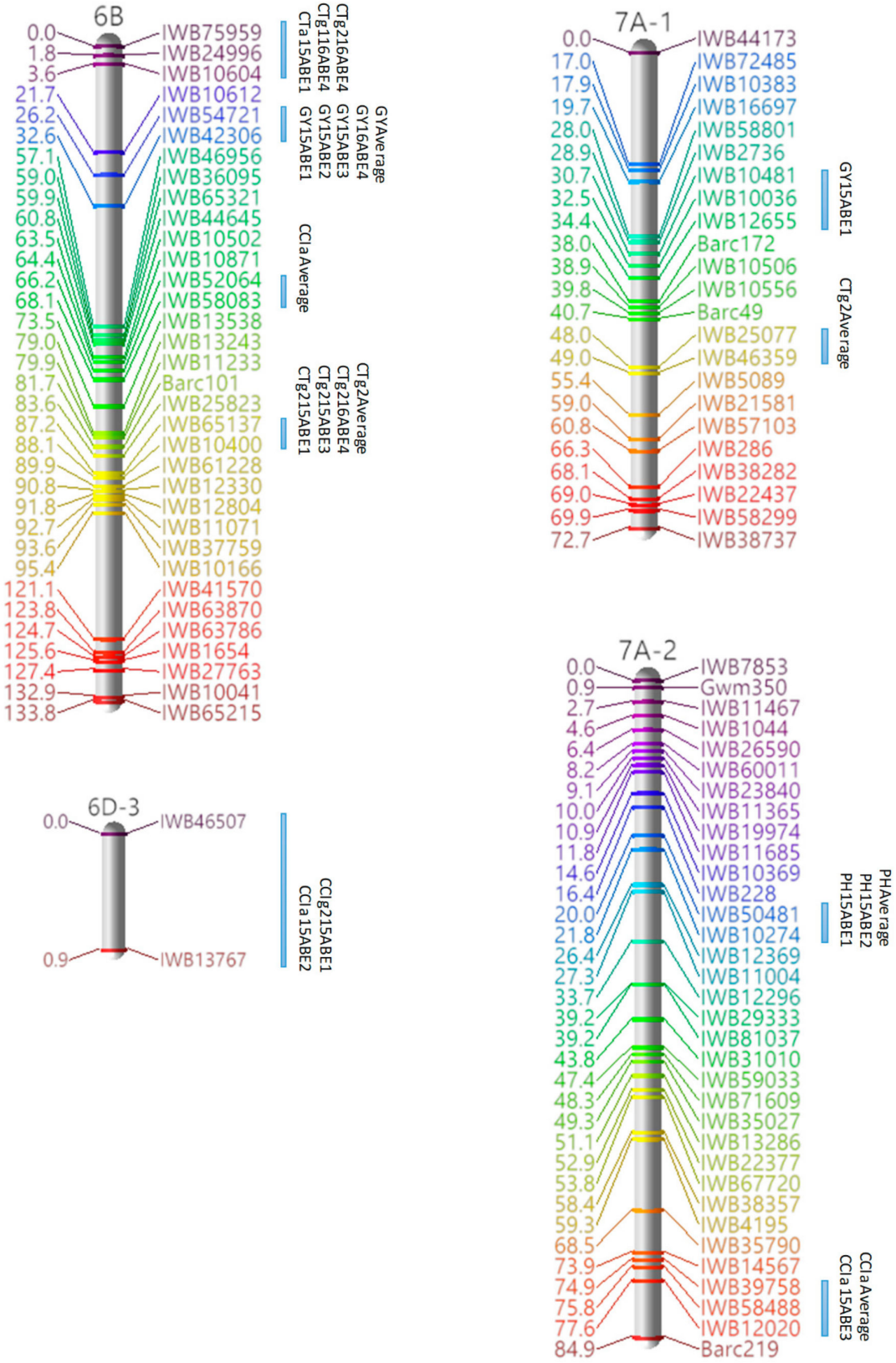

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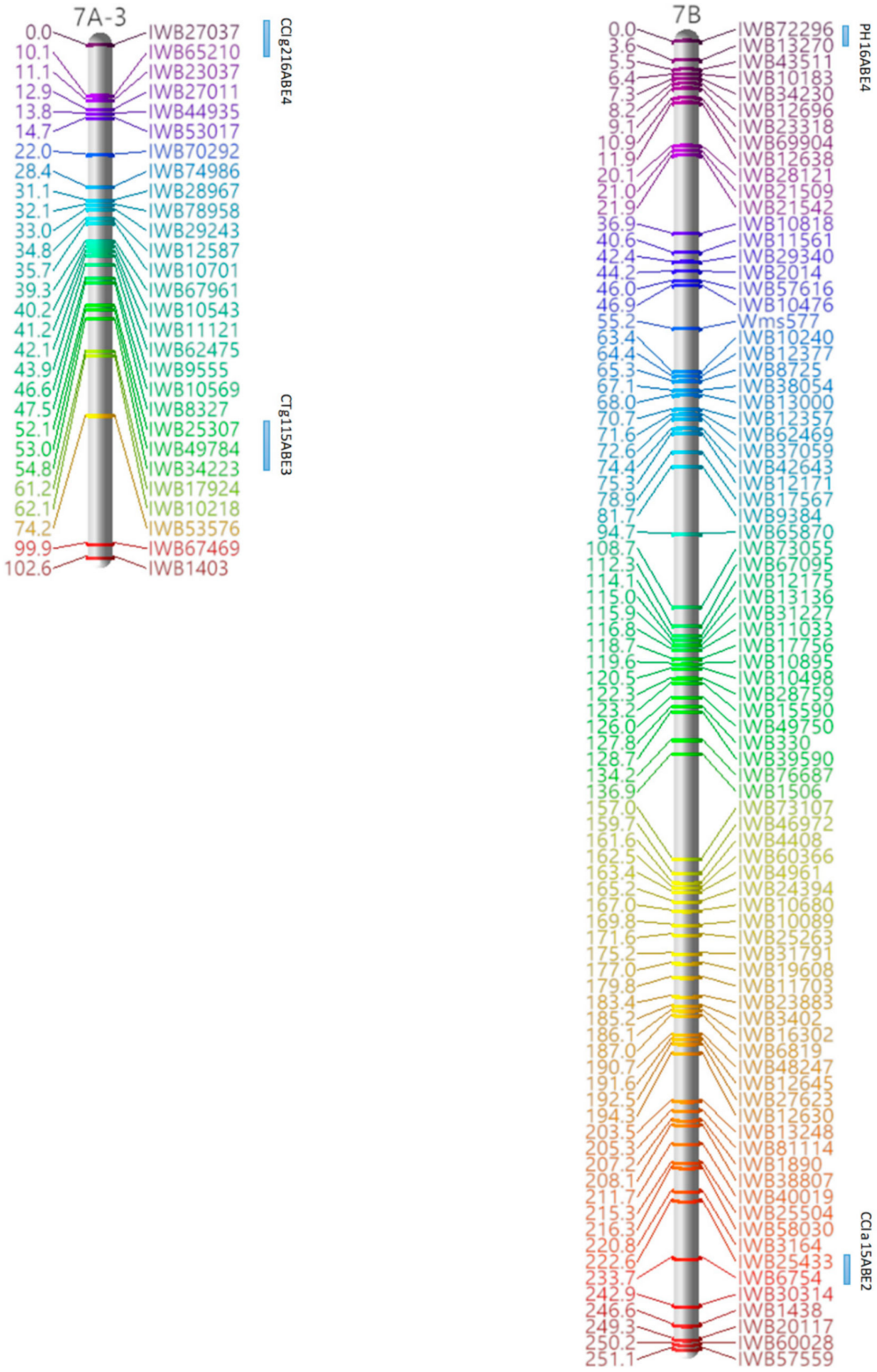

Figure 1. Quantitative trait locus (QTL) for physiological traits (CTa, CTg1, CTg2, CCI_a, CCIg1 and CCIg2), PH, TKW and GY on the linkage groups of the doubled haploid (DH) population from UI Platinum/SY Capstone. 15ABE1, 15ABE2, 15ABE3: trial 1, 2 and 3 in Aberdeen in 2015, respectively; 16ABE4, trial 4 in Aberdeen in 2016; CTa, CTg1, CTg2, canopy temperature during anthesis, mid-grain-filling and late grain-filling stage, respectively; CCIa, CCIg1, CCIg2, chlorophyll content index during anthesis, mid-grain-filling and late grain-filling stage, respectively; PH, plant height; TKW, thousand kernels weight; GY, grain yield.

For CCIg2, 13 QTL were detected on Chr. 1A, 3A-2, 4A-1, 5A, 7A-3, 1B-1, 1B-2, 3B-1, 5B-2, 2D-1, and 6D-3, explaining 10.2%–25.2% of the phenotypic variation across environments (Tables 5 and S4; Figure 1). A QTL on Chr. 5A between *IWB*21197 and *IWB*17983 at 165.38–169.93 cm was found in two environments (15ABE2 and 15ABE4), explaining 14.9%–24.1% of the phenotypic variation.

For PH, 12 QTL were detected on Chr. 1A, 5A, 6A-2, 7A-2, 1B-1, 2B-1, 5B-2, 7B, 2D-1, and 5D-3, explaining 9.9%–21.8% of the phenotypic variation across environments (Tables 6 and S4; Figure 1). A QTL on Chr. 5A between *IWB31050* and *IWB54778* at 108.49–112.13 cm was found in four environments (15ABE1, 15ABE2, 15ABE3 and Average environment), explaining 12.3%–19.6% of the phenotypic variation. Additionally, a QTL on Chr. 7A-2 between *IWB*50481and *IWB*10274 at 20.02– 21.84 cm was found in three environments (15ABE1, 15ABE2 and Average environment), explaining 9.9%–18.3% of the phenotypic variation.

Table 6. QTLs for plant height (PH), thousand kernels weight (TKW) and grain yield (GY) detected in the DH population of UI Platinum/SY Capstone.

Trial		QTL [a]	Peak Marker	LG	Position [b]	Marker Interval	LOD [c]	Addd	R^2 [e]
PH	15ABE1	*Q.PH.ui-6A-2.1*	*IWB70003*	*6A-2*	*110.31*	*IWB31050–IWB54778*	*5.2*	*3.36*	*19.6*
		Q.PH.ui-7A-2	IWB10274	7A-2	21.84	IWB50481–IWB10274	2.7	−2.37	10.9
		Q.PH.ui-2B-1	IWB42693	2B-1	10.01	IWB10588–IWB42693	4.2	3.24	16.1
		Q.PH.ui-5B-2.1	IWB626	5B-2	42.9	IWB36579–IWB18101	4.8	−3.55	18.3
		Q.PH.ui-5B-2.2	IWB2079	5B-2	94.84	IWB19792–IWB1762	3.0	2.57	11.8
		Q.PH.ui-5D-3	IWB17912	5D-3	0	IWB17912–IWB63558	2.6	2.50	10.3
	15ABE2	Q.PH.ui-1A	IWB13768	1A	96.17	IWB34600–IWB67661	3.7	3.12	14.3
		Q.PH.ui-6A-2.1	*IWB70003*	*6A-2*	*110.31*	*IWB31050–IWB54778*	*3.4*	*3.06*	*13.3*
		Q.PH.ui-6A-2.2	IWB40830	6A-2	118.5	IWB40830–IWB52007	4.0	3.32	15.6
		Q.PH.ui-7A-2	IWB10274	7A-2	23.84	IWB50481–IWB10274	2.5	−2.60	9.9
		Q.PH.ui-2D-1	IIWB15442	2D-1	133.01	IWB15442–IWB60397	3.7	3.15	14.4
	15ABE3	Q.PH.ui-1A	IWB13768	1A	96.17	IWB34600–IWB67661	2.7	2.41	10.7
		Q.PH.ui-6A-2.1	*IWB70003*	*6A-2*	*110.31*	*IWB31050–IWB54778*	*3.3*	*2.76*	*12.8*
		Q.PH.ui-1B-1	Barc80	1B-1	14	Barc80–IWB26010	4.8	3.75	18.1
	16ABE4	Q.PH.ui-5B-2.2	IWB2079	5B-2	94.84	IWB19792–IWB1762	3.2	2.68	12.7
		Q.PH.ui-7B	IWB72296	7B	0	IWB72296–IWB13270	4.3	2.99	16.6
	Average [f]	*Q.PH.ui-6A-2.1*	*IWB70003*	*6A-2*	*110.31*	*IWB31050–IWB54778*	*3.6*	*1.88*	*14.2*
		Q.PH.ui-6A-2.2	IWB40830	6A-2	118.5	IWB40830–IWB52007	3.5	1.88	13.7
		Q.PH.ui-7A-2	IWB10274	7A-2	21.84	IWB50481–IWB10274	2.7	−1.52	10.8
		Q.PH.ui-5B-2.1	IWB626	5B-2	42.9	IWB36579–IWB18101	2.8	−1.61	11.2
TKW	15ABE1	Q.TKW.ui-2A-1.1	IWB22006	2A-1	37.57	IWB11289–IWB1047	4.1	−2.45	15.7
		Q.TKW.ui-2A-1.2	IWB51843	2A-1	44.85	IWB14710–IWB51843	2.9	−2.11	11.3
		Q.TKW.ui-3B-1	IWB5790	3B-1	50.52	IWB5790–IWB10800	5.3	−2.83	20.0
		Q.TKW.ui-5D-1	IWB71674	5D-1	34.35	IWB22695–IWB35177	3.4	2.16	13.2
	15ABE2	*Q.TKW.ui-2D-1*	*cfd73*	*2D-1*	*108.19*	*cfd73–IWB1093*	*3.7*	*−2.07*	*14.3*
		Q.TKW.ui-3D-1.1	IWB35432	3D-1	43.71	IWB35432–IWB63148	2.6	−1.70	10.2
		Q.TKW.ui-3D-1.2	IWB45650	3D-1	12	IWB45650–Wms3	5.3	−2.13	19.5
	15ABE3	Q.TKW.ui-2B-4	IWB11240	2B-4	101.17	IWB11240–IWB42141	5.4	−2.54	20.4
		Q.TKW.ui-2D-1	*cfd73*	*2D-1*	*108.19*	*cfd73–IWB1093*	*3.8*	*−1.95*	*14.8*
		Q.TKW.ui-3D-1.1	IWB35432	3D-1	43.71	IWB35432–IWB63148	3.7	−1.88	14.2
		Q.TKW.ui-3D-1.2	IWB45650	3D-1	12	IWB45650–Wms3	4.8	−2.40	18.2
		Q.TKW.ui-5D-1	IWB71674	5D-1	34.35	IWB22695–IWB35177	3.3	1.74	12.8
	16ABE4	Q.TKW.ui-4A-2	IWB21392	4A-2	12	IWB21392–IWB34577	3.9	1.79	15.2
		Q.TKW.ui-5A	IWB17401	5A	203.25	IWB17401–IWB56891	5.4	2.08	20.2
		Q.TKW.ui-2D-1	*cfd73*	*2D-1*	*108.19*	*cfd73–IWB1093*	*4.6*	*−1.68*	*17.5*
		Q.TKW.ui-2D-1.2	IWB22901	2D-1	161.07	IWB22901–Gwm484	5.1	−2.10	19.1
	Average [f]	Q.TKW.ui-2A-1.1	IWB22006	2A-1	37.57	IWB11289–IWB1047	7.4	−1.81	26.5
		Q.TKW.ui-2A-1.2	IWB51843	2A-1	44.85	IWB14710–IWB51843	5.7	−1.72	21.1
		Q.TKW.ui-2A-1.3	IWB10540	2A-1	108.22	IWB12554–IWB5752	5.4	1.48	20.1
		Q.TKW.ui-3B-1	IWB5790	3B-1	50.52	IWB5790–IWB10800	2.8	−1.04	10.9
		Q.TKW.ui-2D-1	*cfd73*	*2D-1*	*108.19*	*cfd73–IWB1093*	*5.7*	*−1.52*	*21.1*
		Q.TKW.ui-5D-1	IWB71674	5D-1	34.35	IWB22695–IWB35177	4.2	1.28	16.0
GY	15ABE1	Q.GY.ui-7A-1	IWB10036	7A-1	32.53	IWB10481–IWB12655	4.8	0.48	18.2
		Q.GY.ui-5B-2	IWB2079	5B-2	94.84	IWB19792–IWB1762	3.8	−0.46	14.6
		Q.GY.ui-6B	*IWB42306*	*6B*	*34.61*	*IWB54721–IWB42306*	*4.4*	*−0.57*	*16.7*
		Q.GY.ui-3D-1	IWB35432	3D-1	43.71	IWB35432–IWB63148	3.2	−0.39	12.7
	15ABE2	Q.GY.ui-2A-1.1	IWB14710	2A-1	41.21	IWB14710–IWB51843	2.5	−0.37	9.9
		Q.GY.ui-5A	IWB11626	5A	120.51	IWB11626–IWB35454	2.9	−0.40	11.3
		Q.GY.ui-2B-4	IWB11240	2B-4	111.17	IWB11240–IWB42141	3.7	−2.04	14.5

Table 7. QTLs for plant height (PH), thousand kernels weight (TKW) and grain yield (GY) detected in the DH population of UI Platinum/SY Capstone.

Trial	QTL [a]	Peak Marker	LG	Position [b]	Marker Interval	LOD [c]	Addd	R^2 [e]
	Q.GY.ui-6B	*IWB42306*	*6B*	*34.61*	*IWB54721–IWB42306*	*5.1*	*−0.56*	*19.2*
15ABE3	Q.GY.ui-2A-1.1	IWB14710	2A-1	41.21	IWB14710–IWB51843	2.7	−0.32	10.8
	Q.GY.ui-3B-1	IWB58000	3B-1	169.8	IWB58000–IWB67913	4.0	−0.87	15.4
	Q.GY.ui-5D-3	Barc320	5D-3	30.31	Barc320–IWB58388	4.8	0.45	18.4
16ABE4	Q.GY.ui-1A.1	IWB13768	1A	96.17	IWB34600–IWB67661	2.9	−0.78	11.6
	Q.GY.ui-1A.2	IWB52960	1A	110.81	IWB78643–IWB31771	5.2	1.16	19.6
	Q.GY.ui-6A-2	IWB34744	6A-2	155.47	IWB34744–IWB199	2.7	−0.39	10.6
	Q.GY.ui-6B	*IWB42306*	*6B*	*34.61*	*IWB54721–IWB42306*	*4.3*	*−0.60*	*16.6*
	Q.GY.ui-1D-1	IWB42629	1D-1	11.94	IWB42629–IWB80211	5.5	0.59	20.4
Average [f]	Q.GY.ui-2A-1.1	IWB14710	2A-1	41.21	IWB14710–IWB51843	3.6	0.20	13.8
	Q.GY.ui-2A-1.2	IWB22006	2A-1	37.57	IWB11289–IWB1047	3.1	−0.19	12.2
	Q.GY.ui-5A	IWB11626	5A	120.51	IWB11626–IWB35454	2.6	−0.18	10.4
	Q.GY.ui-1B-1	Barc80	1B-1	4	Barc80–IWB26010	5.6	0.32	20.8
	Q.GY.ui-1B-2	Barc152	1B-2	59.02	Barc152–IWB30286	2.7	0.18	10.6
	Q.GY.ui-2B-2.1	IWB15495	2B-2	30.98	IWB14855–IWB50665	4.2	−0.23	16.3
	Q.GY.ui-2B-2.2	IWB10507	2B-2	36.44	IWB10507–IWB17472	4.4	−0.23	16.8
	Q.GY.ui-6B	*IWB42306*	*6B*	*34.61*	*IWB54721–IWB42306*	*2.8*	*−0.18*	*11.2*

15ABE1, 15ABE2, 15ABE3: trial 1, 2 and 3 in Aberdeen in 2015, respectively; 16ABE4, trial 4 in Aberdeen in 2016. [a] ui, university of Idaho. Different QTL on the same linkage group was indicated with 1 and 2 after the period following the linkage group. [b] Position of QTL located on linkage group, as CM distance from the top of each linkage group. [c] A LOD threshold of 2.5 was used for declaration of QTL. [d] Positive "additive effect" indicated effect from SY Capstone, negative "additive effect" indicated effect from UI Platinum. [e] Percentage of phenotypic variation explained by the QTL. [f] Average data across the four or five environments was used. LG, linkage group. Italic and bold showed the stable QTL for traits.

For TKW, 15 QTL were detected on the homologous chromosome groups 2 and 5 as well as on Chr. 4A-2, 3B-1, 3D-1, and 7B, explaining 10.2%–31.3% of the phenotypic variation across environments (Tables 6 and S4; Figure 1). A QTL on Chr. 2D-1 between *cfd73* and *IWB1093* at 108.19–110.01 cm was found four environments (15ABE3, 15ABE3, 16ABE4 and Average environment), explaining 14.3%–21.1% of the phenotypic variation. Additionally, a QTL on Chr. 5D-1 between *IWB* 22695 and *IWB*35177 at 33.44–36.17 cm was found in three environments (15ABE1, 15ABE3 and Average environment), respectively, explaining 10.2%–16.2% and 18.2%–31.1% of the phenotypic variation, respectively.

For GY, 18 QTL were detected on the homologous chromosome groups 1 and 5 as well as on Chr. 2A-1, 6A-2, 7A-1, 2B-2, 2B-4, 3B-1, 6B, and 3D-1, explaining 9.8%–20.8% of the phenotypic across environments (Tables 6 and S4; Figure 1). A stable QTL on Chr. 6B between *IWB54721* and *IWB42306* at 26.2–32.61 cm was found in four environments (15ABE1, 15ABE2, 16ABE4 and Average environment), explaining 11.2%–19.2% of the phenotypic variation. In addition, one QTL on Chr. 2A-1 between *IWB*14710 and *IWB*51843 at 41.21–44.85 cm was found in three environments (15ABE2, 15ABE3 and Average environment), each explaining 9.9%–13.8% of the phenotypic variation.

4. Discussion

Improving GY is an essential objective in wheat breeding programs worldwide. Physiological traits, as well as PH and TKW, are critical elements of GY. The wide use of molecular markers has made possible the study of quantitative traits [9,11,23] and detect QTL that allow the development of high-yield cultivars via MAS. Previous studies identified numerous QTL associated with yield-related traits in various populations [1,9,10,19–21,27]. However, the genetic architecture of these traits needs further research. In this study, a DH population was phenotyped for CT (CTa, CTg1, and CTg2), CCI (CCIa, CCIg1, and CCIg2), PH, TKW, and GY under irrigated conditions and genotyped with SNP markers and SSRs to better understand the genetic control of the studied traits.

4.1. Phenotypic Evaluation

In the present study, PH and TKW showed high heritability; CCIa, CCIg1, and CCIg2 moderate heritability; whereas CTa, CTg1, and CTg2 low heritability, results that were in agreement with those reported in previous studies [10,11,47]. Environmental diversity affects CT heritability, which ranges from

low under heat or water-stressed conditions [9] to high under irrigated conditions [28]. GY is a complex trait highly affected by the environment and thus, has low heritability [48]. However, in the present study, the heritability of GY was higher than that reported previously [49]. The higher heritability could be attributed to the lower error variance. Overall, our results suggested that PH and TKW could be used for early generation breeding because of their high heritability, whereas CT and CCI could be also used due to their strong correlation with GY, similarly as reported by Zhang (2013) [49].

4.2. Linkage Map Construction

Molecular markers have been widely applied for genetic map construction, QTL detection, gene cloning, and MAS [15]. SNP markers are the most abundant polymorphisms in plant genomes [32], and thus, allow the high-throughput genotyping compared with previous marker platforms [30,31]. In the present study, we used the 90 K iSelect SNP array combined with SSRs to genotype a spring wheat DH population derived from a cross between UI and SY. Using 9687 polymorphic SNPs, 9330 previously mapped [31] and 357 newly mapped, we constructed a genetic map of 43 LGs that represented all the 21 chromosomes of bread wheat (Table S2) and had a total length of 3633.19 cm and an average marker density of 0.37 cm (Table S2). Our linkage map had a better marker distribution and a higher density compared with those reported in previous studies [11,23,50–55]. However, some gaps were observed in Chr. 1A and 1B-1. The A and B genomes were mapped by 4320 and 4367 markers, respectively, whereas the D genome by 1046 markers (Table S2), suggesting that the former genomes included more polymorphisms. These results were in agreement with those reported in previous studies [11,31,56].

The average number of markers mapped per chromosome was 463.5, ranging from 15 on Chr. 3D to 1125 on Chr. 6A (Table S2). Although 89.4% of mapped SNPs displayed redundancy, only 10.6% was used to construct the linkage map, similarly as in previous studies, since many SNPs were co-located at the same loci [11,57].

4.3. QTL Mapping

Previous studies reported a large number of QTL for several physiological and agronomic traits under different conditions [9–11,27,28]. In the present study, we detected QTL for CTa, CTg1, and CTg2 on Chr. 2B, 4B, 5B-2, and 6B (Tables 4 and S3). Of these, the stable QTL *Q.CTa.ui-4B.1* on Chr. 4B at 27.83–30.56 cm (Table 4; Figure 1) was different from that reported by Gao et al. (2016) [10] linked to *RAC875_c6749_954* at 42.0 cm; the stable QTL *Q.CTg1.ui-5B-2.1* on Chr. 5B at 10.96–13.69 cm was different from that reported by [21] at 52.4–55.7 cm and from that reported by Gao et al. (2016) [10] close to *wsnp_Ex_c10842_17637744* at 54.1 cm; and the stable QTL *Q.CTg2.ui-6B.1* on Chr. 6B at 87.2–88.11 cm has not been reported in any previous studies.

We also detected QTL for CCIa, CCIg1, and CCIg2 on Chr. 2D-1, 3A-2, 4A-1, and 5A (Tables 5 and S3). Of these, the QTL *Q.CCIg1.ui-5A.1* on Chr. 5A tightly linked to *IWB14149* at 91.35 cm was different from that reported by Gao et al. (2015) [11] at 72 cm; and the minor QTL *Q.CCIg2.ui-5A.1* of Chr. 5A has not been reported in any previous studies.

PH is considered as a complex trait, consisted of internode and spike length [9,58]. *Rht-B1b* and *Rht-D1b* (previously known as *Rht1* and *Rht2*) on Chr. 4B and 4D, respectively [43], that result in semi-dwarfism are widely used in wheat breeding. In the present study, both UI and SY carried *Rht-D1b*, but not *Rht-B1b*, and thus, no QTL for PH were identified on Chr. 4B and 4D. However, we detected the stable QTL *Q.PH.ui-6A-2.1* on Chr. 6A-2 that has not been reported in any previous studies as well as two QTL on Chr. 7A-2 and 5B-2 that were consistently detected in two environments, explaining 9.9%–18.3% of the phenotypic variation (Table 7). Additionally, the minor QTL *Q.PH.ui-5A* on Chr. 5A at 41.26 cm was likely the same as that previously reported by Lopes et al. (2013) [9] and Gao et al. (2015) [11]. Additionally, two minor QTL identified for PH and GY on Chr. 1A and 1B-1 might indicate that other genes for PH probably have minor, but significant effects on GY.

Previous studies reported major QTL on Chr. 5A, affecting adaptability and productivity [59–61], as well as QTL for yield-related traits on the homologous chromosome groups of 5, 6, and 7 [62]. In the present study, the stable QTL *Q.TKW.ui-2D-1* on Chr. 2D-1 between *cfd73* and *IWB1093* at 108.19–110.01 cm (Table 5; Figure 1) and the QTL *Q.TKW.ui-3D-1.2* on Chr. 3D-1 at 0–22.27 cm were different from those previously reported for TKW by Gao et al. (2015) [11].

QTL for yield and yield-related traits have been identified on Chr. 4A under drought and other stress conditions [9,28,63,64]. In the present study, we detected QTL for GY on Chr. 1A, 1B-1, 1B-2, 2A-1, 2B-2, 2B-4, 3B-1, 3D, 5A, 5B-2, 5D-3, 6A-2, 6B, and 7A-1 across all environments (Table S3), but not any on Chr. 4A. Differences in QTL locations could be attributed to the environmental conditions, which were more favorable for wheat production in the present study. However, we detected QTL on Chr. 4A-1 with pleiotropic effects on CCIa, CCIg1, and CCIg2. The stable QTL *Q.GY.ui-6B* on Chr. 6B at 26.21–32.61 cm (Table 7; Figure 1) was different from that reported by Zhang (2013) [49] at 51.9–57.3 cm.

Previous studies reported QTL clusters for various traits [10,11,65]. Here, we detected 26 QTL clusters for more than two traits (Table 8; Figure 1) on Chr. 1A, 2A-1(2), 1B-1, 2B-2, 2B-4, 5B-2, 1D-2, and 3D-1. Pleiotropic QTL for GY and PH were detected on Chr. 1A and 1B-1, and analysis of their allelic effects showed that a decrease in GY due to the presence of the SY allele was accompanied by an increase in PH (data not shown). Additionally, pleiotropic QTL for GY and KWT were found on Chr. 2A-1 and 2B-4 (2), and analysis of their allelic effects showed that the presence of the UI allele on Chr. 2A-1 increased TKW and GY (data not shown). Therefore, pleiotropic QTL confirmed the positive correlation between TKW and GY (Table 3). Pleiotropic QTL for GY and CTa and also for CTa and CTg2 were detected on Chr. 2B-2 and 4B (2), respectively. Analysis of their allelic effects showed that the presence of the UI allele reduced CTa and CTg2, but increased GY (data not shown). Thus, pleiotropic QTL on Chr. 2B confirmed the negative correlation between GY and CTa, whereas those on Chr. 4B the positive correlation between CTa and CTg2 (Table 3).

Table 8. Summary of pleiotropic QTLs identified in the SY Capstone/UI Platinum DH population.

Linkage Group	Cluster	Traits	Marker Interval	Position [a]
1A	1	PH, GY	IWB34600–IWB67661	94.35–97.08
1B-1	1	PH, GY	Barc80–IWB26010	0–18.01
	2	CTg1, CTg2, CCIg2	IWB10780–IWB58775	127.09–128
1D-1	1	CCIg1, GY	IWB42629–IWB80211	11.94–23.0
2A-1	1	TKW, GY	IWB11289–IWB1047	36.66–38.48
	2	TKW, GY	IWB56873–IWB51843	43.03–44.85
2B-2	1	CTg2, CCIg1	IWB22675–IWB11319	20.97–25.52
	2	CTa, GY	IWB11092–IWB17472	41.9–43.72
2B-3	1	CTg1, CCIa	IWB18944–Wmc149	0–24.52
2B-4	1	TKW, GY	IWB11240–IWB42141	91.17–111.28
2D-1	1	CTg2, TKW	cfd73–IWB1093	108.19–110.01
	2	CCIa, CCIg1, CCIg2, PH	IWB15442–IWB60397	133.01–134.83
3A-1	1	CTg2, CCIa	IWB33546–IWB14315	0–5.58
3B-1	1	CCIg2, TKW	IWB5790–IWB10800	50.52–54.16
3D-1	1	TKW, GY	IWB35432–IWB63148	43.71–45.53
	2	CCIa, TKW	IWB45650–Wms3	0–22.27
4A-1	1	CCIa, CCIg1, CCIg2	IWB37346–IWB10035	78.04–79.86
4B	1	CTa, CTg2	IWB20226–IWB57507	27.83–30.56
	2	CTa, CTg2	IWB12144–IWB35486	33.29–34.2
5A	1	CCIg1, CCIg2	IWB14149–IWB10765	91.35–93.17
	2	CCIg1, CCIg2	IWB21197–IWB17983	165.38–169.93
5B-2	1	CTg1, CTg2	IWB80334–IWB29709	10.96–13.69
	2	CTa, CCIg2	IWB36033–IWB19921	18.24–20.97
	3	CTa, PH	IWB36579–IWB18101	41.08–44.72
	4	PH, GY	IWB19792–IWB1762	92.11–95.75
6B	1	CTa, CTg1	IWB75959–IWB10604	0–3.64

[a] Position of QTL located on chromosome, as CM distance from the top of each linkage group. PH, plant height; GY, grain yield; TKW, thousand kernels weight; CTa, CTg1, CTg2, canopy temperature during anthesis, mid- and late grain-filling stage, respectively; CCIa, CCIg1, CCIg2, chlorophyll content index during anthesis, mid- and late grain-filling stage respectively.

4.4. Practical Applications in Wheat Breeding

Wheat GY is a complex, quantitative trait, highly affected by the environment; thus, early generation selection for high yield is usually not effective. In the present study, we suggested that CT, CCIa, PH, and TKW could be used for increasing GY using stable QTL, similarly as reported in previous studies [9,11]. GY was significantly positively correlated CCIa, PH, and TKW, negatively correlated with CTa, CTg1, and CTg2; therefore, these traits could be used for early generation and early growth stage selections. Additionally, some stable QTL, such as *Q.CTa.ui-4B.1*, *Q.CTg1.ui-5B-2.1*, *Q.CTg2.ui-6B.1*, *Q.PH.ui-6A-2.1*, *Q.TKW.ui-2D-1*, and *Q.GY.ui-6B*, could be applied in MAS for yield improvement after validation.

5. Conclusions

Genome-wide linkage mapping was used to identify QTLs associated with CTa, CTg1, CTg2, CCIa, CCIa, CCIg1, CCIg2, PH, TKW, and GY using high-density genetic linkage map in a spring wheat DH population derived from a cross between 'UI Platinum' and 'SY Capstone'. The DH population was genotyped using the wheat 90K iSelect platform and SSRs. The linkage map was constructed using a total of 9687 SNP marker and 44 SSRs, with whole linkage map of 3594.0 cm and marker density of 0.37 cm between adjacent markers. A total of 116 QTLs were detected for the nine traits on 33 linkage groups, representing the whole 21 wheat chromosomes, except for Chr. 7D. Among these QTLs, 71 QTL were for CT and CCI, and 45 QTL were for PH, TKW, and GY. Six QTLs were consistently detected more than three irrigated environments, called as stable QTL. 26 QTL clusters were identified for more than two traits, and four QTL-rich chromosome regions on these traits were found on chromosomes 4A-1, 1B-1, 5B-2, and 2D-1. These QTLs, QTL clusters and linked molecular markers may be very useful in assisted selection for improving grain yield in spring wheat breeding.

Supplementary Materials: The following are available online at http://www.mdpi.com/2073-4395/8/5/60/s1, Figure S1: The frequency distribution of canopy temperature (CT) (A), chlorophyll content index (CCI) (B), plant height (PH), thousand kernels weight (TKW) and grain yield (GY) (C) in the DH population from UI Platinum/SY Capstone in the four environments, Table S1: Phenotypic variations for physiological traits, plant height (PH), thousand kernel weight (TKW) and grain yield (GY) in UI Platinum and SY Capstone and their DH population across four trial, Table S2: Summary of the genetic linkage maps constructed with SNP, SSR and STS markers using DH population derived from UI Platinum / SY Capstone, Table S3: The names and positions of 357 newly mapped SNP markers, Table S4: Summary of QTLs detected for physiological traits, plant height (PH), thousand kernels weight (TKW) and grain yield (GY) in the UI Platinum/SY Capstone DH population.

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