DISSERTATION

MAPPING QUANTITATIVE TRAIT LOCI FOR BREAD MAKING QUALITY AND AGRONOMIC TRAITS IN WINTER WHEAT UNDER DIFFERENT SOIL MOISTURE LEVELS

Submitted by

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WE HEREBY RECOMMEND THAT THE DISSERTATION PREPARED UNDER OUR SUPERVISION BY WALID MOHAMED ROUSHDY MOHAMED EL-FEKI ENTITLED MAPPING QUANTITATIVE TRAIT LOCI FOR BREAD MAKING QUALITY AND AGRONOMIC TRAITS IN WINTER WHEAT UNDER DIFFERENT SOIL MOISTURE LEVELS BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY.

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ABSTRACT OF DISSERTATION

MAPPING QUANTITATIVE TRAIT LOCI FOR BREAD MAKING QUALITY AND AGRONOMIC TRAITS IN WINTER WHEAT UNDER DIFFERENT SOIL MOISTURE LEVELS

Drought is a major abiotic stress that affects wheat (*Triticum aestivum* L.) production in many regions of the world. Identifying quantitative trait loci (QTL) controlling important traits such as quality and yield components in winter wheat under reduced soil moisture may help develop cultivars improved for those traits. Our main objective was to identify QTL affecting quality and agronomic traits under fully irrigated and reduced soil moisture conditions.

A population of 185 doubled haploid (DH) lines derived from a cross between CO940610 and 'Platte' was grown in replicated field trials in Fort Collins and Greeley, Colorado, USA in 2007-08 and 2008-09. At each location, two side-by-side trials were planted; one trial was grown under moderate moisture stress ("dry") and one under fully irrigated ("wet") conditions, for a total of four environments. Fifteen quality traits were evaluated under both irrigation treatments: mixograph parameters, single kernel characteristics, polyphenol oxidase activity, and flour color. Seventeen agronomic traits comprising phenological parameters, morphological traits, yield and yield components, pre-harvest sprouting, normalized difference vegetation index, and drought susceptibility index were evaluated.

Moderate to high heritability estimates were observed for most of the quality traits, indicating that a large part of the expression of these traits is genetically

controlled. Heritability of yield-related traits was low to moderate indicating the greater effect of environmental conditions on these traits. Moisture stress affected most of the quality and agronomic traits. Grain yield was reduced by 795.8 kg ha^{-1} (21.4%) at Fort Collins, and by 704.0 kg ha^{-1-} (18.7%) at Greeley in the dry treatments. All kernel characteristics (kernel weight, kernel diameter, and kernel hardness), test weight, and grain protein concentration had higher mean values (P<0.05) under limited irrigation compared to the full irrigation treatments in both years. Thirty-one linkage groups spanning 2,083 cM and covering the 21 chromosomes were constructed from 221 microsatellite, diversity array technology, sequence-tagged-site, and protein markers. The composite interval mapping option of QTL Cartographer software was used in a genome-wide scan to estimate the location and effect of QTL associated with the evaluated traits. A total of 251 QTL were identified on 25 linkage groups representing 19 chromosomes. Individually, the QTL explained from 3.7 to 68.4% of the phenotypic variation, and when combined in multiple-locus models for a given trait and environment, they accounted for up to 73.8% of the phenotypic variation. Regions on chromosomes 1A, 2B, 6A, 7B, and 7D contained QTL for multiple traits. The QTL clusters on linkage groups 2B.1 and 7D.2 seem likely to coincide with the photoperiod response gene *Ppd-B1* and vernalization locus *Vrn-D3*. Genomic regions on chromosomes 1AL, 1BL, 1DL, and 7BS contained QTLs for multiple bread making quality traits. The 1AL, 1BL, and 1DL QTL most likely indicate the effects of the *Glu-A1*, *Glu-B1*, and *Glu-D1* loci. The 7BS QTL region may reflect a novel quality locus or loci. The co-localization of QTL for multiple quality traits suggests that the effects may be due to pleiotropy.

Distribution of QTL for quality traits was relatively balanced between irrigation treatments; 67 QTL (54.7%) were detected under full irrigation and 56 QTL (45.5%) were identified under limited irrigation. For agronomic traits, 64 QTL (50.0%) were detected under full irrigation and 62 (48.4%) under limited irrigation. In general, the same QTL for

most of the quality and agronomic traits were detected in both soil moisture levels. This indicates that the same set of genes controls these traits regardless of the degree of moisture, at least within the range of moisture sampled in this study. This finding is convenient for wheat breeders, who do not need to modify their selection schemes based on the moisture stress of target environments. Colocalized QTL for grain yield in the dry treatment and drought susceptibility index were identified on chromosomes 5B and 7B at Greeley. These regions deserve additional attention to determine the basis of these drought-adaptive traits.

After validation, the identified QTL may facilitate marker assisted breeding strategies or high resolution mapping leading to map-based cloning for the benefit of winter wheat breeding programs.

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LIST OF ABBREVIATIONS

Abbreviation	Description
AACC	American Association of Cereal Chemistry
Agb	Above ground biomass
BLUPs	Best Linear Unbiased Prediction
CSU	Colorado State University
DArT	Diversity array technology
DH	Doubled haploid
Dpm	Days to physiological maturity
Dsi	Drought susceptibility index
Dth	Days to heading
Fcl	Flour color value whiteness
Fcb	Flour color value yellow
Fls	Flag leaf senescence
Fpc	Flour protein concentration at 14% moisture content
Gac	Ash extraction
Gfd	Grain filling duration
Gfr	Grain filling ratio
Gpc	Grain protein concentration at 12% moisture content
Gy	Grain yield
HMW-GS	High molecular weight glutenin subunits
Ht	Plant height
Kw	Kernel weight
Ll	Leaf length
LMW-GS	Low molecular weight glutenin subunits
LOD	Logarithm of odds
Lw	Leaf width

Abbreviation	Description
Mxw	Mixograph peak width
Mrw	Mixograph right width
Mxh	Mixograph peak height
Mxt	Mixograph peak time
Mrs	Mixograph right slope
Ndvi	Normalized difference vegetation index
NIRS	Near-infrared spectroscopy
PCR	P*olymerase chain reaction*
Phs	Pre-harvest sprouting
Ppo	Polyphenol oxidase
QTL	Quantitative trait loci
RED/NIR	Red near-infrared
RIL	Recombinant inbred line
SDS-PAGE	Sodium dodecylsulfate polyacrylamide gel electrophoresis
Sha	Kernel hardness
SKCS	Single kernel characterization system
Skd	Kernel diameter
Skw	Kernel weight
Sl	Spike length
SSR	Simple sequence repeat
STS	Sequence-tagged site
Tw	Test weight
1mg	One-meter grain weight

CHAPTER 1

LITERATURE REVIEW

1.1 Importance of wheat

Common wheat (*Triticum aestivum* L.) is the world's most important food grain (http://faostat.fao.org). It is primarily milled into flour and provides a variety of end products such as bread, noodles, and cookies (Huang et al., 2006; Li et al., 2009; Raman et al., 2009; Sun et al., 2010).

The end use qualities of the grain, referred to here as quality traits, are under genetic and environmental control. Molecular genetic studies to determine this control may increase the efficiency of wheat breeding programs for improved quality (Nelson et al., 2006). There are many methods to quantify end use qualities including measurements of flour yield, protein concentration and composition, kernel texture, and dough mixing properties (Branlard et al., 2001; Zanetti et al., 2001; Ma et al., 2007a; Sun et al., 2010). Several technologies have been used to determine wheat quality characteristics, such as single kernel charachterization system (SKCS), near-infrared spectroscopy (NIR), and the mixograph. These tests are helpful to improve the end use quality required by the wheat breeder, and they provide the basis for many studies in cereal science (Bekes et al., 2001, 2006). Consequently, identifying the mechanisms underlying development of different traits controlling loci is an important challenge worldwide.

There is a need to improve the end use quality traits as well as the agronomic traits of wheat. Many quality traits are correlated to each other and allow the prediction of a significant part of bread making quality (Huang et al., 2006). Development of wheat

varieties with high yield potential and good end use quality under different environmental conditions like drought stress is an essential requirement in wheat breeding.

1.2 The effect of drought stress on wheat quality

Drought stress plays an important role in determining wheat quality (Campbell and Davidson, 1979). Generally, an increase in moisture stress creates a higher protein concentration and decreases the yield due to the reverse relationship between the yield and protein (Sun et al., 2010). Drought stress also influences wheat protein quality. When moisture stress affects wheat, the stage of rapid protein polymerization begins earlier than normal in the kernel (Daniel and Triboi, 2002). Furthermore, drought restricts green leaf area and the plant's ability to fix dry matter during grain filling, thereby causing less starch to accumulate in the grain, resulting in higher grain protein concentration (Weightman et al., 2008).

Drought often reduces yield and grain size, and is considered to reduce grain quality by reducing grain filling (Weightman et al., 2008). Drought stress and its effect on end use quality have been investigated in various studies. Guttieri et al. (2000) evaluated the cultivar x irrigation interaction effects on milling and baking quality properties of six hard red spring wheat cultivars. Cultivars did not differ significantly in the amount of flour yield. However, protein quantity per kernel increased in all cultivars with increasing water deficit.

Griffiths et al. (2009) studied 16 spring wheat cultivars produced under different moisture stress levels. Effects of drought stress on flour extraction and mixograph peak time varied between cultivars. Drought stress reduced noodle brightness and increased noodle yellowness. Mixograph peak time was significantly longer under drought stress (3.7 min) compared to the optimum conditions (2.9 min). In another study to determine the effect of drought stress, severe moisture stress was found to significantly reduce flour yield for some cultivars (Guttieri et al., 2001). Kernel and test weight were not

reduced by moderate drought stress, however they were reduced 9% and 18%, respectively, under severe moisture deficit. The same authors also studied the effect of drought stress on mixograph parameters. Moisture stress significantly reduced flour extraction and increased mixograph peak time.

Weightman et al. (2008) showed that drought stress increased kernel hardness in both seasons of their study. There was a wide range of grain weights and sizes across the doubled haploid (DH) lines in this study, and mean values for both grain weight and diameter were decreased significantly by drought in one of the two seasons. Grain protein concentration was significantly increased by drought stress in both seasons.

1.3 Mapping populations and molecular markers

1.3.1. Mapping populations

The construction of a genetic linkage map requires a segregating plant population. The parents selected for the mapping population should be sufficiently polymorphic at the DNA level that recombination events throughout the genome can be detected. Population sizes used in preliminary genetic mapping studies in the early 1990's generally range from 50 to 250 individuals (Mohan et al., 1997), however larger populations are required for high-resolution mapping. Several different populations may be utilized for mapping including RIL, DH, F2, and backcross (BC). DH populations are frequently used in wheat to map agronomic and quality traits (Suenaga et al., 2003; Eriksen et al., 2004). In this method, maize (*Zea mays* L.) pollen is used to fertilize female wheat plants, followed by embryo rescue, development of haploid plants, and chromosome doubling by dipping plants in a colchicine solution (Matzk and Mahn, 1994). This technique has been used to reduce the length of the crop improvement cycle of crops like canola (*Brassica napus* L.) and wheat by several years (Hansen and Andersen, 1998). The production of DH populations is only possible in species that are amenable to tissue culture (Collard et al., 2005). The major advantage of DH populations

is to produce homozygous lines quickly that can be multiplied and reproduced without the occurrence of genetic change. This allows for the planting of replicated trials across different locations and years. After the mapping population is created, DNA is extracted from each line in the population and analyzed with molecular markers (Suenaga et al., 2003). The markers used for analysis of the mapping population must first be tested on the two parental lines to confirm that they are polymorphic (Santra et al., 2008). Then genotyping of the whole population allows researchers to determine if each individual line is genetically similar to parent A or parent B for a specific marker, allowing the segregation to be determined and recombination events to be inferred.

1.3.2 Molecular markers

The main applications of molecular markers in cereals and other field crops can be divided into two categories: a) assessment of genetic variability and characterization of germplasm; b) identification and characterization of genomic regions controlling quantitative traits (Ribaut et al., 2002). A number of genetic marker systems have been developed for use in different plant species; however, some systems may not be suitable for all purposes. In general, a desirable marker system should detect a high level of polymorphism at specific loci, provide clear, highly repeatable, genetic information in a short period of time, and be easily automated (Liu, 1998). The first available molecular markers used were allozymes, protein variants detected by differences in migration on starch gels in an electric field. Starting in the late 1960's allozyme markers were used extensively and were relatively inexpensive to score in large numbers, but there was often insufficient protein variation for high-resolution mapping. During the mid-1980's, methods became available to evaluate genetic variation directly at the DNA level, leading to DNA based markers in mapping studies (Tanksley, 1993; Liu, 1998).

DNA markers may be divided into three classes based on the method of their detection: (1) hybridization-based; (2) polymerase chain reaction (PCR)-based; and (3)

DNA sequence-based. DNA markers are particularly useful if they reveal differences between individuals of the same or different species. These markers are called polymorphic markers, which may be classified as co-dominant or dominant. This classification is based on whether markers can discriminate between homozygotes and heterozygotes. Co-dominant markers indicate differences in size, whereas dominant markers are either present or absent and cannot distinguish heterozygous from homozygous individuals. Co-dominant markers may have many different alleles, whereas a dominant marker only has two alleles (Collard et al., 2005). Commonly used markers for detection of variation in plants are random fragment length polymorphisms (RFLPs), random amplified polymorphic DNA (RAPDs), amplified fragment length polymorphism (AFLPs), and microsatellite markers also known as simple sequence repeats (SSRs) (Mohan et al., 1997).

It is beyond the scope of this review to discuss the characteristics of all markers. However, we will describe SSRs, diversity array technology (DArTs), and glutenin protein markers, because they were used in this study.

1.3.2.1 Microsatellites (SSR)

Microsatellites or SSR are highly informative, co-dominant markers composed of tandemly repeated di- to tetra-nucleotide sequence flanked by unique sequences in the genome (Roder et al.,1998). The most common form of these repeats is simple di-nucleotide repeats; tri- and tetra-nucleotide repeats are also found in the genome but are less frequent. Polymerase chain reaction primers for the regions flanking the microsatellite are developed, and the target region is amplified followed by high-resolution electrophoresis of microsatellite PCR products. Microsatellites are locus-specific and evenly distributed along chromosomes (Roder et al., 1998). They detect a high level of polymorphism because they target highly variable regions of the genome. They have been widely used in wheat to develop maps for quantitative trait loci (QTL)

(McIntyre et al., 2010), tag resistance genes (Babar et al., 2010), enable marker assisted selection (Olson et al., 2010), and assess genetic diversity in closely related bread wheat germplasm (Huang et al., 2003).

1.3.2.2 Diversity array technology (DArT)

The DNA-based genetic marker analysis methods that depend on gel electrophoresis are limited by their low throughput (Jaccoud et al., 2001). These technologies can genotype agricultural crops with varying degrees of efficiency, but they have various degrees of limitations associated with their capability to quickly develop large numbers of markers. DArT can detect and type DNA variation at several thousand genomic loci without relying on sequence information (Wenzl et al., 2004). DArT analysis generates whole-genome fingerprint scans by scoring the presence versus absence of specific DNA sequence. The technology was developed for rice (*Oryza sativa*) studies, (Jaccoud et al., 2001) and later applied in wheat and other field crops (Akbari et al., 2006). The technology was recently used in QTL studies (Crossa et al., 2007; Griffiths et al., 2009; and Raman et al., 2009) and in an association mapping study (Neumann et al., 2010) in wheat.

1.4 Construction of genetic maps and QTL analysis

1.4.1 Genetic Maps

One of the main uses of DNA markers in plants has been to construct genetic or linkage maps for a number of field crops. A linkage map may be thought of as a 'road map' of the chromosomes derived from two different parents (Paterson, 1991). Linkage maps indicate the position and relative genetic distances between markers along chromosomes. One important use of linkage maps is to identify chromosomal locations containing major genes and QTL associated with traits of interest (Collard et al., 2005). QTL mapping is based on the fact that genes and markers segregate via chromosome recombination during meiosis, therefore allowing their analysis in the offspring

(Paterson, 1991). In a segregating population, there is a mixture of parental and recombinant genotypes. Alleles that are close together or tightly linked will be transmitted together from parent to offspring more frequently than genes or markers that are located further apart. Two commonly used mapping functions that convert recombination frequency into centi-Morgan (cM) distance are the Kosambi mapping function, which assumes that recombination events influence the occurrence of adjacent recombination events, and the Haldane mapping function, which assumes no interference between crossover events. Linkage between markers is usually calculated with an odds ratios (i.e., the ratio of linkage versus no linkage). This ratio is more conveniently expressed as the logarithm of the ratio, and is called a logarithm of odds (LOD) value or LOD score (Risch, 1992). LOD values of >3 are typically used to construct linkage maps. LOD values may be lowered in order to detect linkage over a greater distance or to place additional markers within maps constructed at higher LOD values (Collard et al., 2005). Construction of linkage maps is completed with computer software such as JoinMap (Van Ooijen et al., 2006). Linked markers are grouped together into linkage groups, which represent chromosomal segments or entire chromosomes. Markers are typically not evenly distributed over the chromosome but clustered in some regions and absent in others. The majority of the problems in genetic map construction have been the lack of informative markers with available marker types. Genetic maps are currently available for all chromosomes and homoeologous groups in wheat and a high-density microsatellite consensus map was constructed by combining four independent genetic maps of bread wheat covering 2,569 cM (Somers et al., 2004).

1.4.2 QTL detection

A QTL is a genomic region that is responsible for variation in a quantitative trait of interest (Doerge et al., 2002). Quantitative traits are controlled by a number of genes with small effects, and are typically influenced by the environment (Falconer and

MacKay, 1981). The goal of QTL analysis is to estimate the number, location, and effect of QTL controlling quantitative traits. QTL analysis is based on the principle of detecting an association between variation in phenotype and variation in genotype of a marker. Once a genetic linkage map has been constructed, the chromosomal location of the genetic factor(s) controlling the trait of interest can be located on the map. A number of methods have been developed to detect and characterize QTL, three of which are single factor analysis, simple interval mapping, and composite interval mapping. It is beyond the scope of this review to discuss the difference between all QTL analyses. However, composite interval mapping will be described as it was the primary method used in this study.

1.4.3 Composite interval mapping (CIM)

In the simple interval mapping method, the location of a QTL is determined relative to pairs of flanking markers on a linkage map. Using a maximum likelihood approach, simple interval mapping evaluates the likelihood, expressed as a LOD score that a QTL is located at a specific position, typically at each marker and each 2 cM position between adjacent markers. CIM is an enhancement of simple interval mapping, in which the location of a QTL between a pair of markers is estimated by interval mapping, while the effects of QTL located in other intervals of the genome are accounted for by regression analysis (Zeng, 1993). Zeng (1993) claimed that by utilizing this approach any bias is removed because the test statistic for the QTL of interest is independent of the effects of alternate QTL. Therefore, this method improves the power of detecting and estimating QTL effects. QTL Cartographer is a computer software package that allows composite interval mapping as an option to determine QTL location (Wang et al., 2010). Forward stepwise regression with backward elimination is a method of stepwise regression used in QTL Cartographer (Wang et al., 2010). This method ranks the markers for their effect on the quantitative trait as well as determines whether

adding or deleting a marker makes a significant difference to the fit of the model. When a step is reached where no more markers can be added, all of the markers are retested to determine whether they are still significant with their markers, or co-factors, incorporated in the analysis. CIM calculates a LOD score at each position in an interval. When a peak has exceeded the threshold significance value, a QTL is declared at that location (Zeng, 1994). Typically, a threshold LOD value of 2.5 to 3.0 is used. Significance thresholds can also be determined with permutation tests. Briefly, the phenotypic values of the population are 'shuffled' while the marker genotypic values are held constant (i.e., all marker-trait associations are broken) and QTL analysis is performed to assess the level of false positive marker-trait associations. This process is then repeated (e.g., 500 or 1000 times) and significance levels are determined based on the experiment wise level of positive marker-trait associations.

1.5 Quality traits and their genetic control

1.5.1 Mixograph traits

Bread making quality is evaluated on the basis of flour protein quality, using an instrument such as the mixograph, and through experimental bread baking procedures. Good bread flour has strong gluten which is measured by high protein quantity, high peak time, and high peak height (Campbell et al., 2001). Mixograph results can be translated into several numerical parameters (Huang et al., 2006). Mixograph peak time (Mxt), the time at which the curve reaches its maximum height, corresponds to the optimum mixing time or time to optimum dough development. Mixograph peak height (Mxh) of the center of the curve from the baseline at the time of maximum height provides an indication of flour strength. Mixograph right width (Mrw) is the distance between the upper and the lower line at two minutes after Mxt. Tolerance to over mixing is assessed by several parameters including the height of the curve at a specific time after the peak and the mixograph right slope (Mrs) between the peak and the

descending portion of the curve. This is an indication of the resistance of the dough to breakdown during continued mixing.

QTL for mixograph traits have been mapped in wheat on several chromosomes and locations (Nelson et al., 2006). A compilation of published reports of QTL for mixograph traits and other quality characteristics is presented in Table 1.2.

In a study of 185 DH lines, Huang et al. (2006) found QTL for Mxt on chromosomes 1B, 1D, and 3B; for Mxh on chromosomes 1B, 1D, and 4D; and for Mrs on chromosomes 1D and 4D. The QTL on chromosomes 1B and 1D were associated with *Glu-B1* and *Glu-D1,* respectively. The third QTL on chromosome 3B explained 20.5% of the phenotypic variance. Breseghello et al. (2005) used a population of 101 DH lines evaluated in four environments and found QTL for Mxh on chromosomes 1BS, 1BL, and 2AS and for Mxt on chromosomes 1BL and 3AS. They inferred that the effect detected on 1BS was probably caused by the gliadin locus *Gli-B1*. The gene underlying the QTL for Mxt near 1BL was probably *Glu-B1*. In another study, six QTL were associated with mixograph traits in 78 RIL (Campbell et al., 2001). They identified QTL for Mxt on chromosomes 1D, 4AL, 7AS, and 7DS, and for Mxh on chromosomes 1AL and 1BL. Using a population of DH lines, McCartney et al. (2006) identified mixograph QTL clusters on chromosomes 1B, 4D and 7D. QTL were detected for Mxh on 4D, Mxt on 1B and 1D, Mrs on 1B and 4D, and Mrw on 2B, 4D, and 7D. Some of these QTL mapped near the *Glu-B1* locus on chromosome 1B.

A major quality QTL cluster was identified on chromosome 4D, in the same interval as the largest plant height QTL, probably coincident to the *Rht-D1* locus (McCartney et al., 2005). Another major quality QTL cluster was on chromosome 7D, where a major days to heading QTL co-localized. In a similar study, Zhang et al. (2009d) identified QTL for Mxt on chromosomes 1A, 1B, 1D, and 5D and for Mrw on chromosomes 1A, 1B, 1D in a RIL population evaluated over six environments.

Table 1.1 Allele variations of HMW-GS loci in hexaploid wheat and the subunits encoded.†

Locus	Designation of Alleles	Protein Subunits Encoded	SDS-sedimentation score‡ (Payne's quality score)
Glu-A1	a	1	3
	b	2*	1
	c	null	3
Glu-B1	a	7	1
	b	7 + 8	3
	c	7+ 9	2
	d	6 + 8	1
	e	20	-
Glu-D1	a	2 + 12	2
	b	3 + 12	2
	c	4 + 12	1
	d	5 + 10	4
	h	5 + 12	-

† Obtained from Payne et al., 1987
‡ Scores are ranked from 1 to 4, indicating poor and good bread making quality, respectively. '-' Not available.

QTL for Mxt were associated with glutenin loci *Glu-B1* and *Glu-D1*, and consistent with previous studies (Campbell et al., 2001; Zanetti et al., 2001; Huang et al., 2006; McCartney et al., 2006). The QTL on 1A was associated with the *Glu-A3* locus. The QTL on chromosome 5DS occurred at the same location as the QTL for flour protein concentration which was probably due to the *Ha* locus.

1.5.2 Single kernel characterization system

The single-kernel characterization system (SKCS) instrument (Perten Instruments, Springfield, IL), evaluates wheat kernel characteristics by measuring the weight, electrical current, and force needed to crush the kernels. Kernel weight is analyzed by load cell and expressed in mg; kernel diameter and moisture concentration

Table 1.2 QTL for quality characteristics from published literature.

Trait	Population	QTL location	No. of lines	No. of env	Reference
Mixograph peak time	Grandin x AC Reed (DH)	IBL, 3AS	101	4	Breseghello et al., 2005
	NY6432-18 x Clark's Cream (RIL)	1D, 4AL,7AS, 7DS	78	6	Campbell et al., 2001
	ACKarma X 87E03-S2B1 (DH)	1B, 1D, 3B	185	3	Huang et al., 2006
	Kukri x Janz (DH)	1B, 1D	160	5	Mann et al., 2009
	RL4452 x AC Domain (DH)	1B, 1D	182	3	McCartney et al., 2006
	WPI219 x Opata85 (RIL)	1B	114	5	Nelson et al., 2006
	PDW233 x Bhalegaon4 (RIL)	1B, 4B, 7A	140	5	Patil et al., 2009
	PH82-2 x Neixiang 188 (RIL)	1A, 1B, 1D	214	6	Zhang et al., 2009d
Mixograph peak height	Grandin x AC Reed (DH)	IBS, IBL, 2AS	101	4	Breseghello et al., 2005
	NY6432-18 x Clark's Cream (RIL)	1AL, 1BL	78	6	Campbell et al., 2001
	ACKarma X 87E03-S2B1 (DH)	1B, 1D, 4D	185	3	Huang et al., 2006
	Kukri x Janz (DH)	1A, 1D, 4D, 5D, 7B	160	5	Mann et al., 2009
	RL4452 x AC Domain (DH)	4D	182	3	McCartney et al., 2006
Mixograph right slope	ACKarma X 87E03-S2B1 (DH)	1D, 4D	185	3	Huang et al., 2006
	RL4452 x AC Domain (DH)	1B, 4D	182	3	McCartney et al., 2006
Mixograph peak width	RL4452 x AC Domain (DH)	2B, 4D, 7D	182	3	McCartney et al., 2006
	PDW233 x Bhalegaon4 (RIL)	1A, 7B	140	5	Patil et al., 2009
Mixograph right width	PH82-2 x Neixiang 188 (RIL)	1A, 1B, 1D, 5D	214	6	Zhang et al., 2009d
Single kernel weight	Rye111 x Chinese spring (RIL)	1A, 1D, 2D, 6B	113		Ammiraju et al., 2001
	AC Reed x Grandin (DH)	2BL, 2DS	101	2	Breseghello and Sorrells, 2007
	PH132 x WL711 (RIL)	2BL, 2DL	106	2	Dholakia et al., 2003
	ACKarma X 87E03-S2B1 (DH)	2B, 2D, 3B, 4B, 4D, 6A, 7A	185	3	Huang et al., 2006
	Kukri x Janz (DH)	4B, 4D	160	5	Mann et al., 2009
	Sunco × Tasman (DH)	2B, 4D	163	4	Mares and Campbell, 2001

Table 1.2 Continued**.**

Trait	Population	QTL location	No. of lines	No. of env	Reference
Single kernel weight	Ning7840 x Clark (RIL)	1BS, 4B, 5AS, 6AS, 7AL	132	7	Sun et al., 2010
Single kernel hardness	Récital x Renan (RIL)	1A, 1B, 2A, 2B, 2D, 3A, 3B, 4A, 5A, 5B, 5D, 6A, 6B, 6D	165	3	Groos et al., 2004
	W7984 x Opata 85 (RIL)	5D	115	2	Igrejas et al., 2002
	Neixiang188 x Yanzhan1 (RIL)	1BL, 3B, 4B, 5D, 5A, 5B, 5D	198	2	Li et al., 2009
	Kukri x Janz (DH)	1A, 4D, 5D	160	5	Mann et al., 2009
	WPI219 x Opata85 (RIL)	5D	114	5	Nelson et al., 2006
	Courtot x CV (DH)	1A, 5D, 6D	187	2	Perretant et al., 2000
	Opata-85 x W7984 (RIL)	5D, 6A, 3A	63	2	Pshenichnikova et al., 2008
	W-7984 x Opata85 (RIL)	2AL, 2DL, 5BL, 5DS, 6DS	114	2	Sourdille et al., 1996
	Ning7840 x Clark (RIL)	1DL, 5B, 5DS, 5DL	132	7	Sun et al., 2010
	Beaver x Soissons (DH)	2A, 2D, 3A, 4A, 5A, 5D, 6D	46	2	Weightman et al., 2008
	PH82-2 x Neixiang 188 (RIL)	5D	214	6	Zhang et al., 2009d
Single kernel diameter	W7984 x Opata 85 (RIL)	1B	115	2	Breseghello and Sorrells, 2007
	NY6432-18 x Clark's Cream (RIL)	1A, 2A, 2B, 2DL	78	6	Campbell et al., 1999
	PH132 x WL711 (RIL)	2DL	106	2	Dholakia et al., 2003
	Kukri x Janz (DH)	4B, 4D	160	5	Mann et al., 2009
	Chuan35050 x Shannong483 (RIL)	2A, 5D, 6A	131	4	Sun et al., 2009
	Ning7840 x Clark (RIL)	4AL, 5AL, 5AS, 6AS	132	7	Sun et al., 2010
Grain protein content	Messapia × MG4343 (RIL)	4BS, 5AL, 6AS, 6BS, 7AS 7BS,	65	8	Blanco et al., 2002
	Latino x MG29896 (BIL)	2AS, 6AS, 7BL	92	4	Balnco et al., 2006
	PH132 x WL711 (RIL)	2BL, 7AS	106	2	Dholakia et al., 2001
	Récital x Renan (RIL)	1A, 2A, 3A, 3B, 4A, 4D, 5B, 6A, 7A, 7D	194	6	Groos et al., 2003

Table 1.2 Continued**.**

Trait	Population	QTL location	No. of lines	No. of env	Reference
Grain protein content	Récital x Renan (RIL)	3A, 5B	165	3	Groos et al., 2004
	ACKarma X 87E03-S2B1 (DH)	2D, 4B, 4D, 7B	185	3	Huang et al., 2006
	Neixiang188 x Yanzhan1 (RIL)	1B, 2A, 2B, 2D, 3A, 3B, 4D, 5B, 5D, 7B, 7D	198	2	Li et al., 2009
	Kukri x Janz (DH)	1B, 3A, 7A	160	5	Mann et al., 2009
	Sunco × Tasman (DH)	1B, 2B, 5B,	163	4	Mares and Campbell, 2001
	WPI219 x Opata85 (RIL)	2A, 2D, 6D	114	5	Nelson et al., 2006
	PDW233 x Bhalegaon4 (RIL)	7B	140	5	Patil et al., 2009
	Courtot x CV (DH)	1B, 6A	187	2	Perretant et al., 2000
	PH132 x WL711 (RIL)	2D	100	1	Prasad et al., 1999
	WL711 x PH132 (RIL)	2AS, 2BL, 2DL, 3DS, 4AL, 6BS, 7AS, 7DS	100	5	Prasad et al., 2003
	Chara x WW2449 (DH)	4A	190	2	Raman et al., 2009
	Courtot x Chinese Spring ((DH)	1BL, 6AS	217	5	Sourdille et al., 2003
	Ning7840 x Clark (RIL)	3AS, 4B	132	7	Sun et al., 2010
	DT695 x Strongfield (DH)	1A, 1B, 2A, 2B, 5B, 6B, 7A, 7B	185	6	Suprayogi et al., 2009
	Beaver x Soissons (DH)	1B, 3A, 3B, 4D, 5D, 7A, 7D	46	2	Weightman et al., 2008
Flour protein content	Grandin x AC Reed (DH)	2AS, 2BL 4B, 6B	101	4	Breseghello et al., 2005
	NY6432-18 x Clark's Cream (RIL)	1A, 2B, 7AL,7BL, 7DL	78	6	Campbell et al., 2001
	ACKarma X 87E03-S2B1 (DH)	2D, 4B, 4D, 7D, 7B	185	3	Huang et al., 2006
	Trident x Molineux (DH)	1B, 6A, 6D, 7A, 7D	182	3	Kuchel et al., 2006
	W21MMT70 x Mendos (DH)	5A	92	2	Ma et al., 2007
	RL4452 x AC Domain (DH)	1B, 4D, 6A, 6B	182	3	McCartney et al., 2006
	WPI219 x Opata85 (RIL)	2D, 6D	114	5	Nelson et al., 2006
	Chara x WW2449 (DH)	1A, 1B, 4A, 5B	190	2	Raman et al., 2009

Table 1.2 Continued**.**

Trait	Population	QTL location	No. of lines	No. of env	Reference
Flour protein content	PH82-2 x Neixiang 188 (RIL)	3A, 5D	214	6	Zhang et al., 2009d
Test weight	Wichita x Cheyenne (RIL)	3A	98	7	Campbell et al., 2003
	ACKarma X 87E03-S2B1 (DH)	2D, 4A, 4D, 5A, 7A	185	3	Huang et al., 2006
	SeriM82 x Babax (RIL)	2B, 3B, 4D, 7A	194	8	McIntyre et al., 2010
	Karl92 x TA4152-4 (AB)	2D	190	2	Narasimhamoorthy et al., 2006
Polyphenol oxidase	Zhongyou 9507 x CA9632 (DH)	2A, 2D	71	2	He et al., 2007
	Sunco × Tasman (DH)	2A, 2D	163	4	Mares and Campbell, 2001
	Zhongyou9507 x CA9632 (DH)	2AL	71	2	Sun et al., 2005
	Jennah Khetifa x Cham1 (RIL)	2A, 2B	110	4	Watanabe et al., 2004
	Jennah Khetifa x Cham1 (RIL)	2AL	110	4	Watanabe et al., 2006
Flour color L	Trident x Molineux (DH)	7B	182	3	Kuchel et al., 2006b
	Sunco × Tasman (DH)	1B, 4B, 5B, 5D	163	4	Mares and Campbell, 2001
	Cranbrook × Halberd	1A, 5D	163	6	
	CD87 × Katepwa	1B, 2D, 5B	180	2	
	Schomburgk x Yarralinka (RIL)	3A, 7A	150	3	Parker et al., 1998
	Chara x WW2449 (DH)	1B, 5B	190	2	Raman et al., 2009
	Huapei3 x Yumai57 (DH)	1B, 4B, 7B	168	3	Zhang et al., 2009a
	PH82-2 x Neixiang 188 (RIL)	1A, 1B, 3B, 4A, 7A	240	6	Zhang et al., 2009b
Flour color b	Trident x Molineux (DH)	7B	182	3	Kuchel et al., 2006b
	Sunco × Tasman (DH)	3B, 4B, 5B, 7A	163	4	Mares and Campbell, 2001
	Cranbrook × Halberd	2D, 5D, 7A	163	6	
	CD87 × Katepwa	2D, 3A, 6A, 7B	180	2	
	Chara x WW2449 (DH)	3B 4A	190	2	Raman et al., 2009
	Huapei3 x Yumai57 (DH)	2B, 3D, 4D, 5A	168	3	Zhang et al., 2009a
	PH82-2 x Neixiang 188 (RIL)	1B, 7A	240	6	Zhang et al., 2009b

are measured by electrical current and expressed in mm and as a percentage, respectively; and kernel hardness is evaluated by pressure force and expressed as an index of –20 to 120.

1.5.2.1 Kernel weight and kernel diameter

Among the various kernel related traits, single kernel weight (Skw) is one of the most important, since it is phenotypically the most stable component of yield and is also positively correlated with flour yield (Varshney et al., 2000). A study by Marshall et al. (1986) showed that changes in kernel shape and size may result in increases in flour yield of up to 5%. Furthermore, Berman et al. (1996) reported a high correlation between kernel size and flour yield. The high heritability estimates of kernel weight in most studies have proved that this trait is phenotypically a very stable kernel characteristic (Giura and Saulescu, 1996). Identifying molecular markers linked to QTL controlling kernel characteristics under different moisture levels may help wheat breeders to accelerate breeding programs to improve end use quality in wheat.

Several studies reported QTL for kernel weight and kernel diameter using different population types and environmental conditions. For kernel weight, chromosomes 1A, 1B, 3B, 4A, 5B, 5D, 6D and 7A were found to carry QTL for this trait in multiple studies (Giura and Saulescu, 1996; Campbell et al., 1999; Varshney et al., 2000; Mann et al., 2009) (Table 1.2).

Breseghello and Sorrells (2007) evaluated kernel weight and diameter in two RIL and DH populations developed from soft x hard kernel crosses over two years. They identified QTL for kernel diameter on 1B, and for kernel weight on 2BL, 2DS, and 4A. They also mentioned that some of the QTL detected in this study may have a pleiotropic effect on grain quality. The 2DS QTL caused an increase in kernel size and weight.

Recently, Sun et al. (2010) found significant positive correlations between Tw, Skw and Skd. For Skw, they identified major QTL regions on chromosomes 1BS, 4B,

5AS, 6AS, and 7AL. The most consistent QTL for Skw were identified on chromosomes 6AS and 7AL. For Skd, six QTL were identified on chromosomes 4AL, 5AL, 5AS, and 6AS, which together explained 42–71% of the phenotypic variation in different locations.

Campbell et al. (1999) conducted a QTL analysis using 78 RIL lines evaluated over six environments. The markers associated with Skw were located on chromosomes 1A, 1B, 3B, and 7A. All markers that were associated with Skw also had significant associations with either kernel length or Skd. QTL for Skd was located on chromosomes 1A, 2A, 2B, and 2DL. Furthermore, Dholakia et al. (2003) revealed two QTL for Skw on chromosomes 2BL and 2DL and one QTL for Skd on chromosome 2DL in a population of 106 RIL. They also found positive significant correlation between kernel weight and width in their study.

Mann et al. (2009) identified QTL for Skw and Skd on chromosomes 4B and 4D consistent with the location of the *Rht-B1b* and *Rht-D1b* genes, respectively, where the influence of the *Rht* genes resulted in reduced seed weight and diameter. Similarly, Huang et al. (2006) identified QTL for Skw on chromosomes 4B and 4D, in addition to other QTL on chromosomes 2B, 2D, 3B, , and 7A.

Recently, Sun et al. (2009) studied several quality traits in a population of 131 RIL. Three QTL were identified for Skd on chromosomes 2A, 5D, and 6A in different environments, explaining 6.3 to 20.0% of phenotypic variation. The QTL on 6A was a relatively stable locus, which was consistent in two environments, while the QTL on 2A and 5D were detected in one environment. They also identified QTL for Skw on chromosomes 1D, 2A, 5D, and 6A.

1.5.2.2 Kernel hardness

The main effect of hardness on bread making quality is related to higher starch damage during milling. The major determinant of hardness is the *Ha* locus located on chromosome arm 5DS, carrying two tightly linked genes, *Pina-D1* and *Pinb-D1*. Those

genes encode the lipid-binding proteins puroindoline(a) and puroindoline(b), respectively, (Martin et al., 2001). These genes are responsible for synthesis of the proteins, which have distinct compositions in soft and hard wheat cultivars. The effect of grain hardness on bread quality has been reported in several studies (Li et al., 2009; Mann et al., 2009). Martin el al. (2001) showed that *Pina-D1* gives harder endosperm, lower milling yield and higher water absorption compared to *Pinb-D1*.

Several studies have investigated QTL for kernel hardness (Sha) in different populations and environments (Table 1.2). Sourdille et al. (2003) identified QTL for Sha on chromosomes 1AL, 5DS, and 6AL. Similarly, Turner et al. (2004) identified QTL for the same trait on chromosomes 5D and another on 1B. Furthermore, Sourdille et al. (1996) identified QTL on chromosomes 2AL, 2DL, 5BL, 5DS, and 6DS. Generally, the previous studies demonstrate the importance of the *Ha* locus on chromosome 5D, but also show that QTL for Sha are distributed on many other chromosomes.

Weightman et al. (2008) studied the effect of drought stress on Sha using a DH wheat population evaluated over two years. As expected from previous studies, the major QTL for hardness on 5D was detected in both seasons and across both irrigation treatments. In addition, other QTL for hardness were found on chromosomes 2A, 2D, and 3A under all moisture levels

In a study to determine the effect of drought stress on kernel characteristics, Pshenichnikova et al. (2008) conducted an experiment using 63 RILs evaluated over two seasons. Three QTL were identified for Sha on chromosome 5DS, apparently corresponding to *Ha.* They also detected two QTL on chromosomes 6AL and 3AL. The QTL located on 6AL is highly significant under both moisture stress conditions. Similarly, Igrejas et al. (2002) studied QTL controlling kernel hardness in a population of 115 RIL population. The researchers observed a QTL on chromosome 5D for kernel hardness that was consistent in the both years of the study.

The studies completed by Groos et al. (2003, 2004) provided an insight on Sha in the same population. They evaluated Sha using both SKCS and NIR. Eleven QTL were identified for NIR-Hardness, on 1A, 2A, 2D,3A, 4A, 5A, 5B,5 D, 6A, and 6D. For SKCS-hardness they detected QTL on chromosomes 1B, 2B, 2D, 3A, 3B, 4A, 5A, 5B, 6B, and 6D. The QTL on chromosome 1A is close to the protein loci *Gli-A1* and *Glu-A3* and could be due to an effect of one of these genes on hardness.

Li et al. (2009) constructed a linkage map using 250 SSR and five glutenin loci to identify QTL for Sha and evaluated in two environments. Several QTL for Sha were identified on chromosomes1BL, 3B, 4B, 5D, 5A, 5B, and 5D, which individually explained 2.6 to 27.7% of the phenotypic variation. The QTL on 5D seems with be coincident to the *Ha* locus.

1.5.3 Grain and flour protein concentration

1.5.3.1 Near infrared spectroscopy

Near infrared spectroscopy (NIR) provides a method for a rapid and accurate analysis of the composition of a sample. Grain protein concentration (Gpc) is an important grain quality trait in bread wheat. Gpc is considered a quantitative trait controlled by several genes distributed throughout the hexaploid wheat genome (Borner et al., 2002; Groos et al., 2003; Prasad et al., 2003), and influenced by genotype, environmental factors, and nutrient availability.

A major objective for wheat breeders is to increase grain yield while maintaining or increasing the Gpc. Improvement for both traits has been limited by the negative relationship between Gpc and grain yield in wheat (Simmonds, 1995). On the other hand, Groos et al. (2003) revealed no negative relationships between yield and grain protein concentration.

1.5.3.2. Grain protein concentration

Wheat has the highest grain protein concentration (Gpc) among cereals, ranging from 8 to 16%. Protein is the second most abundant substance in wheat kernels next to starch. Wheat proteins are classified as albumins, globulins, gliadins, and glutenins based on their solubility (Branlard et al., 2001).The two main seed storage protein groups of wheat are gliadins and glutenins, which are the major components of wheat gluten structure. Gluten proteins, which comprise up to 85% of endosperm proteins, are the major components influencing the viscoelastic properties of the dough and baking quality (Gianibelli et al., 2001; Eagles et al., 2004). These proteins are built up from a number of subunits linked by disulfide bonds. Gliadins are important in dough viscosity and extensibility, and glutenins affect dough strength. The glutenin proteins are classified as low or high molecular weight based on their subunit composition. The low molecular weight (LMW) glutenin proteins are encoded by the *Glu-3* orthologous genes on 1AS, 1BS, and 1DS (Singh and Shepherd, 1988). The high molecular weight (HMW) glutenin proteins are encoded by the *Glu-1* orthologous genes on 1AL, 1BL, and 1DL (Payne, 1987). The gliadins are encoded by the *Gli-1* and *Gli-3* genes on 1AS, 1BS, and 1DS and the *Gli-2* genes on 6AS, 6BS, and 6DS (Payne et al., 1987). These proteins can be extracted from wheat flour and separated into two groups by sodium dodecylsulfate polyacrylamide gel electrophoresis (SDS–PAGE).

Several researchers found that as the glutenin to gliadin ratio increased there was an increase in dough strength and loaf volume (Uthayakumaran et al., 2000). Wheat with hard kernels and strong gluten are used for leavened bread, while wheat with soft kernels and weak gluten are used for flatbreads (McCartney et al., 2006). Due to the relationships between protein concentration and end use quality, and taking into account the effects of environmental stresses on protein concentration, accurate predictions of bread making quality can be made.

Environmental factors, such as temperature, soil moisture and nitrogen nutrition have major effects on protein concentration (Daniel and Triboi, 2002). For example, drought stress was associated with protein concentration, and therefore, end use quality of wheat, in three Colorado locations (Zheng et al., 2009). Wheat from the lowest rainfall location had the highest grain and flour protein concentrations and the fully irrigated location had the lowest protein concentration in that study.

The HMW-GS of wheat have been studied by many researchers in detail because of their important role in determining bread making quality. The HMW-GS account for 10 to 20% of total prolamins and only 5 to 15% of total flour protein (Singh and Khatkar, 2005). The LMW-GS represent about one-third of the total seed protein and around 60% of total glutenins (D'Ovidio and Masci, 2004). Genetic studies have shown that the allelic composition of these proteins is correlated with differences in dough physical properties (Payne et al., 1987; Table 1.1). Zheng et al. (2009) reported the effects of HMW and LMW alleles on bread making quality of recent Great Plains cultivars.

QTL for Gpc have been identified on chromosomes 4B, 5A, 6A, 6B, and 7B in durum wheat (Blanco et al., 1996). Weightman et al. (2008) studied the effect of drought stress on Gpc in a DH wheat population over two years. Under moderate moisture stress they identified QTL on chromosomes 1B, 4D, 5A, 7A, and 7D, while under the well watered condition they found QTL on chromosomes 3A, 3B, 5D, and 7A. As observed in previous studies, Gpc increased under drought stress treatment.

Blanco et al. (2002) constructed an RFLP map from a wheat population of 65 RIL evaluated in eight environments. Six chromosome arms were associated with variation in Gpc: 4BS, 5AL, 6AS (two loci), 6BS, 7AS and 7BS. Of the seven QTL, four were detected in two environments. However, detection in only two environments indicates that individual QTL seem to be sensitive to environmental factors. Furthermore, Blanco

et al. (2006) evaluated 92 backcross inbred durum wheat lines in four environments. They found QTL for Gpc on chromosomes 2AS, 6AS, and 7BL. On the other hand, Huang et al. (2006) found QTL on other chromosomes for Gpc on 2D, 4B, and 7D in a DH population evaluated in three environments.

Suprayogi et al. (2009) evaluated a durum wheat population of 185 DH lines under three moisture levels. They identified eight QTL for Gpc on chromosomes 1A, 1B, 2A, 2B, 5B, 6B, 7A, and 7B. However, they were not consistent in all environments. The QTL located on chromosome 7A were consistent in all environments even under the most severe drought stress condition. The QTL on 2A was expressed in three environments. The effect of genotype by environment (G x E) interactions was high, as shown by the low correlation of means among environments and the moderate heritability estimate across environments of (0.51 to 0.70).

One hundred ninety-four RIL were evaluated by Groos et al. (2003) in six environments to identify QTL for Gpc. They found QTL on chromosomes 1A, 2A, 3A, 3B, 4A, 4D, 5B, 6A, 7A and 7D. Similarly, Li et al. (2009) identified 16 QTL for Gpc detected in the two environments and distributed on chromosomes 1B, 2A, 2B, 2D, 3A, 3B, 4D, 5B, 5D, 7A, 7B and 7D. Among them, 3A, 4D, 5B, and 7B were detected in both environments. Mann et al. (2009) identified QTL for Gpc in 165 DH lines evaluated in five environments on chromosomes 1B, 3A, and 7A. The average protein concentration for the sites ranged from 10.5 to 14.6%.

Patil et al. (2009) evaluated a 140 RIL durum wheat population in five environments. A significant QTL on chromosome 7B was detected in the same position as QTL reported by Blanco et al. (2002) and Groos et al. (2003). Recently, Sun et al. (2010) identified QTL for Gpc in a set of 132 RIL evaluated in seven environments. Two QTL were detected on chromosomes 3AS and 4B and explained 19 to 36% of the phenotypic variance for Gpc in different experiments.

Several studies have been conducted to identify QTL for flour protein concentration (Fpc). Campbell et al. (2001) evaluated 78 RIL in six environments. The primary QTL for flour protein quantity were on 1A, 2B, 7AL, 7BL, and 7DL. Kuchel et al. (2006) found QTL on chromosomes 1B, 6A, 6D, 7A, and 7D in a DH population tested in three environments. The QTL on 6A was identified in all environments in the same position for QTL associated with flour yield. Similarly, Nelson et al. (2006) identified a region on chromosome arm 6DS containing the *Gli-D2* gliadin locus that consistently influenced Gpc and Fpc. They also identified other QTL on chromosomes 2A and 2D.

A population of 182 DH lines was evaluated in three environments and the results showed QTL on chromosomes 1B, 4D, 6A, and 6B for Fpc (McCartney et al., 2006). On the other hand, Zhang et al. (2009c) identified QTL on chromosomes 3A and 5D for Fpc in a RIL population evaluated in six environments.

1.5.4 Test weight

Test weight (Tw) is used as an indicator of overall grain quality and to determine the price of wheat in many countries. When grain density is lower, more volume is required to store and transport the grain, which adds more expense to the wheat growers.

Five QTL associated with Tw were reported in a study by Huang et al. (2006). They found QTL on chromosomes 2D, 4A, 4D, 5A, and 7A. Of five QTL detected for Tw, two QTL on chromosomes 5A and 7A were colocalized with QTL for grain yield, and another QTL on chromosome 4DS was located in the same position as a QTL for plant height. The QTL on 7A was located in a similar position to a QTL for Tw on chromosome 7AS detected by Elouafi and Nachit (2004) in a durum wheat population. Campbell et al. (1999) found four QTL for Tw on chromosomes 2B, 2DL, 4AL, and 7AS, however, they were not consistent over environments. McCartney et al. (2005) identified 10 QTL associated with Tw in a DH population evaluated under different moisture levels. The

most significant Tw QTL were detected on chromosomes 3B and 4D, and other minor Tw QTL were located on chromosomes 1B, 1D, 2D, 3D, 4D, and 5D, but were not consistent across environments.

1.5.5 Flour color

Flour color is an important criterion of wheat quality and is important in determining the quality of the end product (Parker et al., 1998). Flour color is genetically controlled, and factors such as brightness and yellowness of flour have been targets for selection in many wheat quality studies (Zhang et al., 2009c). Color readings are usually expressed as L* (brightness), a* (red-green chromaticity), and b* (yellow-blue chromaticity) of the flour sample. A pure white flour should have zero values for a* and b*, and 100 for L* (Zhang et al., 2009c). Variation in flour color exists among wheat genotypes. Furthermore, environmental stresses and milling processes may impact flour color.

In a study to determine flour color, Kuchel et al. (2006) used a Minolta color meter to evaluate 182 DH over three environments. Flour color traits were significantly (P<0.01) correlated with flour protein concentration. A major QTL for flour color b* (Fcb) was identified on chromosome 7B and explained 48% of the phenotypic variation. A QTL associated with Fcb has also been reported on chromosome 7B (Mares and Campbell, 2001).

Mares and Campbell (2001) identified several QTL for flour color L* (Fcl) on chromosomes 1A ,1B, 2D , 4B, 5B, and 5D in three DH populations, and on chromosomes 2D, 3A, 3B, 4B, 5B, 5D, 6A, 7A, and 7B for Fcb. Most of these regions were consistent over different sites and years. The QTL located on chromosome 4B was associated with both Fcl and Fcb, and also appeared to correspond to a QTL for plant height and grain size. Similarly, Parker et al. (1998) identified a QTL located on chromosome 7A that was associated with flour color.

1.5.6. Polyphenol oxidase activity (Ppo)

Ppo enzymes are “copper-containing metallo-enzymes, which are encoded in the nucleus and then transported into the plastids” (Anderson and Morris, 2003). Ppo is the main factor involved in darkening of wheat products (Feillet et al., 2000; Simeone et al., 2002), especially Asian noodles (Kruger et al., 1994; Baik et al., 1995; Mares and Campbell, 2001; Fuerst et al., 2006). Therefore, the development of wheat cultivars with low grain Ppo activity is an important objective in wheat breeding programs (Mares and Campbell, 2001).

Several reports identified Ppo QTL on group 2 chromosomes especially on chromosomes 2A and 2D (Jimenez and Dubcovsky, 1999; Anderson and Morris, 2001; Sun et al., 2005; He et al., 2007). Furthermore, a QTL of minor effect was detected on chromosome 2B in many studies (Demeke et al., 2001; Watanabe et al., 2004). Mares and Campbell, (2001) identified a highly significant region on chromosome 2D associated with variation in Ppo levels that accounted for 39% of the phenotypic variation. Measurements of grain Ppo activity were not correlated with Fcl (r = 0.051). In a similar study, Watanabe et al. (2004) identified two QTL located on chromosomes 2A and 2B responsible for Ppo activity.

1.6 Phenological parameters: Days to heading, days to physiological maturity, grain filling duration, grain filling rate, and flag leaf senescence

Flowering time is a critical trait in wheat; optimum flowering time can help wheat plants escape from dry conditions late in the season and freeze risk in early spring, thereby maintaining optimum grain yield. Flowering time in wheat is genetically controlled by several genes. There are five wheat vernalization loci: *Vrn-A1* on chromosome 5AL (Galiba et al., 1995), *Vrn-B1* on chromosome 5BL (Iwaki et al., 2002), *Vrn-D1* on chromosome 5DL (Nelson et al., 1995b), *Vrn-B3* on chromosome 7BS (Yan et al., 2006), and *Vrn-D3* on chromosome 7DS (Wang et al., 2009). Winter wheat life

cycle from planting to maturity is passed by several important physiological and morphological stages, including seedling emergence, stem elongation, heading, flowering, and maturity (Chen et al., 2009). Wheat is exposed to a period (6 to 8 weeks) of low temperature (2 to 8 C°) to increase accelerate t he transition from vegetative to reproductive stages which known as vernalization. After vernalization the reproductive developmental rate that regulates the phase change of plant growth will be mainly affected by genes in the photoperiod pathway (Wang et al., 2009). The major genes affecting photoperiod response in wheat, *Ppd-A1*, *Ppd-B1*, and *Ppd-D1*, were mapped to the homoeologous positions on the short arms of group 2 chromosomes (Scarth and Law, 1983). Optimum flowering time in wheat makes maximum use of resources available throughout the growing season, unless biotic or abiotic stresses affect specific stages of plant development, which can lead to a negative effect on grain yield and quality (Worland, 1996).

McCartney et al. (2005) found four QTL for days to physiological maturity (Dpm) on chromosomes 4A, 4D, and 7D. The most significant QTL was located on chromosome 7D, had a LOD score of 17.5, and explained 25.7% of the phenotypic variation. The 7D QTL mapped to a similar region as a QTL for days to heading (Dth), which was mapped by Börner et al. (2002). In a similar study, Huang et al. (2006) identified three QTL for Dpm on chromosomes 2D, 5D and 7D.

Cuthbert et al. (2008) evaluated a population of 178 DH spring wheat lines over 12 environments. They identified QTL for grain filling duration (Gfd) on chromosomes 2D, 3A, 5A, 5B, and 7B; for Dth on chromosomes 1B, 2D, 3A, 5A, 6B, 7B, and 7D; and for Dpm on chromosomes 1B, 3B, 5A, 5B, 6B, 7A, 7B, and 7D. Four of the QTL identified for Dth coincident with QTL for Dpm which can be explained by the highly significant correlation between the two traits.

Zhang et al. (2009a) identified six QTL for Dth on chromosomes 1B, 2B, 5D, 6D, 7A, and 7D in three environments. The 5DL QTL seems likely to be coincident with the vernalization gene *Vrn-D1*. This *Vrn* locus was identified in another mapping population (Nelson et al., 1995; Borner et al., 2002).

Griffiths el al. (2009) developed four DH populations (Table 1.3) that represent diversity in European winter wheat germplasm. Several QTL were detected across environments for Dth on chromosomes 1B, 1DL, 2A, 3A, 3B, 4B, 4D, 5A, 5B, 6A, 6B, 7A, 7B and 7D. The major effects identified on the group 7 chromosomes were due to vernalization genes, *Vrn-B3* and *Vrn-D3* located on chromosome 7B and 7D, respectively. Similarly, Sourdille et al. (2003) identified QTL for days to heading on chromosomes 5A, 7B, and 7D using different types of populations.

Börner et al. (2002) evaluated a set of 114 wheat RIL over four years. For Dth major QTL were identified on chromosome 2DS, 3AL, and 5DL, and minor QTL were detected in the distal region of chromosome arm 7DS. QTL on chromosomes 2BS and 2DS seem to be coincidental with the major photoperiod genes *Ppd2* and *Ppd1*, respectively, while the QTL detected on 5DL correspond to *Vrn-D1*. This vernalization response locus had been discovered previously by Nelson et al. (1995) in the same mapping population. In two environments minor QTL for Dth were detected on chromosome 7DS, probably corresponding to *Vrn-D3*. In another study, 136 RIL were evaluated over five environments and used to determine QTL for Dth (Lin et al., 2008). They identified QTL on chromosomes 1B, 1D, 2B, 2D, 4A, and 7B. The major QTL for Dth was detected on chromosome 7BS. In the same interval, Kuchel et al. (2006) mapped a photoperiod QTL associated with heading date under short day winter conditions.

Table 1.3 QTL for agronomic characteristics from published literature.

Trait	Population	QTL location	No. of lines	No. of env	Reference
Days to heading	Chinese Spring x Kanto107 (RIL)	4A	98	2	Araki et al., 1999
	Norstar x Manitou (DH)	2B, 4A, 6A	142	1	Baga et al., 2009
	Opata 85 x W7984 (RIL)	2DS, 3AL, 5DS, 5DL, 7DS	114	11	Börner et al., 2002
	TA4152-60 x ND495 (DH)	5AL, 5BL	120	4	Chu et al., 2008
	Superb x BW278 (DH)	1B, 2D, 3A, 5A, 6B, 7B, 7D	178	12	Cuthbert et al., 2008
	Avalon x Cadenza (DH)	1B, 1D, 2A, 3A, 4B, 5A, 6A, 6B, 7A	202	3	Griffiths et al., 2009
	Charger x Badger (DH)	1B, 2A, 3B, 6B	93	7	
	Spark x Rialto (DH)	1B, 1D, 2A, 3A, 3B, 4B, 5A, 6A, 7A, 7D	129	10	
	Savannah x Rialto (DH)	1D, 3A, 7D	126	3	
	Renan x Recital (RIL)	2B, 2D, 5A, 5B, 7A, 7D	194	3	Hanocq et al., 2004
	Prinz x W-7984 (AB)	2A, 2D, 3B, 5A, 5B, 6A 7B	72	4	Huang et al., 2003
	Trident x Molineux (DH)	1AL, 2AS, 6DS 7AS	182	18	Kuchel et al., 2006
	Nanda 2419 x Wangshuibai (RIL)	1B, 1D, 2B, 2D, 4A, 7B	136	5	Lin et al., 2008
	Kofa x Svevo (RIL)	2A, 2B, 7B	249	16	Maccaferri et al.,2008
	Ning7840 x Clark (RIL)	3BL, 5B, 6B	132	5	Marza et al., 2006
	SeriM82 x Babax (RIL)	1B, 1D, 4A, 5D	194	8	McIntyre et al., 2010
	Karl92 x TA4152-4 (AB)	2D, 3D	190	2	Narasimhamoorthy et al., 2006
	WPI219 x Opata85 (RIL)	2D	114	5	Nelson et al., 2006
	Courtot x Chinese Spring ((DH)	2BS, 5AL, 7BS, 7BL, 7DL	217	5	Sourdille et al., 2003
	Heshangmai x Yu8679 (RIL)	1B, 2B, 3B, 5D, 6D	142	4	Wang et al., 2009
	Huapei3 x Yumai57 (DH)	1B, 2B, 5D, 6D, 7A, 7D	168	3	Zhang et al., 2009
Days to physiological maturity	ACKarma X 87E03-S2B1 (DH)	2D, 5D, 7D	185	3	Huang et al., 2006
	Superb x BW278 (DH)	1B, 3B, 5A, 5B, 6B, 7A, 7B, 7D	178	12	Cuthbert et al., 2008
	Ning7840 x Clark (RIL)	4A, 4D, 7D	132	5	Marza et al., 2006

Table 1.3 Continued**.**

Trait	Population	QTL location	No. of lines	No. env	Reference
Days to physiological maturity	Heshangmai x Yu8679 (RIL)	1B, 2A, 2B, 3D, 4B,6D	142	4	Wang et al., 2009
Grain filling duration	Opata 85 x W7984 (RIL)	5AL, 5B, 6AS	114	11	Börner et al., 2002
	Superb x BW278 (DH)	2D, 3A, 5A, 5B, 7B	178	12	Cuthbert et al., 2008
	Heshangmai x Yu8679 (RIL)	1A, 3B, 5D, 6D	142	4	Wang et al., 2009
Grain filling rate	Dharwar x Sitta (RIL)	4A	127	7	Kirigwi et al., 2007
	Heshangmai x Yu8679 (RIL)	1A, 1B, 2A, 3A, 3B, 3D, 4D, 5B, 6D	142	4	Wang et al., 2009
Flag leaf senescence	Beaver x Soissons (DH)	2B, 2D	48	2	Verma et al., 2004
Plant height	Opata 85 x W7984 (RIL)	1AS, 2DS, 4AL, 6A	144	3	Borner et al., 2002
	Courtot x Chinese Spring (DH)	3D, 4B, 4D, 5A, 5B, 6B, 6D, 7A, 7B	275	3	Cadalen et al., 1997
	Wichita x Cheyenne (RIL)	3A	98	7	Campbell et al., 2003
	TA4152-60 x ND495 (DH)	4DS, 5AL	120	4	Chu et al., 2008
	CA9613 x H1488 (DH)	1A, 1D, 2A, 2B, 3D, 4A, 6A, 7D	108	4	Hai et al., 2008
	ACKarma X 87E03-S2B1 (DH)	4BL, 4DS, 5DL, 7BS	185	3	Huang et al., 2006
	ND3338 x F390 (RIL)	1B, 4B, 6A , 6D, 7A	240	2	Liu et al., 2002
	Kofa x Svevo (RIL)	1BS, 2BL, 3AL, 3BS, 7BS	249	16	Maccaferri et al., 2008
	Ning7840 x Clark (RIL)	2B, 2D, 3B, 4B, 6A	132	3	Marza et al., 2006
	RL4452 × AC Domain (DH)	2D, 4B, 4D, 5B, 7A, 7B	182	8	McCartney et al., 2005
	SeriM82 x Babax (RIL)	1D, 2B, 4A, 4B, 5B, 5D	194	8	McIntyre et al., 2010
	Courtot x Chinese Spring ((DH)	4BS, 4DL, 7AL, 7BL	217	5	Sourdille et al., 2003
	Chuan-Mai18 x Vigour18 (RIL)	2AS, 6AS	460	2	Spielmeyer et al., 2007
	Heshangmai x Yu8679 (RIL)	1D, 2D, 3D, 4D	142	4	Wang et al., 2009
Spike length	Opata 85 x W7984 (RIL)	1BS, 4AS, 4AL, 5AL	114	4	Borner et al., 2002
	TA4152-60 x ND495 (DH)	1AL, 1AS, 1B, 2BL, 2BS, 3BL, 4B,5B, 7A, 7BS	120	4	Chu et al., 2008
	Nanda2419 x Wangshuibai (RIL)	1A, 2D, 4A, 5B, 7D	136	2	Ma et al., 2007

Table 1.3 Continued**.**

Trait	Population	QTL location	No. of lines	No. of env	Reference
Kernel weight	Opata 85 x W7984 (RIL)	3AS, 5AL, 6BS, 7DS	114	11	Börner et al., 2002
	NY6432-18 x Clark's Cream (RIL)	1AS, 1BS, 3B, 7A	78	6	Campbell et al., 1999
	Superb x BW278 (DH)	2D, 3B, 5A, 7A	178	12	Cuthbert et al., 2008
	CA9613 x H1488 (DH)	2B, 7B	108	4	Hai et al., 2008
	Prinz x W-7984 (AB)	2A, 2D, 4D, 5B, 7A, 7B, 7D	72	4	Huang et al., 2003
	Trident x Molineux (DH)	6A, 7D	182	18	Kuchel et al., 2007
	Rye Selection111 x Chinese Spring (RIL)	3A	100	6	Kumar et al., 2006
	Chuang35050 x Shannong483 (RIL)	1D, 5D, 6A, 7D	131	6	Li et al., 2007
	Nanda 2419 x Wangshuibai (RIL)	2B, 7B	136	5	Lin et al., 2008
	RL4452 × AC Domain (DH)	2A, 3D, 4A, 4B, 4D, 6D	182	8	McCartney et al., 2005
	Opata-85 x W7984 (RIL)	1B, 2D	63	2	Pshenichnikova et al., 2008
	Chara x WW2449 (DH)	6B, 7A	190	2	Raman et al., 2009
	Chuan35050 x Shannong483 (RIL)	1D, 2A, 5D, 6A	131	4	Sun et al., 2009
	Heshangmai x Yu8679 (RIL)	1B, 2A, 2D, 3B, 4A, 4D, 5A, 6D, 7D	142	4	Wang et al., 2009
	PH82-2 x Neixiang 188 (RIL)	1B, 4A, 5D, 7A	214	6	Zhang et al., 2009c
Harvest index	Superb x BW278 (DH)	1A, 3A, 3B, 5A, 5B	178	12	Cuthbert et al., 2008
	WL711x PH132 (RIL)	2BL, 3AL, 4AL	100	6	Kumar et al., 2007a
	Opata85 x W7984 (RIL)	2DS, 3BL, 4BL, 6AL	110	6	Kumar et al., 2007b
	SeriM82 x Babax (RIL)	1B, 1D, 4D, 6A, 7A	194	8	McIntyre et al., 2010
Above ground biomass	Dharwar x Sitta (RIL)	4A	127	7	Kirigwi et al., 2007
	Nanda 2419 x Wangshuibai (RIL)	1B, 5B, 5D, 7A, 7D	136	5	Lin et al., 2008
Grain yield	Chinese Spring x Kanto107 (RIL)	4A	98	2	Araki et al., 1999
	Wichita x Cheyenne (RIL)	3A	98	7	Campbell et al., 2003

Table 1.3 Continued**.**

Trait	Population	QTL location	No. of lines	No. of env	Reference
Grain yield	Superb x BW278 (DH)	1A, 2D, 3B, 5A	178	12	Cuthbert et al., 2008
	Récital x Renan (RIL)	2B, 3B, 4A, 4B, 5A, 5B, 7D	194	6	Groos et al., 2003
	Prinz x W-7984 (AB)	1B, 2A, 2D, 5B	72	4	Huang et al., 2003
	ACKarma X 87E03-S2B1 (DH)	5A, 7A, 7B	185	3	Huang et al., 2006
	Dharwar x Sitta (RIL)	4A	127	7	Kirigwi et al., 2007
	Trident x Molineux (DH)	1B, 2D, 3D, 4D, 6A, 6D	182	18	Kuchel et al., 2007
	WL711x PH132 (RIL)	1DL, 2DL, 3BL, 4AS, 4DL, 7AS, 7AS	100	6	Kumar et al., 2007a
	Opata85 x W7984 (RIL)	1AL, 2AS, 2DS, 4BL, 6DL	110	6	Kumar et al., 2007b
	Chuang35050 x Shannong483 (RIL)	1D, 2D, 3B, 6A	131	6	Li et al., 2007
	Kofa x Svevo (RIL)	2B, 3B, 7B	249	16	Maccaferri et al.,2008
	Sunco × Tasman (DH)	2B, 4D		4	Mares and Campbell, 2001
	Ning7840 x Clark (RIL)	1AL, 1B, 2BL, 4AL, 4B, 5A, 5B, 6B, 7A, 7DL	132	5	Marza et al., 2006
	RL4452 × AC Domain (DH)	2A, 2B, 3D, 4A, 4D	182	8	McCartney et al., 2005
	SeriM82 x Babax (RIL)	6D, 7A	194	8	McIntyre et al., 2010
	Chinese Spring X SQ1 (DH)	1AS, 1BL, 2BS, , 4AS, 4AL, 4BS, 4BL, 4DL,5AL, 5BS, 5BL, 5DS, 5DL,6BL, 7AL, 7BS, 7BL	96	24	Quarrie et al., 2005
Pre-harvest Sprouting	NY6432-18 x 'Clark's Cream' (RIL)	1A	78	6	Anderson et al., 1993
	NY18 x NY6432-10 (RIL)	3B, 4A, 5D, 6B	138	7	Anderson et al., 1993
	AC Domain x 'White-RL4137 (DH)	3A, 3B, 3D, 5D	174	3	Fofana et al., 2008
	Cranbrook x Halberd (DH)	2AL, 2DL, 4AL	157	2	Mares and Marva. 2001
	AUS1408 x SW95-50213 (DH)	4AL	95	2	Mares et al., 2005
	SUN325B/QT7475 (DH)	3BL	92	2	Mares et al., 2009
	SPR8198 x 9HD2329 (RIL)	1AS, 2AL, 2DL, 3AL, 3BL	90	6	Mohan et al., 2009
	Cayuga x Caledonia (DH)	2B, 2D, 3D, 6D	206	16	Munkvold et al. 2009
	'CN19055 x ''Annuello'' (RIL)	4AL	319	4	Ogbonnaya et al., 2008
	Cascades x AUS1408	4AL, 5BL	83	3	Tan et al., 2006

Chu et al. (2008) developed a population of 120 DH lines and identified two major QTL for Dth on chromosomes 5AL and 5BL. The QTL on 5A explained 41% of phenotypic variation and probably corresponded to *Vrn-A1*, which was also indicated by Galiba et al. (1995) and Hanocq et al. (2004). The 5B QTL explained 15% of phenotypic variation and may correspond to *Vrn-B1*.

Flag leaf senescence (Fls) is the outcome of different biochemical and physiological process which determine the final stage of leaf development. Fls is affected either by internal hormonal factors affecting ageing or by external environmental factors such as temperature or drought. Flag leaf photosynthesis in wheat contributes about 30 to 50% of the assimilates for grain filling (Verma et al., 2004). The same authors evaluated DH under different moisture stress to identify QTL for flag leaf senescence. They identified QTL on chromosomes 2B and 2D.

1.7. Plant height

Plant height is an important trait for wheat breeding because it is related to plant biomass and lodging resistance. Appropriate plant height is an important trait to achieve the desired yield level in wheat. Tall wheat cultivars are more sensitive to lodging whereas semi-dwarf cultivars are shorter, less sensitive to lodging and usually partition more dry matter to the grain (Huang et al., 2006).

There have been several QTL mapping studies on wheat plant height *(*Ht), resulting in QTL on most of the 21 chromosomes that are associated with this trait under different moisture levels (Sourdille et al., 2003).

Maccaferri et al. (2008) evaluated a RIL wheat population in 16 environments over two years in different Mediterranean locations (10 rainfed and 6 irrigated locations) (Table 1.3). They identified five major QTL for Ht, on chromosomes 1BS in seven environments, 2BL in nine environments, 3AL in 10 environments, 3BS in 11

environments, and 7AS in 6 environments. The QTL were inconsistent over environments, especially under different moisture levels.

Cadalen et al. (1998) detected nine QTL associated with wheat Ht in a DH population. These QTL were distributed on chromosomes 3D, 4B, 4D, 5A, 5B, 6B, 6D, 7A, and 7B. Two of these QTL, on 4B and 4D, were associated with dwarfing loci *Rht-B1* and *Rht-D1,* respectively, which have major effects on plant height in wheat. Yu and Bai (2010), observed similar results in a wheat RIL population, where they detected four QTL for Ht on chromosomes 3D, 5A, and 4D. The QTL on 4D showed larger effects on Ht and explained 40 to 59% of phenotypic variation.

In another study by Hai et al. (2008) a population of 108 DH lines were evaluated in four environments. They identified 10 QTL on chromosomes 1A, 1D, 2A, 2B, 3D, 4A, 6A, and 7D. Only one common QTL on 2A was identified across the four environments and it explained more than 23% of the total phenotypic variation for Ht. Similarly, Borner et al. (2002) reported the same QTL locations (1A, 4A, and 6A), in addition to another QTL on 6AS.

McCartney et al. (2005) evaluated a population of 182 DH lines in eight environments and revealed six QTL controlling Ht on chromosomes 2D, 4B, 4D, 5B, and 7A. The strongest height QTL was on chromosome 4D. This QTL had a LOD score of 30.9 and an R^2 value of 47.5%. The 4B and 4D QTL were mapped near the two major genes, *Rht-B1* and *Rht-D1*, respectively.

In a study to evaluate a spring wheat population of 140 RIL segregating at *Rht-B1* and *Rht-D1* under different moisture levels, Butler et al. (2005) found that the two loci had major effects on Ht in all four environments with R^2 values of 35.9 to 70.0 %.

1.8. Yield and yield components

Grain yield has been an important focus of plant breeding programs around the world, under both well watered and drought stress conditions. Drought stress has drastic

negative effects on grain yield and yield components (Cseuz et al., 2009; Inagaki et al., 2007). Grain yield is a complex quantitative trait controlled by a number of genes, each with a small effect on the final product and is highly influenced by the environment.

Borner et al. (2002) constructed a high density RFLP map to identify QTL associated with yield and yield components under a range of conditions. The highest number of QTLs was detected for spike length on chromosomes 1BS, 4AS, 4AL, and 5AL, detected in 9 of 11 environments.

Groos et al. (2003) evaluated 194 RIL (Table 1.3) at six locations to detect QTL for grain yield and kernel weight. Seven QTL were detected for yield on chromosomes 2B, 3B, 4A, 4B, 5B, and 7D. However, only the QTL on 7D was considered to be stable since it was observed in four of the six environments evaluated. Nine QTL were identified for kernel weight on chromosomes 1D, 2B, 2D, 3A, 5B, 6A, 6D, 7A, and 7D, while only the QTL on 2B, 5B, and 7A were considered to be stable. QTL for kernel weight and yield co-located on chromosomes 5B and 7D.

An advanced backcross population was used to identify QTL for yield and yield components in four environments (Huang et al., 2003). Eleven QTL were detected for grain yield on chromosomes 1B, 2A, 2D, and 5B, explaining from 9.6 to 21.6% of the phenotypic variation. They also identified seven QTL for kernel weight on chromosomes 2A, 2D, 4D, 5B, 7A, 7B, and 7D. QTL for other yield components detected in this study were distributed on chromosomes 2D, 3B, 4D, 5B, 6A and 7B.

Huang et al. (2004) studied seven agronomic traits in a 111 BC_2F_3 families (Table 1.3). In total, 57 QTL were detected for yield and kernel weight. Nine QTL were identified for yield on chromosomes 1A, 3D, 4D, 5A, 5B, 6B, and 6D while 14 QTL were identified for kernel weight on chromosomes 1B, 1D, 2A, 2D, 3A, 3B, 3D, 4B, 6A, 7A, and 7D.

Lin et al. (2008) established field trials in five seasons with a population of 108 DH lines. Three QTL for grain weight per spike were identified on chromosomes 1A, 2B,

and 2D, respectively. Two QTL for kernel weight were identified on chromosomes 2B and 7B, explaining nearly 14% of the total phenotypic variance in all environments. Five QTL for biomass were located on chromosomes 1B, 5B, 5D, 7A, and 7D, respectively, explaining a total of 31% of the phenotypic variance.

Cuthbert et al. (2008) evaluated yield and yield components in a DH spring wheat population. QTL analysis of the mapping population detected 53 QTL across environments for grain yield, yield components, and agronomic traits. They identified QTL for grain yield on chromosomes 1A, 2D, 3B, and 5A, thousand grain weight on chromosomes 2D, 3B, 5A, and 7A, and harvest index on chromosomes 1A, 3A, 3B, 5A, and 5B. This study identified five major grain yield QTL on four chromosomes that were consistent across the environments evaluated and coincident with QTL for at least one yield component.

A mapping population of 182 DH lines was used to construct a linkage map based largely on SSR makers. It was grown in a total of 18 year-site combinations (environments) (Kuchel et al., 2007). QTL significantly associated with grain yield were identified on chromosomes 1B, 2D, 3D, 4D, 6A and 6D in one or more environments. Another QTL located at 6A, was found to be associated with kernel weight at two environments. They also identified QTL for kernel weight on chromosome 7D.

Ma et al. (2007) evaluated a population of 136 RIL over two environments to determine QTL for spike length. Five chromosome regions were associated with spike length in this population. A major QTL was detected in two environments on chromosome 7D, which explained 29.7 to 36.3% of the phenotypic variation. Other QTL were distributed on chromosomes 1A, 2D, 4A, and 5B. The 1A location has been associated with spike length in three different mapping populations (Sourdille et al., 2000; Börner et al., 2002; Marza et al., 2006).

A durum wheat population of 249 RIL was evaluated over 16 environments under different drought conditions (Maccaferri et al., 2008). Two major grain yield QTL were identified in several environments on chromosomes 2B and 3D, with R^2 values up to 44.7%. The QTL on 2B, located in the distal region of chromosome 2BL, had a LOD score of 2.5 in eight environments with R^2 ranging from 3.5 to 12.4%. The second major grain yield QTL located on the distal region of chromosome 3BS, was detected in seven environments with R^2 values ranging from 4.8 to 18.1%.

Wang et al. (2009) evaluated a set of 142 RIL (Table 1.3) in four environments. Twenty-one QTL controlling kernel weight on chromosomes 1B, 2A, 2D, 3B, 4A, 4D, 5A, 6D and 7D were identified across the four environments. Two common QTL on 1B and 2A were found across all four environments. The detected QTL on 2A for kernel weight in this population in the interval *Xbarc1165*- *Xbarc124* seemed to correspond with the QTL results previously detected by Campbell et al. (1999).

1.9. Pre-harvest sprouting

Pre-harvest sprouting (Phs) in wheat is the germination of grain in the spike while still in the field, usually in response to rain (Fofana et al., 2008). Wheat fields may receive rainfall before harvest and become more susceptible to sprouting damage. Phs causes decrease of grain quality and results in financial losses to wheat producers (Mares, 2009). Flour produced from sprouted wheat kernels produces lower quality flour due to starch damage, so that the end product has a smaller volume and a compact, sticky crumb structure (Mohan et al., 2009). Tolerance to Phs is therefore a highly desirable trait by plant breeders.

Phs tolerance is a quantitative trait influenced by many environmental factors and controlled by several dormancy related genes (Fofana et al., 2008). Different types of markers have been used to identify QTL associated with Phs tolerance in wheat (Anderson et al.,1993; Kato et al., 2000; Zanetti et al., 2000; Mares and Mrva, 2001;

Groos et al., 2002; Mares et al., 2005; Fofana et al., 2009; Mares et al., 2009). Anderson et al. (1993) were the first to report QTL associated with Phs resistance in wheat. They found regions related to Phs tolerance on chromosomes 1A, 3B, 4A, 5D, and 6B in two white winter wheat RIL populations.

Fofana et al. (2009) identified 11 QTL for Phs resistance on group 3 chromosomes and on chromosome 5D in two DH populations. The phenotypic variation (R^2) explained by these QTLs ranged between 7% and 44%. QTL located on chromosomes 3A, 3B, 3D and 5D were identified and correlated with seed color. In another study, a DH wheat population grown in 16 environments was used to detect 15 different Phs QTL, including a major QTL on 2B that was significant in all environments tested and explained from 5 to 31% of the trait variation in a given environment (Munkvold et al., 2009). Mares et al. (2009) reported a highly significant QTL located on the long arm of chromosome 3B that explained up to 19% of the phenotypic variation for Phs in DH population.

The previous studies suggest that Phs tolerance and seed dormancy are controlled by multiple genes. Similar studies involving QTL using other mapping populations identified a number of QTL involving most of the 21 wheat chromosomes (Groos et al., 2002; Imtiaz et al., 2008; Chen et al., 2008; Mohan et al., 2009).

1.9.1. Seed color and environmental effects on pre-harvest sprouting

Red kernel wheats tend to have more tolerance to Phs than white wheat, however, some studies have shown that sources of resistance to Phs in white wheat can also be acquired (Anderson et al., 1993 and Mares et al., 2005). Furthermore, some white kernel genotypes have high levels of Phs tolerance (Wu et al., 1999). Wheat grain dormancy is affected by the pleiotropic effects of *R* (Red grain color) genes located on the long arms of the group 3 chromosomes which confer red pericarp color; and have major effects on the embryo. Several studies were conducted to find sources of Phs

resistance related to seed color, especially in white wheat germplasm, which are the most susceptible to Phs (Groos et al., 2002). Mares and Marva (2001) reported QTL associated with grain dormancy in an Australian DH population; they identified QTL on chromosome arms 2AL, 2DL, and 4AL. Mares et al. (2005) found a QTL on chromosome 4A using a DH population derived from white and red-grained bread wheat genotypes. Two significant QTL for grain dormancy located on chromosomes 4AL and 5BL were reported by Tan et al. (2006).

1.10. Normalized difference vegetation index (Ndvi)

Estimates of wheat biomass and related traits such as leaf length, as well as yield, require time and labor. There is a need for an indirect measurement that is easy and rapid to use so that many field plots can be screened under different environmental conditions. Ndvi the one of the most used techniques in remote sensing applications for agriculture because of its relationship with vegetation indices (Calera et al., 2004). The index is used as an indirect evaluation of wheat biomass, leaf area index, light-absorption, and photosynthesis capacity (Araus et al., 2001; Slafer, 2005). Therefore, measurements of Ndvi in wheat fields may be used to estimate final biomass and yield. To the best of our knowledge, this study will be the first to report QTL analysis for this trait under different moisture levels.

1.11. Drought susceptibility index (Dsi)

Water deficit is the main environmental factor limiting wheat productivity in many parts of the world (Kirigwi et al., 2007). Therefore, developing wheat cultivars with improved drought tolerance is an important approach to solve this problem. It is difficult to make progress for grain yield and its components under drought as they are complex traits influenced by different environmental factors. Fischer and Maurer (1978) proposed the Dsi, which is the yield of a genotype under drought conditions as a function of the yield without drought, as an estimate of genotype adaptability over a range of moisture

levels. It provides a measure of drought tolerance based on yield reduction under stress, when compared with yield under full irrigation. A low Dsi corresponds to high drought tolerance (Du et al., 2009). Only a limited number of studies have investigated Dsi by conducting QTL analysis, especially in wheat (Peleg et al., 2009). Kirigwi et al. (2007) identified QTL for Dsi on chromosome 4A in a wheat RIL population of 127 lines.

CHAPTER 2

Mapping quantitative trait loci for bread making quality traits in winter wheat under different soil moisture levels

ABSTRACT

Improved bread making quality is an essential goal of many wheat (*Triticum aestivum* L.) breeding programs. In addition to genetic factors, environmental conditions including drought stress play an important role in determining wheat quality. The main objective of this study was to identify quantitative trait loci (QTL) for quality traits in a winter wheat mapping population under different levels of soil moisture availability. A population of 185 doubled haploid (DH) lines derived from a cross between the hard white winter wheats CO940610 and 'Platte' was evaluated in field experiments in Fort Collins and Greeley, Colorado, USA in 2007-08 and 2008-09, respectively. At each location, two side-by-side trials were grown; one trial was grown under moderate moisture stress and one under fully irrigated conditions, for a total of four environments. Harvested grain was evaluated for traits important for end use quality, including mixograph parameters, single kernel characteristics, grain protein concentration, polyphenol oxidase activity, and flour color. Heritability estimates of most of the quality traits were high, indicating that a large part of the expression of these traits was genetically controlled. A linkage map based on 108 simple sequence repeat, 105 Diversity Array Technology, 3 sequence tag sites, and 5 protein markers was constructed with Join Map 4 software. The map consisted of 31 linkage groups covering the 21 chromosomes and spanning 2,083 cM. QTL detection was performed with the software Windows QTL Cartographer version 2.5, using the composite interval mapping

option. A total of 123 QTL for 15 quality traits with R^2 values up to 68.4% were detected on 18 chromosomes. Distribution of QTL was relatively balanced between the two irrigation levels, and Platte contributed the favorable allele for most of the QTL. Some QTL for correlated traits mapped to the same regions, forming QTL clusters. Twenty-seven QTL were generally consistent across environments and were mapped to three major QTL clusters on chromosomes 1A, 1B, and 1D; most likely they reflect the effects of the high molecular weight glutenin loci *Glu-A1*, *Glu-B1*, and *Glu-D1* on these chromosomes. A minor QTL cluster occurred close to the low molecular weight glutenin locus *Glu-D3* on chromosome 1D. Other QTL clusters for quality traits were located on linkage groups 2B.1, 6A, and 7D.2. These QTL may be due to the photoperiod response gene *Ppd-B1*, gliadin locus *Gli-A2*, and vernalization locus *Vrn-D3*, respectively, which reside in the same chromosome regions. Another QTL cluster located on chromosome 7BS included several QTL for mixograph parameters, grain ash concentration, grain protein concentration, and flour color b*. The largest and most consistent QTL for polyphenol oxidase activity was located on chromosome 2AL, linked to the *Ppo33* locus. This study confirms previous reports on the importance of high and low molecular weight glutenin loci and the effects of specific alleles at those loci on breadmaking quality traits. Also in agreement with previous studies, the relative effects of these alleles did not vary greatly with moisture stress over the range evaluated in these trials. The effects of the developmental genes *Ppd-B1* and *Vrn-D3* on quality traits had not been well documented previously. This study suggests that these genes have major effects on multiple quality traits, most likely through their effects on maturity. The results of this study may guide breeding programs in the choice of parents for improving quality and in conducting marker-assisted selection in segregating generations. Some of our findings may lead to further experiments to advance understanding of the genetic control of quality traits.

2.0 INTRODUCTION

Bread making quality of wheat is a complex set of traits influenced by a number of environmental, genetic, and biochemical factors. Drought stress plays an important role in determining wheat quality (Campbell and Davidson, 1979). Generally, an increase in drought stress results in higher protein concentration, improved bread-making quality, and a decrease in grain yield due to the inverse relationship between yield and protein (Sun et al., 2010). Development of wheat cultivars with both high yield potential and good bread making quality across a range of soil moisture conditions is a major aim in wheat breeding programs. Wheat end use quality can be characterized by several quality parameters, mixograph traits, single kernel characterization, test weight, average kernel weight, grain protein concentration, flour color, and polyphenol oxidase activity.

A number of genes are known to affect bread making quality of wheat. These include genes encoding high molecular weight glutenin subunit (HMW-GS) proteins (*Glu-A1*, *Glu-B1*, and *Glu-D1*), located on the long arms of group 1 chromosomes (Payne, 1987). Low molecular weight glutenin subunit proteins (LMW-GS) are encoded by genes at the *Glu-A3*, *Glu-B3*, and *Glu-D3* loci on the short arms of group 1 chromosomes. Genes coding for gliadin proteins are located on the short arms of group 1 and 6 chromosomes (Gao et al., 2007). HMW-GS are generally known to have major effects on bread-making quality (Payne et al., 1987). The LMW-GS (Gianibelli et al., 2001) and gliadins (Branlard, 2009) also influence bread-making quality, but their effects are less well documented because of the greater difficulty in evaluating allelic differences. Zheng et al. (2009, 2010) reported the effects of *Glu-1* and *Glu-3* alleles on bread making quality of recent Great Plains cultivars and advanced lines. Endosperm texture is controlled by a major locus, the Hardness (*Ha*) locus, on chromosome arm 5DS of bread wheat. The locus carries two tightly linked genes, *Pina-D1* and *Pinb-D1* (Gross et al., 2004; Li et al., 2009).

Quantitative trait locus (QTL) analysis based on molecular marker maps has been used to detect genomic regions that control mixograph parameters (Huang et al., 2006; Mann et al., 2009; Patil et al., 2009; Zheng et al., 2010), kernel characteristics (Ammiraju et al., 2001; Breseghello and Sorrells, 2006; Li et al., 2009; Sun et al., 2010), grain and flour protein concentration (Zanetti et al., 1999; Perretant et al., 2000; Blanco et al., 2002; Groos et al., 2003; Prasad et al., 2003; Breseghello et al., 2005; Li et al., 2009), flour color (Kuchel et al., 2006; Raman et al., 2009), and polyphenol oxidase activity (Watanabe et al., 2006; He et al., 2007). However, only a few of those studies were conducted in both well watered and moisture stress conditions. For semi-arid wheat-growing regions like the western Great Plains, stability of QTL across a range of moisture conditions is important information for wheat breeders for improving quality traits.

For this study, a doubled haploid (DH) population was developed from the cross of a high-quality wheat cultivar ('Platte') and an experimental line with exceptionally poor bread making quality, but high yield potential (CO940610). Our objectives were (1) to evaluate a doubled haploid mapping population for multiple quality traits in environments differing in moisture stress; (2) to develop a genome-wide molecular marker linkage map for the population; (3) to conduct quantitative trait locus (QTL) analysis to determine the location and size of QTL and their stability across environments.

2.1 MATERIALS AND METHODS

2.1.1. Mapping population

A doubled haploid (DH) wheat population was produced by crossing parents CO940610 and 'Platte', with CO940610 as the female. CO940610 is a hard white winter wheat experimental line developed by the CSU Wheat Breeding Program from the cross KS87H22/MW09. The first parent of CO940610 has a genetic composition that is approximately one-half TAM 105 (Porter et al., 1980), which explains at least part of its excellent dryland yield (S. Haley, personal communication). Clark's Cream (described in Anderson et al., 1993) constitutes approximately half of the MW09 parent, and thus it is possible that CO940610 had pre-harvest sprouting tolerance from that cultivar. However, based on observations in CSU's Wheat Quality Laboratory, CO940610 has poor bread making quality. Platte is a hard white winter wheat developed by Agripro (Junction City, KS), with pedigree N84-1104/'Abilene'. It is known for its adaptation to irrigated production systems and excellent bread making quality, but is considered to have poor tolerance to pre-harvest sprouting.

Parents were evaluated as part of the Wheat CAP Coordinated Agriculture Project, (CAP) funded by USDA-CSREES. Allelic variation between the CO940610 and Platte at selected major genes is presented in Table 2.1.

The DH population was produced by Agripro in 2005 and 2006 based on the method described by Laurie and Bennett (1988). In this method, maize pollen is used to fertilize female CO940610/Platte F_1 wheat plants, followed by embryo rescue, development of haploid plants, and chromosome doubling by soaking plants in a colchicine solution. Seed of the 214 DH lines used in this study was first increased in the greenhouse at CSU, then in Yuma, Arizona, during the 2005-06 and 2006-07 growing seasons.

Table 2.1. Allelic variation for selected major genes for CO940610 and Platte winter wheat*

Characteristic	Locus or trait	Allelic variation	
		CO940610	Platte
Grain texture	*PinA*	+	+
	PinB	-	-
Gluten strength	*Glu-A1*	c (null)	b (2*)
	Glu-B1	b (7+8)	e (20x+20y)
	Glu-D1	a (2+12)	d (5+10)
	Glu-A3	c	c
	Glu-B3	h	g
	Glu-D3	b	c
Waxy	*Wx-D1*	+	+
	Wx-A1	+	+
	Wx-B1	+	+
Grain protein	*Gpc-B1*	-	-
Disease resistance	*Lr37/Yr17/ Sr38*	-	-
	H9	-	-
	Lr21	-	-
Stripe Rust - HTAP	*barc101*	172	Null
	barc136	272	261
Aluminum tolerance	Al tolerance	T	S
Vernalization requirement	Heading	Late	Late
	VRN-A1	*vrn-A1*	*vrn-A1*
	VRN-B1	*vrn-B1*	*vrn-B1*
	VRN-D1	*vrn-D1*	*vrn-D1*
Height	*Rht-B1*	*Rht-B1b*	*Rht-B1b*
	Rht-D1	*Rht-D1a*	*Rht-D1a*
Rye translocation	*1RS*	*non-1RS*	*non-1RS*

* For most of these loci and traits, the source of the information is the Wheat CAP website (http://maswheat.ucdavis.edu/wheatcap.htm). Alleles for *Glu-A3*, *Glu-B3*, and *Glu-D3* were determined by Scott Reid, CSU Department of Soil and Crop Sciences, based on protein and polymerase chain reaction (PCR) markers in comparison with published report (Appelbee et al., 2009).

Where,

Grain texture: A negative in either *Pina* or *Pinb* results in hard texture. Both positives results in soft.

Gluten strength: *Glu-D1a* (2+12) is associated with weak gluten, *Glu-D1d* (5+10) is associated with strong gluten.

Waxy endosperm: One negative *Wx* allele is sufficient for a partial Waxy phenotype.

Grain protein: Positive indicates the presence of the *T. diccocoides* allele for high grain protein content.

Lr37/Yr17/Sr38: Positive indicates presence of the 2NS/2AS translocation carrying this set of three resistance genes.

Hessian fly resistance: Positive indicates presence of the *H9* allele.

Leaf rust resistance: Positive indicates presence of the Lr21 allele.

Stripe rust, high temperature adult plant (HTAP) resistance: The 172 - 272 haplotype is associated with the resistant allele of Stephens.

Aluminum tolerance: T indicates the presence of the Atlas tolerant allele, S indicates susceptible genotype.

VRN: One dominant allele at any of the three loci is sufficient for a dominant spring growth habit.

Dwarfing genes *Rht-1*: The a allele is for tall, and the b allele is for semi-dwarf.

Drought tolerance: The presence of the 1RS translocation on 1AL or 1BL enhances drought tolerance.

The full set of 214 lines was used for marker evaluation and linkage Map construction. A subset of 186 lines was evaluated in the field trials, and 185 lines were included in the QTL analysis after eliminating one line that had a large number of non-parental alleles.

2.1.2. Experimental design and trial management

From the total population of 214 DH lines, 186 were planted in field trials. In addition, two occurrences of each parent, 'Lakin' (a hard white winter cultivar selected from the cross 'Arlin'/KS89H130 and released by Kansas State University), and 'Ripper' (a hard red winter cultivar selected from the cross CO940606/TAM107-R2 and released by CSU (Haley et al., 2007) were included in the field evaluations. Trials were grown in two locations in Colorado: the Agriculture Research, Development and Education Center (ARDEC) of CSU in Fort Collins in 2007-08 and the USDA-Agricultural Research Service Limited Irrigation Research Farm in Greeley in 2008-09. Entries were arranged in an incomplete block Latinized row-column design created with CycDesign 3.0 (www.cycdesign.co.nz) with two replications. At each location two side-by-side trials were grown; one trial was grown under moderate moisture stress ("dry") and one under fully irrigated ("wet") conditions, for a total of four environments. Each plot consisted of two rows 3.88 m long with 23 cm spacing between rows and 28 cm between plots. The plots were planted at a density of 140 seeds/plot in both years. The trial in Fort Collins was irrigated with a linear overhead sprinkler irrigation system and at the Greeley site drip irrigation was used for more precise water distribution. At both sites the two adjacent treatments were irrigated equally after planting and in early spring, but the dry treatment received less supplemental water during stem elongation and no additional water post-anthesis.

2.1.3. Quality trait evaluation

The quality evaluations were conducted in the CSU Wheat Quality Lab in the fall and winter following harvest.

2.1.3.1. Flour sample preparation

Sixty grams of seed from each plot were weighed, tempered to 15.5% moisture concentration (based on the moisture concentration obtained from SKCS), and then

ground to flour with a Brabender Quadrumat® Jr. Mill. (C.W.Brabender Instruments, Inc. South Hackensack, NJ) following the AACCI Method 26-50 (AACCI, 2004). Samples were weighed on a 14% moisture basis and all mixing experiments were carried out following the AACCI Method 54-40A (AACCI, 2004). The water absorption *W* (mL), which is the actual amount of water added to 10 g flour to perform a Mixograph experiment was determined with the “Cheyenne Protein-Absorption Curve". The curve was developed at the USDA-ARS Grain Quality and Structure Research Unit in Manhattan, KS, and is as follows

Predicted water absorption= 42.70086063 + (1.68908775*Protein14)

where Protein14=percent flour protein concentration (14% moisture basis) measured by near-infrared spectroscopy (NIRs).

2.1.3.2. Flour NIR

A sample of wheat kernel flour was placed in a transport module in a quartz cup (NIRSystems, part number 0IH–0379) using a Foss-Tecator NIR Systems Model 6500 (Foss North America, Eden Prairie, MN) in reflectance mode, 450–2498 nm. The output traits are flour protein concentration and ash concentration at 14% moisture concentration.

2.1.3.3. Mixograph traits

Mixing tests were performed on 10 g flour samples with a 10g-mixograph (National Manufacturing Division, TMCO, Lincoln, NE). Mixograph characteristics were determined with the commercial sowftware program Mixsmart® version 3.80 (National Manufacturing Division, TMCO, Lincoln, NE). Samples were weighed on a 14% moisture basis, water was added to the flour from a buret, and the bowl containing the flour and water was inserted into the mixograph, where the flour and water were mixed together to form a dough. As the dough is mixed, the mixograph records a curve on the

device screen. The mixograph determines dough and gluten properties of flour by measuring the resistance of the dough against the mixing action of pins.

The mixograph curve indicates gluten strength, optimum dough development time, mixing tolerance (tolerance to over-mixing), and other dough characteristics (Fig. 2.1). All mixing characteristics except mixing time are reported on a 100-Mixograph unit scale (% height). Mixograph parameters were automatically estimated by Mixsmart® software. In addition to Mxt, mixograph traits included were mixograph right width (Mrw), mixograph right slope (Mrs), mixograph peak height (Mxh), and mixograph peak width (Mxw). For the mixograph evaluation, higher values of peak time, peak height, right width, peak width, and right slope are considered favorable.

2.1.3.4. Single Kernel Characterization System (SKCS)

A 10-g sample of wheat kernels was prepared by removing broken kernels, weed seeds, and other foreign material. The sample was poured into the access hopper of the SKCS instrument model 4100 (Perten Instruments, Springfield, IL). The SKCS instrument analyzes kernels individually and records the results on the computer hard disk. The following characteristics were analyzed: kernel weight (Skw) was measured by load cell and reported in mg; kernel diameter (Skd) was analyzed by electrical current and expressed in mm; kernel hardness (Sha) was analyzed by pressure force and expressed as an index scale of 0 = extremely soft to 100 = extremely hard.

2.1.3.5. Whole grain NIR

A sample of wheat kernels was placed in a transport module in a rectangular quartz cup (NIRSystems, part number 0IH–0379) using a Foss-Tecator NIR systems Model 6500 instrument (Foss North America, Eden Prairie, MN) in reflectance mode, 450–2498 nm. The output traits were grain protein concentration at 12% moisture concentration (Gpc), kernel hardness, kernel ash (Gac), and milling extraction according to AACCI method 39-10 and 39-11 (AACCI, 2004).

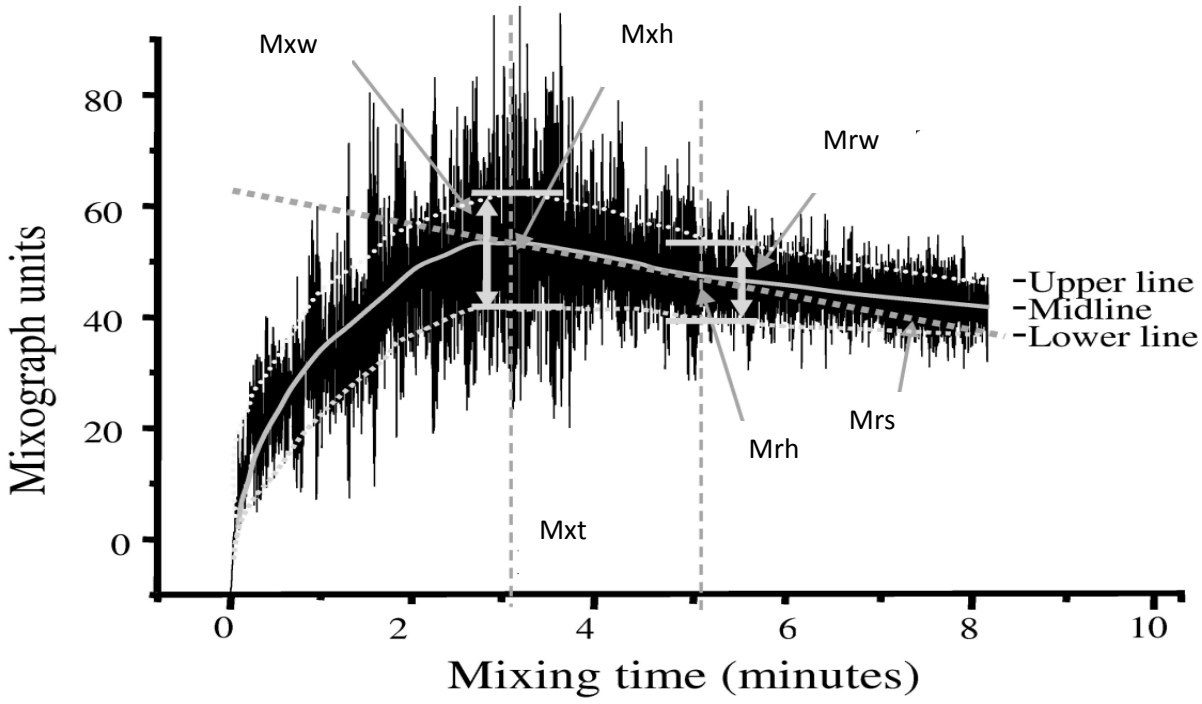


Fig.. 2.1. Illustration of mixograph characteristics. Mxt=Mixograph peak time, Mxh= Mixograph peak height, Mrs=Mixograph right slope, Mrw=Mixograph right width, Mxw= mixograph peak width.

2.1.3.6. Test weight

A kernel sample was poured into a closed hopper centered over a cylindrical container. The valve was quickly opened to allow the grain to fill the container. A standard stroker held in both hands with the flat sides in a vertical position was used to remove the excess grain from the top of the kettle with three full-length, zigzag motions. A container having dimensions of 5.5 cm diameter x 4.5 cm length was used in this test, and the weight was estimated in Kg/hL.

2.1.3.7. Flour Color

To measure flour color the Minolta Chroma Meter CR-310 (Minolta Camera Co Ltd; Japan) was used. Flour color results were reported in terms of 3-dimensional color

values of the parameters L*, a*, and b*. The L* value indicates the brightness, with 0 to 100 representing darkness to brightness. The a* value gives the degree of the red–green color, with a higher positive a* value indicating more red. The b* value indicates the degree of the yellow–blue color, with a higher positive b* value indicating more yellow.

2.1.3.8. Polyphenol oxidase

This assay is based on the ability of polyphenol oxidase (Ppo) of wheat kernels to oxidize an L-DOPA substrate to a red-colored product (He et al., 2007). Fresh stock solution of 5 mM L-DOPA (3, 4-dihydroxyphenylalanine) and 50 mM MOPS (3-(N-morpholino) propane sulfonic acid) buffer (pH 6.5) was added to five whole wheat seeds in a 2 ml tube. A 1.5 ml quantity of solution was dispensed into each tube, and the tubes were then shaken with an orbital shaker for 60 minutes. Mixing is required because oxygen is needed for the reaction to proceed. After incubation, 1 mL of solution was transferred to a SmartSpec™ 3000 UV/Vis Spectrophotometer (BioRad, Hercules, CA) following the AACC Method 22-85.01. Absorbance was measured at 475 nm wave length. This value indicates the amount of oxidation product converted from the substrate and indirectly estimates Ppo activity.

2.1.4. Statistical analysis

Analysis of variance was conducted with PROC MIXED of SAS 9.1 (SAS Institute, Cary, NC) to determine the significance of sources of variation and to calculate Best Linear Unbiased Predictions (BLUPs) for each line. Data were analyzed for each treatment separately, and then combined over treatments within locations. Entries were considered random and treatments were considered fixed. To adjust for spatial variation, row, row-column, and anisotropic adjustments were evaluated to determine the best method based on the lowest value of the Akaike's information criterion (AIC). This procedure is described in more detail in Butler et al. (2005).

The following analyses were conducted with BLUPs. The traits were evaluated for normality with the Kolmogorov-Smirnov test of the SAS UNIVARIATE procedure. Frequency distributions were obtained in Microsoft Excel of Microsoft ® Office 2007 (Microsoft ® Corporation, Redmond, WA) to visually assess normality and to investigate the occurrence of transgressive segregation. Pearson correlation coefficients among quality and agronomic traits were obtained with the CORR procedure of SAS. Proc GLM was used to estimate the heritability from the analysis of variance of progeny-mean data using the following formulas:

For a single trait evaluated in a single environment (treatment within a location) with r= 2 replications and t= 185 entries

Source	df	Expected mean square
Reps	r-1	$\sigma^2 + t\,\sigma^2_R$
Entries	t-1	$\sigma^2 + r\,\sigma^2_G$ = MS1
Error	(r-1) (t-1)	σ^2 = MS2

$\sigma^2_G = (\sigma^2 e + r\sigma^2_G) / r = (MS1 - MS2)/r$

$\sigma^2_P = (\sigma^2_e + r\sigma^2_G / r) = MS1/r$

$h^2 = \sigma^2_G / (\sigma^2_G + \sigma^2_e/r) = 1 - (MS2/MS1)$, Where σ^2_e is the error mean square, $r\sigma^2_G$ is entries mean square, and r is number of replication

For a single trait evaluated in n= 4 environments (2 environments x 2 locations), r= 2 replications, and 185 entries

Source	df	Expected mean square	
Env	n-1	$\sigma^2 + r\,\sigma^2_{GE} + t\,\sigma^2_{R(E)} + rt\,\sigma^2_E$	
Rep (Env)	n(r-1)	$\sigma^2 + r\,\sigma^2_{R(E)}$	
Entries	t-1	$\sigma^2 + r\,\sigma^2_{GE} + rn\sigma^2_G$	= MS1
Env x Entries	(n-1)(t-1)	$\sigma^2 + r\,\sigma^2_{GE}$	= MS2
Error	n(r-1)(t-1)	σ^2	= MS3

When the Env x Entries term was significant (P<0.05):

$\sigma^2_G = ((\sigma^2e + r\sigma^2_{GE} + rn\,\sigma^2_G) - (\sigma^2e + r\sigma^2_{GE}))\,/\,rn = (MS1 - MS2)/rn$

$\sigma^2_{GE} = ((\sigma^2e + r\sigma^2_{GE}) - (\sigma^2e))\,/\,r = (MS2 - MS3)/r$

$\sigma^2_P = (\sigma^2_e + r\sigma^2_{GE} + rn\,\sigma^2_G)\,/\,rn = MS1/rn$

$h^2 = \sigma^2_G\,/\,((\sigma^2_G + \sigma^2_{GE}\,/\,n) + (\sigma^2/\,rn)) = 1 - (MS2/MS1)$

When the Env x Entries term was not significant (P>0.05):

$\sigma^2_G = ((\sigma^2e + r\sigma^2_{GE} + rn\,\sigma^2_G) - (\sigma^2e))\,/\,rn = (MS1 - MS3)/r$

$\sigma^2_{GE} = ((\sigma^2e + r\sigma^2_{GE}) - (\sigma^2e))\,/\,r$

$\sigma^2_P = (\sigma^2_e + r\sigma^2_{GE} + rn\,\sigma^2_G)\,/\,rn$

$h^2 = \sigma^2_G\,/\,((\sigma^2_G) + (\sigma^2_e\,/\,rn)) = 1 - (MS3/MS1)$

Exact confidence intervals for heritability estimates on a progeny mean basis were calculated according to Knapp et al. (1985). For a 90% confidence interval, α= 0.05 for each of the upper and lower confidence limits.

Upper limit: 1-{1/ [(M1/M2)* $F_{0.05}$, df1, df2]} or 1-{1/ [(M1/M3)* $F_{0.05}$, df1, df2]} depending on the significant of Env x Entries.

Lower limit: 1-{1/ [(M1/M2)* $F_{0.95}$, df1, df2]} or 1-{1/ [(M1/M3)* $F_{0.95}$, df1, df2]} depending on the significant of Env x Entries.

2.1.5. DNA and protein extraction

2.1.5.1. DNA extraction

DNA was extracted from each DH line and the two parents of the population. An approximately 400 to 500 mg leaf segment was collected from a seedling at the 1 to 2 leaf stage into a 2.0 ml tube. The tubes were placed temporarily in liquid nitrogen, then stored in a -80 ℃ freezer until further processing. Th e leaf tissue was ground in the tubes with a pestle after adding liquid nitrogen. DNA was extracted and purified using a wheat extraction protocol (Riede and Anderson, 1996) with the following modifications.

Samples were incubated at 65 °C for 30 min in extraction buffer [0.5 *M* NaCl, 0.1 *M* Tris pH 8.0, 0.05 *M* ethylenediaminetetra-acetic acid (EDTA), 8.4 g L^{-1} sodium dodecyl sulfate (SDS), 3.8 g L^{-1} sodium bisulfate] and mixed by inversion every 10 min for one hour. Three hundred µL of 24:1 chloroform: isoamyl alcohol was added to each tube and mixed to form an emulsion. After centrifugation, the aqueous phase was transferred to a new tube, and DNA was precipitated by adding 2 volumes of 100% ethanol. Pelleted DNA was washed in 1 ml of 70% ethanol, air-dried, and resuspended in 400 µL TE buffer (10 m*M* Tris, 1 m*M* EDTA, pH 8.0). DNA concentrations were calculated by measuring absorbance at 260 nm on a Nanodrop ND1000 Spectrophotometer (Thermo Scientific, Wilmington, DE) and the DNA quality was evaluated on a 1.0% agarose gel containing one lane of Lamba DNA/HindIII and stained with ethidium bromide. DNA was diluted to 50 ng/µL in TE (1.0 mM tris, 0.1 mM EDTA, pH 8.0). Protein extraction was performed using the Pfluger et al. (2001) protocol.

2.1.6. Molecular marker evaluation

Parental DNA was screened for SSR polymorphisms by the USDA-ARS Regional Small Grains Genotyping Laboratory in Fargo, ND. Loci indicated as polymorphic in that analysis were re-evaluated in the parents in the labs of Drs. P. Byrne and N. Lapitan at CSU. Markers that were confirmed as polymorphic, along with several sequence-tagged site (STS) markers were evaluated in the whole population of 214 DH lines in the Byrne and Lapitan labs. Primer sequences for those loci were obtained from GrainGenes (www. wheat.pw.usda.gov) or in the references listed in Table 2.2.

To evaluate SSR and STS markers, we performed polymerase chain reactions (PCR) in 96-well micro-plates using a touchdown (TD) thermal cycler program with different target annealing temperatures (Williams et al., 2002). The PCR reactions were carried out in a 12 µL volume containing 2.15 µL of sterile water, 1X Thermopol reaction buffer (10 mM KCL, 10 mM $(NH_4)_2$ SO_4, 20 mM tris-HCL), 200 µM of

deoxyribonucleoside-5' triphosphate (dNTPs), 125 ng of template DNA, 0.2 µM of each primer, and 0.4 unit Taq DNA polymerase.

SSR markers were either separated on agarose gels followed by ethidium bromide staining or by sodium dodecyl sulfate polyacrylamide gel electrophoresis (SDS-PAGE) with silver staining according to the method of (Bassam et al., 1991). Six glutenin protein markers were evaluated in this population (Table 2.1) according to methods described by Shan et al. (2007). To obtain DArT marker data we sent DNA of the 214 lines and the two parents to the Diversity Array Company in Yarralumla, ACT, Australia.

DArT markers with ambiguous parental scores or low polymorphic information content values clustered together (less than 1 cM in distance) were deleted from the data set. The complete data set consisted of 444 markers (130 SSR, 306 DArT, 3 STS, and 5 protein). To evaluate segregation distortion of markers we conducted chi-square analysis with the Excel program.

2.1.7. Linkage map construction

Data for all marker types for 214 DH lines were compiled and analyzed with Join Map 4 software (Van Ooijen, 2006). Using the regression mapping option, we constructed maps of 31 linkage groups with LOD ≥ 8 using the Haldane mapping function to calculate the centiMorgan (cM) distances. There were weak linkages (LOD<3) between some groups, for example 1A.1 and 1A.2 or 7D.1 and 7D.2; therefore, we did not incorporate them into a single chromosome group. As an example, 1A.1 and 1A.2 indicates that there were two linkage groups for chromosome 1A and they were numbered in order according to the marker position on consensus maps (www. wheat.pw.usda.gov).

2.1.8. QTL analysis

QTL detection was performed with the software Windows QTL Cartographer version 2.5 (Wang et al., 2010).

Table 2.2. Source of different markers used in this study.

Marker type	Reference
SSR (gwm)	Roder et al., 1998
SSR (gdm)	Pestsova et al., 2000
SSR (wmc)	Somers et al., 2004
SSR (cfd)	Guoyomarch et al., 2002; Sourdille et al., 2003
SSR (barc)	Song et al., 2005
Ppo33	Sun et al., 2005
Sr24 #12 and 50	Mago et al., 2005
Glu-A1, *Glu-B1*, *Glu-D1*, *Glu-A3*, *Glu-B3*, and *Glu-D3*	Graingenes website: http://wheat.pw.usda.gov/GG2/index.shtml
Vrn-D3	Wang et al., 2009

Composite interval mapping (CIM) analysis was using forward and backward step-wise regression and the parameter setup of ‘‘model 6 standard analysis’’, with 5 control markers, and a window size of 10 cM. Rather than using an arbitrary LOD threshold to declare QTL significance, the threshold was obtained through permutation analysis. Permutation analysis (n=1,000) was conducted for each trait in each of four environments to determine the appropriate LOD threshold to obtain a 0.1 genome-wise probability level of a Type I error in this data set. QTL position was estimated as the point on the LOD curve having a peak score greater than the threshold value. A total of 18 unlinked markers were analyzed for significance (P<0.001) using Proc GLM of SAS.

Percent phenotypic variance explained (%R^2) was obtained by multiplying the R^2 values provided in the Cartographer results by 100. For this analysis, a major QTL was considered to have %R^2>20%, an intermediate QTL to have %R^2 of 5 to 20%, and a minor QTL to have %R^2<5%. The QTL were designated as QX.cob-Y, where X denotes the phenotypic trait abbreviation, cob referred to Colorado, Byrne lab, and Y represents the chromosome on which the QTL was located. To determine the effects of all significant QTL simultaneously, multiple-locus models were calculated with the SAS GLM procedure. For each QTL detected by CIM, the closest marker locus was added in stepwise fashion to determine the multiple-locus model for each trait. The 1-LOD support intervals for QTL locations were calculated by finding the points on either side of the estimated QTL position that corresponded to a decrease in LOD score of 1 unit. The genetic maps, QTL positions, and support intervals were drawn using the computer program Map Chart 2.2 (Voorrips, 2002).

2.2 RESULTS

2.2.1. Marker analysis

Of the 769 SSR markers screened, 458 (59.6%) were polymorphic between CO940610 and Platte. Five glutenin protein markers were polymorphic between the two parents: C0940610 possesses the alleles *Glu-A1c* (null), *Glu-B1b* (7+8), *Glu-D1a* (2+12), *Glu-B3h*, and *Glu-D3b*, while Platte carries the alleles *Glu-A1b* (2*), *Glu-B1e* (20x+20y), *Glu-D1d* (5+10), *Glu-B3g*, and *Glu-D3c*. One hundred and thirty-three SSR markers, three STS and five glutenin protein markers were used to genotype the 185 DH lines. Three hundred and twenty-three DArT markers were surveyed, of which 14 were eliminated for having low polymorphic information content and three eliminated for not having parental scores. Three hundred and six were polymorphic between the parents and were integrated with SSR and protein marker data.

2.2.2. Construction of linkage map

Thirty-one linkage groups covering the 21 chromosomes were constructed from 108 SSR, 105 DArT, 3 STS, and 5 protein markers, after removal of markers <1 cM apart (Fig. 2.2). In eliminating closely spaced markers, preference was given to retaining SSRs and markers with fewer missing scores. The groups had a minimum LOD score for linkage of 8.0. Eighteen markers were either unlinked or formed small linkage groups that could not be assigned to chromosomes; these were excluded for estimation of the length of the linkage map. Each of the 31 groups contained at least one SSR marker to anchor it to a chromosome, except the 1A.2, 2B.2, and 6B.2 groups. These chromosome assignments were based on information provided by Diversity Array Technology. In general, marker order was consistent with previously published maps (www. wheat.pw.usda.gov). The linkage map spanned 2,083 cM, covering 81.8% of the wheat genome relative to the SSR consensus map of Somers et al. (2004).

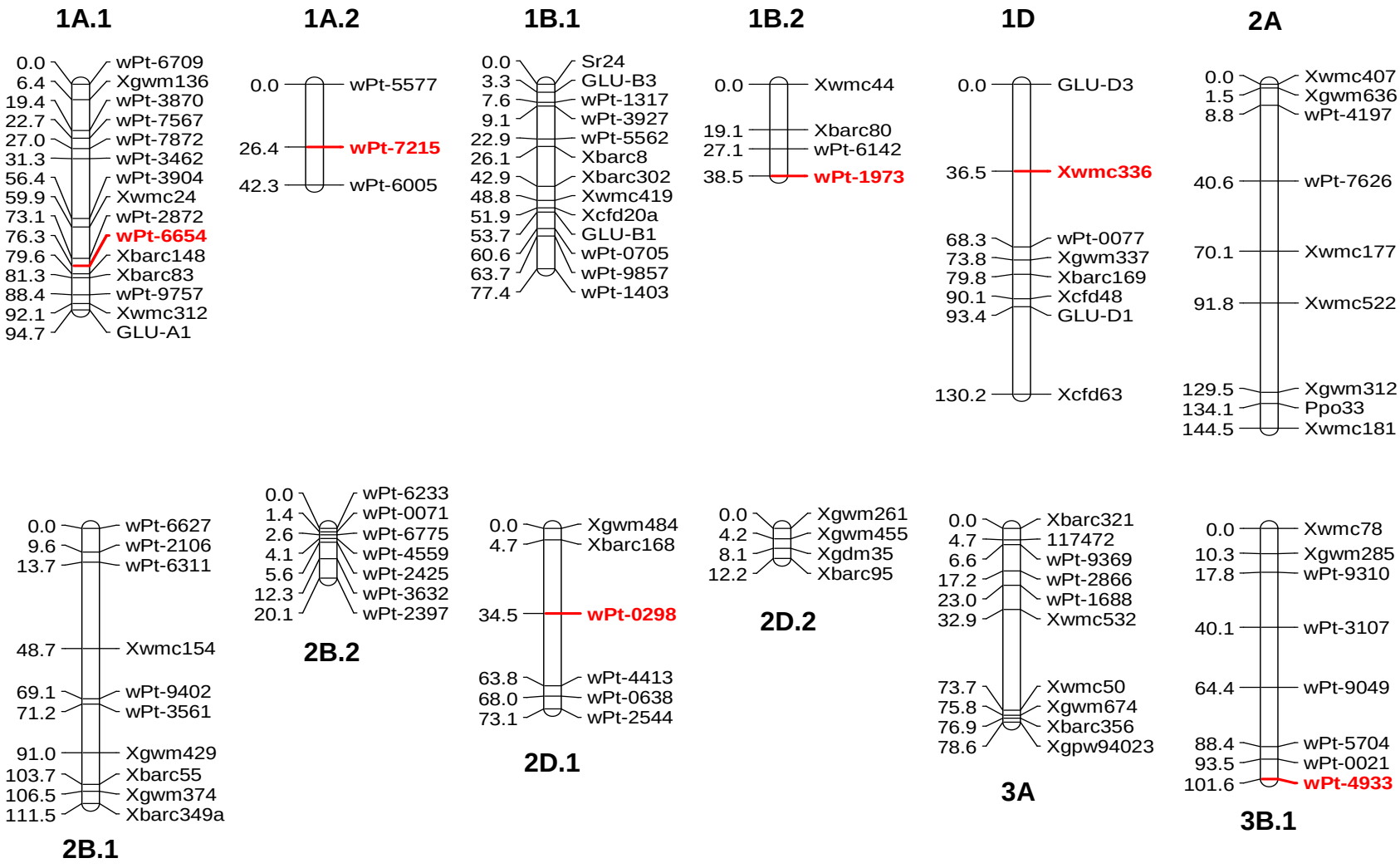


Fig. 2.2. Integrated linkage map based on the CO940610/Platte population. Cumulative distances between markers are given in cM, calculated from recombination frequencies according to Haldane mapping function. Bold red markers are significantly distorted at *P*<0.01.

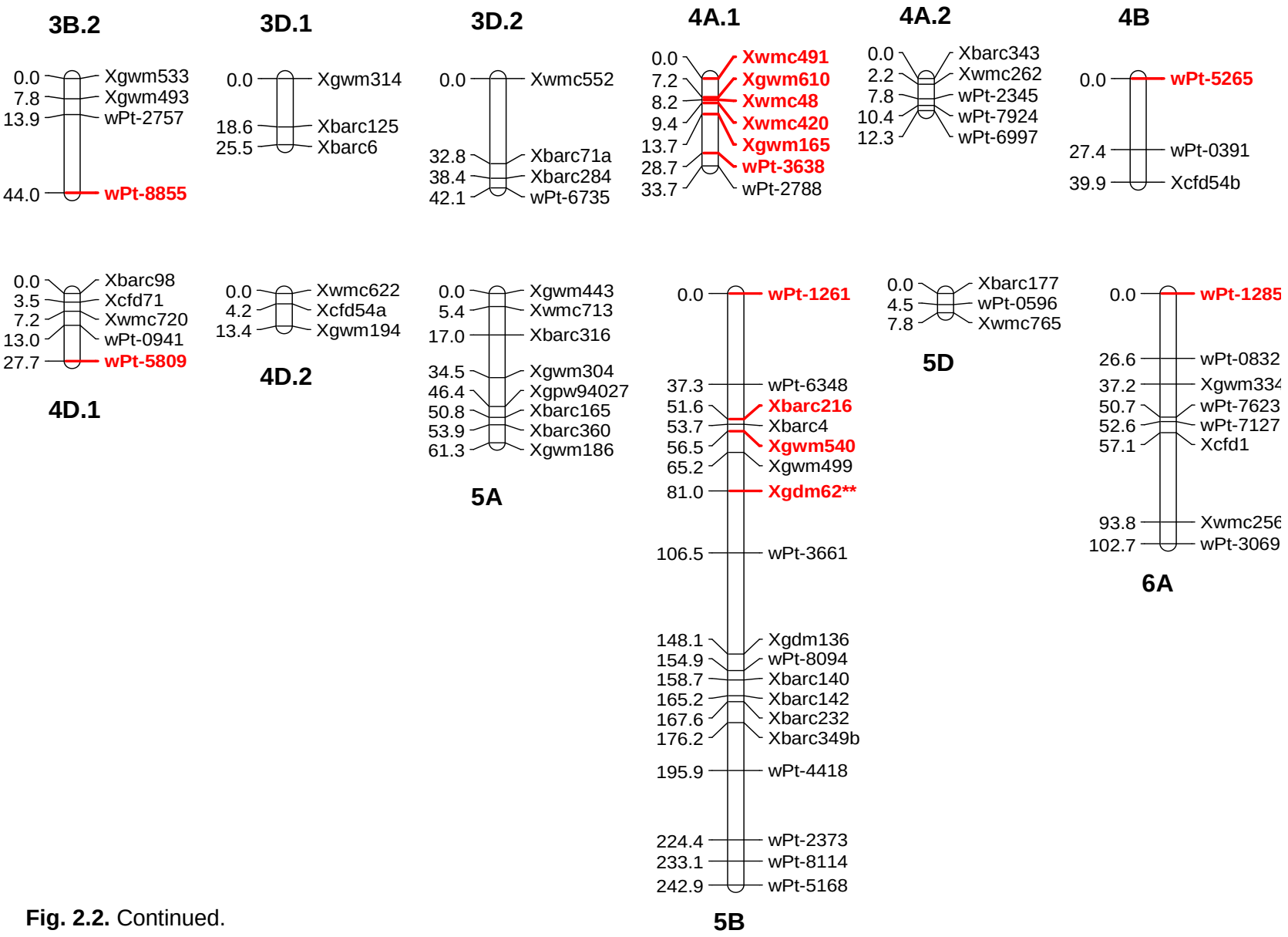


Fig. 2.2. Continued.

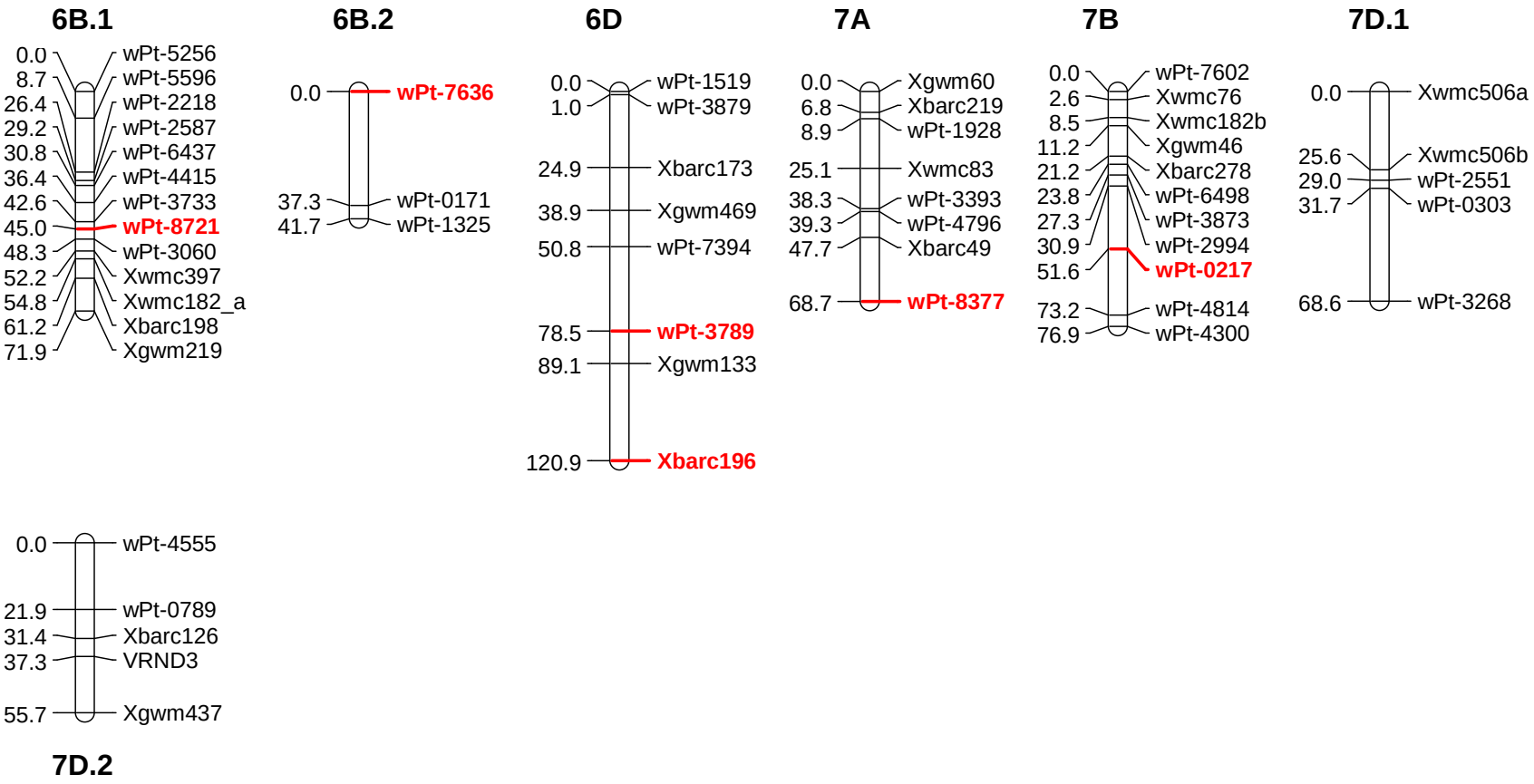


Fig. 2.2. Continued.

The average interval between markers was 9.4 cM. Linkage groups for the A genome chromosomes ranged from 12.3 cM (4A.2) to 144 cM (2A) and covered a total of 638.8 cM (30.7% of the total map length). The B genome chromosomes ranged from 20.1 cM (2B.2) to 242.9 cM (5B) and covered a total of 866.4 cM (41.6% of the total map length). Linkage groups for the seven D genome chromosomes ranged from 7.8 cM (5D) to 130.1 cM (1D) and covered a total of 577.2 cM (27.7% of the total map length). Linkage groups 1A.2, 3D.1, 4B, 4D.2, 5D, and 6B.2 had limited genome coverage (2 to 3 markers/chromosome). There were weak linkages (LOD<3) between some groups, for example 1A.1 and 1A.2 or 7D.1 and 7D.2; therefore, we did not incorporate them into a single chromosome group. In general, the A genome had the greatest marker density, with 73 markers and an average density of one marker per 8.7 cM. The B genome contained 94 markers with an average density of one marker per 9.2 cM, while the D genome had 54 markers with an average density of one marker per 10.6 cM. Clustering of markers was observed on certain chromosomes, for example on chromosomes 1A.1, 1B.1, and 5B (Fig. 2.2). A total of 195 of the 221 markers (88.2%) segregated in a normal Mendelian fashion (1:1 maternal:paternal allele ratio). Segregation distortion (P<0.01) was detected for 10 SSR and 16 DArT marker loci which were distributed on 17 linkage groups. Clustering of distorted loci occurred on chromosomes 4A and 5B due to an excess of CO940610 alleles (Table A1 and Fig. 2.2).

2.2.3. Trait means

The 15 quality traits were classified into five categories for the ease of discussion: Mixograph traits, SKCS traits, NIRs traits, polyphenol oxidase, and flour color. Analysis of variance revealed highly significant differences (P<0.01) for most traits among DH lines and between moisture treatments within locations (Tables 2.3 and 2.4). When frequency distributions of BLUPs were plotted, all traits were seen to vary over a wide range (Fig. A.1). Transgressive segregation was apparent in most cases, thus

indicating the presence of favorable alleles in both parents. Normal or approximately normal distribution of BLUPs was observed for most traits (Fig. A.1). Lines grown at Fort Collins and Greeley under limited irrigation had higher means for quality traits than those grown under full irrigation, with the exception of grain ash content and mixograph right width. The lower precipitation in 2008 compared to 2009 could be a major environmental difference between the two locations (Table A.2). When the parents were compared Platte had higher trait values for grain protein concentration and most of the mixograph traits under both moisture conditions in both years of the study; however, CO940610 exhibited higher trait values for most of the SKCS traits and polyphenol oxidase activity in all environments (Table 2.5). Both parents produced higher grain protein concentration under limited irrigation.

2.2.4. Correlation among traits

Significant correlations among many pairs of traits were observed in this population (Tables 2.6 and 2.7). Grain protein concentration, single kernel characteristics, flour color, and mixograph properties were mostly significantly (P<0.05) correlated with each other (Tables 2.6 and 2.7). Grain protein concentration was negatively correlated with Gy, Mrs, Mrw, and Mxt (r=-0.25 to -0.52, P<0.01) and positively correlated with Mxh (r=0.23, P<0.01) in 08FW, while in 09GW it was negatively correlated with Mxt and Mrs (r=-0.21 and -0.29, P<0.01), and positively correlated with Mxh and Mxw (r=0.59 and 0.25, P<0.01). In 08FD grain protein concentration was negatively correlated with Mrs (r=-0.22, P<0.01) and positively correlated with Mxh (r=0.34, P<0.01), whereas in 09GD it was negatively correlated with Mrs and Mrw (r=0.21, P<0.01), and positively correlated with Mxh (r=0.21, P<0.01). Flour color L and b were negatively correlated in the four environments (r=-0.26 to -0.57, P<0.01). As expected, single kernel hardness and NIR hardness were positively correlated with each

Table 2.3. Means, standard errors, and ranges for quality traits of the CO940610/Platte population (n=185) at Fort Collins under two irrigation levels in the 2007-08 growing season.

Env	Full irrigation (08FW)				Limited irrigation (08FD)				*P* for difference between treatments
Variable†	Mean	Std Error	Min	Max	Mean	Std Error	Min	Max	
Mxt (min)	2.43	0.05	1.29	4.39	2.79	0.07	1.22	4.85	<0.001
Mxh (mu)	56.59	0.44	51.41	62.76	58.20	0.64	49.87	66.58	<0.003
Mxw (mu)	23.71	0.24	19.96	29.85	26.79	0.61	24.14	31.98	<0.001
Mrw (mu)	14.70	0.47	5.98	24.23	14.16	0.53	4.94	27.56	<0.001
Mrs (mu)	-5.31	0.15	-9.81	-1.62	-3.29	0.06	-4.31	-2.49	<0.001
Skw (mg)	32.59	0.38	24.24	40.31	33.99	0.24	26.75	41.33	<0.041
Skd (mm)	2.81	0.01	2.31	3.08	2.93	0.02	2.42	3.19	<0.001
Sha	73.12	0.94	60.38	85.84	75.07	0.85	65.48	85.31	<0.001
Gpc (%)	13.84	0.08	12.60	15.92	14.59	0.23	12.48	16.66	<0.001
Gac (%)	1.45	0.01	1.29	1.60	1.41	0.01	1.22	1.59	<0.023
Tw (g)	77.19	0.22	72.91	79.59	78.41	0.26	77.67	78.53	<0.021
Ppo	0.29	0.01	0.15	0.47	0.32	0.01	0.19	0.56	<0.001
Fcl	91.33	0.03	90.22	91.88	91.30	0.06	90.06	91.45	<0.081
Fcb	10.53	0.08	9.05	14.44	10.19	0.06	8.86	13.85	<0.001

† Mxt, Mixograph peak time; Mxh, Mixograph peak height; Mxw, Mixograph peak width; Mrw, Mixograph right width; Mrs, Mixograph right slope; ; Skw, single kernel weight; Skd, single kernel diameter; Sha, single kernel hardness; Gpc, grain protein concentration at 12% moisture; Gac, grain ash concentration; Tw, test weight; Ppo, polyphenol oxidase activity; Fcl, Flour color L; Fcb, Flour color b; mu= mixograph unit using a 100-unit scale.

Table 2.4. Means, standard errors, and ranges for quality traits of the CO940610/Platte population (n=185) at Greeley under two irrigation levels in the 2008-09 growing season.

Env	Full Irrigation (09GW)				Limited irrigation (09GD)				*P* for difference between treatments
Variable†	Mean	Std Error	Min	Max	Mean	Std Error	Min	Max	
Mxt (min)	3.42	0.11	1.69	6.36	3.76	0.07	1.33	4.89	<0.001
Mxh (mu)	51.08	0.41	46.10	55.54	57.24	0.67	51.99	64.52	<0.001
Mxw (mu)	22.46	0.22	20.48	26.63	27.04	0.29	23.21	31.78	<0.001
Mrw (mu)	17.73	0.28	8.92	25.88	15.35	0.46	7.64	23.95	<0.001
Mrs (mu)	-3.24	0.19	-7.77	-0.64	-6.24	0.18	-10.88	-2.18	<0.001
Skw (mg)	34.94	0.36	25.65	43.28	35.11	0.24	24.22	42.08	<0.034
Skd (mm)	2.83	0.01	2.42	3.11	2.86	0.01	2.44	3.07	<0.024
Sha	67.98	0.58	54.13	80.95	71.72	0.50	57.33	82.13	<0.001
Gpc (%)	11.40	0.14	10.0	14.30	14.36	0.15	12.77	16.44	<0.001
Gac (%)	1.56	0.01	1.34	1.85	1.59	0.01	1.40	1.97	<0.064
Tw (g)	77.62	0.19	72.88	80.39	78.37	0.12	71.77	80.52	<0.001
Ppo	0.21	0.01	0.104	0.38	0.22	0.01	0.123	0.40	<0.053
Fcl	91.59	0.05	90.81	92.16	91.21	0.04	90.49	91.83	<0.053
Fcb	9.93	0.07	8.24	12.20	9.62	0.05	8.34	11.80	<0.001

† Mxt, Mixograph peak time; Mxh, Mixograph peak height; Mxw, Mixograph peak width; Mrw, Mixograph right width; Mrs, Mixograph right slope; Skw, single kernel weight; Skd, single kernel diameter; Sha, single kernel hardness; Gpc, grain protein concentration at 12% moisture; Gac, grain ash concentration; Tw, test weight; Ppo, polyphenol oxidase activity; Fcl, Flour color L; Fcb, Flour color b; mu= mixograph unit using a 100-unit scale.

Table 2.5. Means for observed quality characteristics for the two parents, CO940610 and Platte, under two irrigation levels in the 2007-08 and 2008-09 growing seasons.

Env‡ / Variable†	08FD		08FW		09GD		09GW	
	CO940610	Platte	CO940610	Platte	CO940610	Platte	CO940610	Platte
Mxt (min)	2.82	3.10	2.28	2.51	2.91	2.82	3.66**	2.72
Mxh (mu)	54.09	58.79**	55.30	57.44*	56.30	59.07**	48.50	53.37**
Mxw (mu)	26.07	28.28	22.22	24.20	25.77	27.27	20.89	25.59**
Mrw (mu)	13.96	19.94**	11.80	19.38**	17.42	19.24	17.85	21.19*
Mrs (mu)	-3.07	-3.53	-4.87	-4.61	-5.28	-5.50	-2.50	-1.24
Skw (mg)	36.13*	33.65	35.17**	31.32	35.30	34.81	37.43	34.47
Skd (mm)	2.94	2.94	2.83	2.85	2.81	2.91**	2.84	2.90**
Sha	76.71**	69.30	75.82**	70.17	77.81**	64.74	67.36**	64.85
Gpc (%)	13.92	16.03**	13.17	14.72**	13.41	15.16**	10.99	11.79*
Gac (%)	1.39	1.40	1.45	1.43	1.57	1.62	1.54	1.53
Tw (g)	78.36	78.49	77.18	78.93**	77.68	79.21*	76.79	79.19**
Ppo	0.39**	0.25	0.38**	0.21	0.31*	0.21	0.31**	0.16
Fcl	91.22	91.35*	91.16	91.63**	90.88	91.42**	91.17	91.97**
Fcb	11.11**	9.27	10.93**	9.33	10.27**	8.69	10.20**	8.79

*, ** The parental mean with asterisks is significantly higher than the other parental mean at the 0.05 and 0.01 levels of probability, respectively for each environment.

† Mxt, Mixograph peak time; Mxh, Mixograph peak height; Mxw, Mixograph peak width; Mrw, Mixograph right width; Mrs, Mixograph right slope; Skw, single kernel weight; Skd, single kernel diameter; Sha, single kernel hardness; Gpc, grain protein concentration at 12% moisture; Gac, grain ash concentration; Tw, test weight; Ppo, polyphenol oxidase activity; Fcl, Flour color L; Fcb, Flour color b; mu= mixograph unit using a 100-unit scale .

‡ The four environments obtained from different moisture levels during the two growing seasons: Fort Collins limited irrigation (07FD), Fort Collins full irrigation (07FW), Greeley limited irrigation (08GD), and Greeley full irrigation (08GW)

Table 2.6. Pearson correlation coefficients among quality characteristics of the CO940610/Platte population (n=185) at Fort Collins under different irrigation levels in the 2007-08 growing season.†

Env		Full irrigation															
	Variable‡	Gy	Mxt	Mrs	Mxh	Mxw	Mrw	Fcl	Fcb	Skw	Skd	Sha	Gpc	Gac	NIRha	Tw	Ppo
Limited irrigation	Gy		0.17*	0.31**	-0.19**	-0.07	0.22**	0.02	0.11	0.15*	-0.02	0.26**	-0.52**	-0.22**	0.34**	0.21*	-0.04
	Mxt	0.18**		0.79**	-0.16	0.31**	0.83**	-0.04	0.13	-0.07	-0.12	0.19**	-0.25**	0.07	0.21**	-0.14*	-0.05
	Mrs	0.19**	0.38**		-0.14*	0.33**	0.84**	0.01	0.15	-0.09	-0.14*	0.21**	-0.36**	0.01	0.29**	-0.16*	-0.09
	Mxh	-0.24**	-0.24**	-0.58**		0.45**	0.05	-0.26**	0.18**	-0.05	0.07	0.17*	0.23**	0.05	0.13	-0.07	-0.06
	Mxw	0.07	0.26**	0.48**	-0.51**		0.47**	0.04	-0.01	-0.06	-0.06	-0.04	0.08	0.05	-0.01	-0.14*	-0.03
	Mrw	0.27**	0.79**	0.36**	-0.09	-0.09		-0.07	0.16*	-0.15*	-0.17**	0.24**	-0.24**	0.05	0.24**	-0.22**	-0.08
	Fcl	0.08	-0.12	-0.02	-0.10	-0.01	-0.09		-0.57**	0.18**	0.11	-0.68**	-0.14*	-0.03	-0.41**	0.15*	0.07
	Fcb	0.10	-0.05	0.02	0.05	-0.01	-0.02	-0.29**		-0.22**	-0.19**	0.59**	-0.23**	-0.24**	0.52**	-0.25**	-0.08
	Skw	0.15*	0.19**	0.03	-0.01	-0.01	0.11	0.05	-0.12		0.89**	-0.46**	-0.03	0.04	-0.05	0.39**	0.19**
	Skd	0.14*	0.14*	-0.03	0.07	0.05	0.09	-0.01	-0.09	0.89**		-0.31**	0.09	0.01	-0.04	0.44**	0.11
	Sha	0.14*	0.03	0.12	0.04	-0.03	0.09	-0.36**	0.52**	-0.53**	-0.35**		-0.14	-0.08	0.66**	-0.06	-0.23**
	Gpc	-0.52**	-0.13	-0.22**	0.34**	0.09	-0.12	-0.13*	-0.31**	-0.04	-0.01	-0.21**		0.30**	-0.36**	0.09	0.03
	Gac	-0.52**	-0.13	-0.22**	0.34**	0.09	-0.12	-0.13	-0.31**	-0.04	-0.01	-0.21**	0.60**		-0.11	-0.20**	0.04
	NIRha	0.41**	0.15*	0.15*	0.01	0.08	0.19**	-0.28**	0.50**	0.04	0.12	0.59**	-0.37**	-0.37**		-0.02	-0.09
	Tw	0.23**	0.11	0.07	-0.01	0.05	0.13	-0.01	0.06	0.18*	0.19*	0.08	-0.11	0.11	0.26**		0.02
	Ppo	-0.08	-0.03	0.01	0.04	0.02	-0.05	-0.02	-0.02	0.25**	0.17*	-0.27**	0.07	0.07	-0.04	-0.02	

† The upper right half of the table refers to the fully irrigated treatment and the lower left half of the table refers to the limited irrigation treatment.
*, **, significant at the 0.05 and 0.01 levels of probability, respectively.
‡ Gy, grain yield; Mxt, Mixograph peak time; Mrs, Mixograph right slope; Mxh, Mixograph peak height; Mxw, Mixograph peak width; Mrw, Mixograph right width; Fcl, flour color value whiteness; Fcb, flour color value yellow; Skw, single kernel weight; Skd, single kernel diameter; Sha, single kernel hardness; Gpc, grain protein concentration at 12% moisture content; Gac, grain ash; NIRha, hardness from near infrared spectroscopy; Tw, test weight; Ppo, polyphenol oxidase activity

Table 2.7. Pearson correlation coefficients among quality characteristics of the CO940610/Platte population (n=185) at Greeley under different irrigation levels in the 2008-09 growing season.†

Env		Full irrigation															
	Variable‡	Gy	Mxt	Mrs	Mxh	Mxw	Mrw	Fcl	Fcb	Skw	Skd	Sha	Gpc	Gac	NIRha	TW	Ppo
Limited irrigation	Gy		0.12	0.20**	-0.31**	-0.22	-0.01	0.11	0.06	0.39**	0.35**	0.05	-0.36**	-0.30**	0.14	0.35**	0.06
	Mxt	0.14*		0.56**	-0.48**	0.12	0.46**	-0.08	0.07	0.09	-0.01	0.06	-0.21**	-0.01	0.09	-0.06	-0.04
	Mrs	0.21**	0.79**		-0.45**	0.21**	0.61**	0.10	-0.08	-0.01	-0.08	0.01	-0.29**	-0.06	0.09	0.06	0.02
	Mxh	-0.12	-0.38**	-0.47**		0.39**	-0.05	-0.22**	-0.08	-0.14*	-0.04	0.19**	0.59**	0.26**	0.06	0.04	0.06
	Mxw	-0.03	0.14*	-0.09	0.51**		0.50**	0.04	-0.09	-0.22**	-0.19**	0.06	0.25**	0.14*	0.05	0.01	0.05
	Mrw	0.26**	0.76**	0.80**	-0.21**	0.02		0.05	0.01	-0.19**	-0.21**	0.17*	0.01	0.09	0.22**	-0.08	-0.01
	Fcl	0.23**	-0.08	0.04	-0.15*	-0.01	0.03		-0.32**	0.12	0.14	-0.49**	-0.29**	-0.15*	-0.27	0.13	0.01
	Fcb	0.24**	0.01	0.05	0.07	-0.01	0.05	-0.26**		-0.03	-0.12	0.35**	-0.31**	0.34**	0.29**	-0.11	0.05
	Skw	0.25**	0.15	0.09	0.07	0.07	0.09	-0.04	0.06		0.90**	-0.53**	-0.25**	-0.23**	-0.25**	0.43**	0.32**
	Skd	0.19**	0.13	0.05	0.13	0.09	0.05	-0.01	0.01	0.91**		-0.49	-0.18**	-0.24**	-0.24**	0.49**	0.28**
	Sha	0.24**	0.14	0.15*	0.06	-0.02	0.17*	-0.32**	0.45**	-0.38**	-0.29**		0.07	0.03	0.66**	0.03	-0.19**
	Gpc	-0.66**	-0.12	-0.21**	0.21**	0.15*	-0.21**	-0.27**	-0.29**	-0.23**	-0.10	-0.10		0.52**	-0.08	-0.18**	-0.01
	Gac	-0.50**	-0.05	-0.11	0.05	0.02	-0.13	-0.31**	-0.25**	-0.23**	-0.24**	-0.10	0.58**		-0.06	-0.46	-0.05
	NIRha	0.16*	0.11	0.15*	0.16*	0.14	0.18**	-0.15*	0.39**	0.06	0.09	0.53**	-0.07	-0.07		0.08	0.08
	Tw	0.43**	0.17*	0.18**	0.12	0.05	0.22**	0.19**	0.14*	0.30**	0.38**	0.24**	-0.24**	-0.50**	0.25**		0.04
	Ppo	-0.05	-0.04	0.02	0.02	0.02	0.01	-0.02	0.01	0.14*	0.13	-0.21**	0.03	0.04	-0.07	-0.09	

† The upper right half of the table refers to the fully irrigated treatment and the lower left half of the table refers to the limited irrigation treatment.
*, **, significant at the 0.05 and 0.01 levels of probability, respectively.
‡ Gy, grain yield; Mxt, Mixograph peak time; Mrs, Mixograph right slope; Mxh, Mixograph peak height; Mxw, Mixograph peak width; Mrw, Mixograph right width; Fcl, flour color value whiteness; Fcb, flour color value yellow; Skw, single kernel weight; Skd, single kernel diameter; Sha, single kernel hardness; Gpc, grain protein concentration at 12% moisture content; Gac, grain ash; NIRha, hardness from near infrared spectroscopy; Tw, test weight; Ppo, polyphenol oxidase activity

other in all environments, but the magnitude of the correlation was only moderate (r=0.53 to 0.66, P<0.01).

2.2.5. Heritability of quality traits

Heritability estimates of quality traits were moderate to high, indicating that a large part of the expression of these traits was genetically controlled. Heritability estimates in individual environments ranged from 0.361 for Mxw in 09GW to 0.929 for Fcb in 08FW (Table 2.8). Flour color b showed the highest heritability among quality traits in the four environments (0.872 to 0.929), with an overall heritability estimate of 0.951 for the combined data. Of the mixograph traits, Mxt, Mrs, and Mrw showed high heritability (0.712 to 0.957), and moderate heritability estimates were obtained for Mxh and Mxw (0.491 to 0.782) when combined across the four environments. All single kernel characteristics shared high heritability estimates (0.882 to 0.943) over the four environments

2.2.6. QTL analysis

Composite interval mapping analysis produced a total of 123 putative major and minor QTL for quality traits (Table 2.9, Fig. 2.3). For all categories of traits, QTL frequency was highest in the B genome with 54 QTL (43.9% of total QTL number); another 30 (24.4%) and 39 (31.7%) QTL were found in genomes A and D, respectively. Distribution of QTL was relatively balanced between irrigation levels, with 67 QTL (54.7%) detected under full irrigation and 56 QTL (45.5%) detected in the limited irrigation treatment. The QTL distribution in homoeologous chromosomes for Group 1 through Group 7 was 37 (30.1%), 16 (13.0%), 11 (8.9%), 5 (4.1%), 9 (7.3%), 11 (8.9%), and 34 (27.6%), respectively. QTL for quality traits were distributed among 19 linkage groups, with none detected on 1A.2, 1B.2, 2B.2, 2D.2, 3B.2, 3D.2, 4A.2, 4B, 4D.2, 5D, 6D, and 7D.1. The highest number of QTL were identified for Skw (15 QTL), while the lowest number of QTL was identified for flour color L (two QTL).

Table 2.8. Heritability estimates for quality characteristics of the CO940610/Platte population in four Colorado environments in the 2007-08 and 2008-09 growing seasons.†

Environment / Variable‡	08FD	09GD	08FW	09GW	Four environments & (90% confidence interval)
Gy	0.571	0.689	0.608	0.618	0.729 (0.668 - 0.776)
Mxt	0.857	0.867	0.925	0.822	0.941 (0.928 – 0.957)
Mrs	0.818	0.732	0.818	0.715	0.765 (0.712 – 0.806)
Mxh	0.616	0.489	0.527	0.569	0.735 (0.675 – 0.782)
Mxw	0.391	0.468	0.533	0.361	0.585 (0.491 – 0.658)
Mrw	0.798	0.716	0.835	0.698	0.881 (0.854 – 0.902)
Skw	0.849	0.871	0.787	0.842	0.931 (0.916 – 0.943)
Skd	0.784	0.858	0.760	0.848	0.909 (0.889 – 0.925)
Sha	0.791	0.814	0.883	0.811	0.903 (0.882 – 0.920)
Gpc	0.548	0.523	0.544	0.609	0.739 (0.680 – 0.785)
Gac	0.761	0.734	0.726	0.765	0.871 (0.842 – 0.894)
Fcl	0.854	0.619	0.824	0.602	0.781 (0.732 – 0.819)
Fcb	0.917	0.872	0.929	0.917	0.951 (0.940 – 0.960)
Tw	0.743	0.768	0.749	0.768	0.777 (0.727 – 0.816)
Ppo	0.762	0.652	0.779	0.702	0.884 (0.858 – 0.904)

† Gy, grain yield; Mxt, Mixograph peak time; Mrs, Mixograph right slope; Mxh, Mixograph peak height; Mxw, Mixograph peak width; Mrw, Mixograph right width; Fcl, Flour color L, Fcb, Flour color b; Skw, single kernel weight; Skd, single kernel diameter; Sha, single kernel hardness, Gpc, grain protein concentration at 12% moisture, Gac, grain ash concentration; Tw, test weight, Ppo, polyphenol oxidase activity.

‡ The four environments obtained from different moisture levels during the two growing seasons: Fort Collins limited irrigation (08FD), Fort Collins full irrigation (08FW), Greeley limited irrigation (09GD), and Greeley full irrigation (09GW)

Table 2.9. QTL detection for quality characteristics of the CO940610/Platte population in four Colorado environments in the 2007-08 and 2008-09 growing seasons.

QTL	Environment†	Marker interval	Nearest marker	Peak position (cM)	LOD	a‡	R^2 (%)
Mixograph peak time							
QMxt.cob-1A.1	08FW	*wPt-9757 - Xwmc312*	*wPt-9757*	90.4	4.54	0.13	4.9
QMxt.cob-1B.1		*Xcfd20a - Glu-B1*	*Glu-B1*	53.7	17.39	-0.29	22.6
QMxt.cob-1D		*Xcfd48 - Glu-D1*	*Glu-D1*	92.1	21.11	0.32	29.3
QMxt.cob-2D.1		*wPt-4413 - wPt-0638*	*wPt-4413*	58.5	3.63	0.13	4.7
QMxt.cob-6B.1		*wPt-2587 - wPt-6437*	*wPt-6437*	30.8	2.69	0.11	3.0
QMxt.cob-7B		*Xwmc76 - Xwmc182b*	*Xwmc182b*	6.6	5.91	-0.15	6.2
Multiple-QTL model							68.9
QMxt.cob-1B.1	09GW	*Xcfd20a - Glu-B1*	*Glu-B1*	55.7	12.89	-0.37	24.1
QMxt.cob-1D		*Xcfd48 - Glu-D1*	*Glu-D1*	92.1	21.69	0.39	25.8
QMxt.cob-7D.2		*Xbarc126 - Vrn-D3*	*Xbarc126*	31.4	2.61	0.15	4.7
Multiple-QTL model							56.4
QMxt.cob-1A.1	08FD	*Xwmc312 - GLU-A1*	*Xwmc312*	92.1	7.22	0.18	6.2
QMxt.cob-1B.1		*Glu-B1 - Xcfd20a*	*Glu-B1*	55.7	22.52	-0.37	25.9
QMxt.cob-1D		*Glu-D1 - Xcfd48*	*Glu-D1*	92.1	24.45	0.38	27.1
QMxt.cob-7B		*Xwmc182b - Xgwm46*	*Xgwm46*	10.5	7.75	-0.19	6.8
Multiple-QTL model							68.3
QMxt.cob-1A.1	09GD	*Xwmc312 - Glu-A1*	*Xwmc312*	92.1	6.00	0.16	4.7
QMxt.cob-1B.1		*Xcfd20a - Glu-B1*	*Glu-B1*	53.7	25.41	-0.39	26.3
QMxt.cob-1D		*Xcfd48 - Glu-D1*	*Glu-D1*	92.1	26.32	0.39	28.2
QMxt.cob-6A		*Xcfd1 - Xwmc256*	*Xcfd1*	71.1	2.99	0.13	3.3
QMxt.cob-6B.1		*wPt-2587 - wPt-6437*	*wPt-6437*	30.8	2.82	0.11	2.3
QMxt.cob-7B		*wPt-7602 - Xwmc76*	*Xwmc76*	4.6	7.68	-0.19	6.8
QMxt.cob-7D.2		*wPt-0789 - Xbarc126*	*Xbarc126*	29.9	3.33	0.12	2.7
Multiple-QTL model							73.8

† The four environments were different moisture levels during the two growing seasons: Fort Collins limited irrigation (08FD), Fort Collins full irrigation (08FW), Greeley limited irrigation (09GD), and Greeley full irrigation (09GW).

‡ Additive effect: Positive values indicate an increasing effect of Platte alleles and negative values indicate an increasing effect of CO940610 alleles.

Table 2.9. Continued.

QTL	Environment†	Marker interval	Nearest marker	Peak position (cM)	LOD	a‡	R^2 (%)
Mixograph peak height							
QMxh.cob-1A.1	08FW	*Xwmc312 - Glu-A1*	*Glu-A1*	94.1	12.19	0.94	21.3
QMxh.cob-1B.2		*Xbarc80 - wPt-6142*	*Xbarc80*	19.2	3.10	-0.44	4.7
QMxh.cob-1D		*Xcfd48 - Glu-D1*	*Xcfd48*	90.1	4.93	0.56	7.7
QMxh.cob-3B.1		*wPt-3107 - wPt-9049*	*wPt-9049*	54.1	2.67	0.51	6.3
QMxh.cob-4A.1		*Xwmc48 - Xwmc420*	*Xwmc420*	9.4	3.42	0.47	5.0
Multiple-QTL model							38.7
QMxh.cob-1A.1	09GW	*Glu-A1 - Xwmc312*	*Glu-A1*	92.1	4.62	0.53	8.3
QMxh.cob-1D		*Xgwm337 - Xbarc169*	*Xgwm337*	75.8	6.33	0.67	13.0
QMxh.cob-2B.1		*Xwmc154 - wPt-9402*	*Xwmc154*	56.7	3.69	0.54	8.4
Multiple-QTL model							33.1
QMxh.cob-1A.1	08FD	*wPt-9757 - Xwmc312*	*Xwmc312*	90.4	10.24	1.23	15.6
QMxh.cob-4A.1		*Xgwm610 - Xwmc48*	*Xgwm610*	6.0	3.14	0.76	6.6
Unlinked locus		Chromosome 7A or 7B	Xwmc606		0.0009	0.81	8.0
Multiple-QTL model							34.7
QMxh.cob-1A.1	09GD	*Glu-A1 - Xwmc312*	*Glu-A1*	92.1	7.72	0.78	13.0
QMxh.cob-1B.1		*Xbarc302 - Xwmc419*	*Xbarc302*	44.9	3.78	-0.56	6.4
QMxh.cob-1D		*Xbarc169 - Xcfd48*	*Xbarc169*	87.8	9.22	0.91	17.2
QMxh.cob-2B.1		*Xwmc154 - wPt-9402*	*Xwmc154*	56.7	3.91	0.59	7.2
Multiple-QTL model							33.2
Mixograph peak width							
QMxw.cob-1A.1	08FW	*Xwmc312 - Glu-A1*	*Xwmc312*	92.1	7.27	0.68	14.3
QMxw.cob-1B.1		*Xcfd20a - Glu-B1*	*Xcfd20a*	51.9	3.02	-0.43	5.7
Multiple-QTL model							23.0

† The four environments were different moisture levels during the two growing seasons: Fort Collins limited irrigation (08FD), Fort Collins full irrigation (08FW), Greeley limited irrigation (09GD), and Greeley full irrigation (09GW).

‡ Additive effect: Positive values indicate an increasing effect of Platte alleles and negative values indicate an increasing effect of CO940610 alleles. For unlinked loci, presumed chromosome locations are provided, and in the LOD column *P*-values from SAS PROC GLM are listed.

Table 2.9. Continued.

QTL	Environment†	Marker interval	Nearest marker	Peak position (cM)	LOD	a‡	R^2 (%)
Mixograph peak width							
QMxw.cob-1A.1	09GW	*Xbarc148 - Xbarc83*	*Xbarc83*	81.3	4.17	0.30	8.3
QMxw.cob-3B.1		*Xgwm285 - wPt-9310*	*wPt-9310*	16.3	3.01	-0.34	6.4
QMxw.cob-5B		*Xbarc4 - Xgwm540*	*Xgwm540*	56.5	3.70	0.29	7.3
Multiple-QTL model							20.7
QMxw.cob-1A.1	08FD	*Xbarc148 - Xbarc83*	*Xbarc83*	83.3	2.56	0.48	7.9
QMxw.cob-1B.1		*wPt-0705 - wPt-9857*	*wPt-9857*	63.7	2.97	-0.42	6.2
Multiple-QTL model							12.7
QMxw.cob-1A.1	09GD	*wPt-6654 - Xbarc148*	*Xbarc148*	78.3	8.77	0.70	18.2
Mixograph right width							
QMrw.cob-1A.1	08FW	*Xwmc312 - Glu-A1*	*Xwmc312*	92.1	4.47	1.21	6.8
QMrw.cob- 1B.1		*Xcfd20a - Glu-B1*	*Glu-B1*	53.7	15.01	-2.37	26.6
QMrw.cob-1D		*Xbarc169 - Xcfd48*	*Xbarc169*	85.8	11.78	1.88	16.8
QMrw.cob-6A		*wPt-7127 - Xcfd1*	*Xcfd1*	65.1	5.62	1.43	9.7
QMrw.cob-7B		*wPt-7602 - Xwmc76*	*wPt-7602*	0.0	4.12	-1.17	6.5
Multiple-QTL model							64.4
QMrw.cob-1A.1	09GW	*Xbarc148 - Xbarc83*	*Xbarc148*	79.6	2.59	0.52	4.0
QMrw.cob-1B.1		*Xcfd20a - Glu-B1*	*Glu-B1*	53.7	6.27	-0.83	10.1
QMrw.cob-1D		*Xcfd48 - Glu-D1*	*Glu-D1*	93.4	7.36	0.89	12.0
QMrw.cob-2B.1		*wPt-9402 - wPt-3561*	*wPt-9402*	66.7	3.14	-0.64	5.9
QMrw.cob-2D.1		*Xbarc168 - wPt-0298*	*wPt-0298*	20.7	2.85	0.65	6.1
QMrw.cob-6A		*wPt-7127 - Xcfd1*	*Xcfd1*	63.1	4.23	0.75	8.2
Multiple-QTL model							45.0

† The four environments were different moisture levels during the two growing seasons: Fort Collins limited irrigation (08FD), Fort Collins full irrigation (08FW), Greeley limited irrigation (09GD), and Greeley full irrigation (09GW).

‡ Additive effect: Positive values indicate an increasing effect of Platte alleles and negative values indicate an increasing effect of CO940610 alleles.

Table 2.9. Continued.

QTL	Environment†	Marker interval	Nearest marker	Peak position (cM)	LOD	a‡	R^2 (%)
Mixograph right width							
QMrw.cob-1A.1	08FD	*Xbarc148 - Xbarc83*	*Xbarc148*	79.6	2.81	0.91	3.4
QMrw.cob-1B.1		*Xcfd20a - Glu-B1*	*Glu-B1*	53.7	15.65	-2.30	22.8
QMrw.cob-1D		*Xcfd48 - Glu-D1*	*Glu-D1*	92.1	6.76	1.48	9.3
QMrw.cob-5B		*Xbarc4 - Xbarc216*	*Xbarc4*	53.6	2.95	0.94	3.8
QMrw.cob-6A		*Xcfd1 - Xwmc256*	*Xcfd1*	73.1	6.83	1.79	13.7
QMrw.cob-7B		*wPt-7602 - Xwmc76*	*wPt-7602*	0.0	3.88	-1.11	4.0
Multiple-QTL model							57.6
QMrw.cob-1B.1	09GD	*Xcfd20a - Glu-B1*	*Glu-B1*	55.7	16.56	-2.07	24.5
QMrw.cob-1D		*Xgwm337 - Xbarc169*	*Xgwm337*	73.8	10.57	1.54	14.2
QMrw.cob-6A		*wPt-7127 - Xcfd1*	*Xcfd1*	71.1	5.96	1.36	11.1
QMrw.cob-7B		*Xwmc76 - Xwmc182b*	*Xwmc182b*	6.6	4.94	-1.03	6.3
QMrw.cob-7D.2		*wPt-0789 - Xbarc126*	*wPt-0789*	25.9	3.39	0.89	4.4
Multiple-QTL model							56.3
Mixograph right slope							
QMrs.cob-1B.1	08FW	*Xcfd20a - Glu-B1*	*Glu-B1*	53.7	18.79	-0.94	26.5
QMrs.cob-1D		*Xcfd48 - Glu-D1*	*Xcfd48*	90.1	11.79	0.68	15.4
QMrs.cob-7B		*wPt-7602- Xwmc76*	*wPt-7602*	0.0	7.12	-0.52	8.8
QMrs.cob-7D.2		*Xbarc126 - Vrn-D3*	*Vrn-D3*	33.4	3.39	0.38	4.4
Multiple-QTL model							57.4
QMrs.cob-1B.1	09GW	*Xcfd20a - Glu-B1*	*Glu-B1*	53.7	8.92	-0.42	14.7
QMrs.cob-1D		*Glu-D3 - Xwmc336*	*Glu-D3*	24.0	3.31	0.26	5.4
QMrs.cob-6A		*wPt-7623 - wPt-7127*	*wPt-7127*	59.1	3.54	0.27	5.9
Multiple-QTL model							29.4

† The four environments were different moisture levels during the two growing seasons: Fort Collins limited irrigation (08FD), Fort Collins full irrigation (08FW), Greeley limited irrigation (09GD), and Greeley full irrigation (09GW).

‡ Additive effect: Positive values indicate an increasing effect of Platte alleles and negative values indicate an increasing effect of CO940610 alleles.

Table 2.9. Continued.

QTL	Environment†	Marker interval	Nearest marker	Peak position (cM)	LOD	a‡	R^2 (%)
Single kernel weight							
QSkw.cob-1A.1	08FW	*wPt-3904 - Xwmc24*	*wPt-3904*	56.4	2.67	0.51	4.2
QSkw.cob-2B.1		*wPt-3561 - Xgwm429*	*Xgwm429*	87.2	9.18	1.05	17.8
QSkw.cob-2D.1		*wPt-4413 - wPt-0638*	*wPt-4413*	58.5	4.68	-0.76	9.4
QSkw.cob-6A		*Xwmc256 - wPt-3069*	*Xwmc256*	89.1	5.22	-0.77	9.8
QSkw.cob-7D.2		*Xbarc126 - Vrn-D3*	*Vrn-D3*	37.3	5.04	-0.71	8.1
Multiple-QTL model							38.3
QSkw.cob-1A.1	09GW	*wPt-2872 - wPt-6654*	*wPt-2872*	71.9	3.83	0.74	6.5
QSkw.cob-2B.1		*wPt-3561 - Xgwm429*	*Xgwm429*	83.2	2.99	0.71	5.9
QSkw.cob-2D.1		*wPt-4413 - wPt-0638*	*wPt-4413*	56.5	2.96	-0.72	6.3
QSkw.cob-3B.1		*Xgwm285 - wPt-9310*	*Xgwm285*	10.3	4.26	0.77	6.8
QSkw.cob-6A		*Xwmc256 - wPt-3069*	*Xwmc256*	93.1	10.09	-1.27	17.8
QSkw.cob-7D.2		*Xbarc126 - Vrn-D3*	*Vrn-D3*	35.4	3.29	-0.65	5.1
Multiple-QTL model							41.5
QSkw.cob-1A.1	08FD	*wPt-2872 - wPt-6654*	*wPt-2872*	75.1	3.94	0.66	7.4
QSkw.cob-1B.1		*Xcfd20a - Glu-B1*	*Glu-B1*	55.7	6.52	-0.79	10.7
QSkw.cob-2D.1		*Xbarc168 - wPt-0298*	*Xbarc168*	20.7	2.84	-0.65	7.2
QSkw.cob-3B.1		*Xgwm285 - wPt-9310*	*Xgwm285*	10.3	2.89	0.56	5.1
QSkw.cob-6A		*Xwmc256 - wPt-3069*	*Xwmc256*	93.8	6.56	-0.85	12.1
QSkw.cob-7D.2		*Xbarc126 - Vrn-D3*	*Xbarc126*	33.4	2.71	-0.54	4.8
Multiple-QTL model							37.4
QSkw.cob-1A.1	09GD	*Xbarc148 - Xbarc83*	*Xbarc83*	83.3	4.79	0.78	8.4
QSkw.cob-1B.1		*Xcfd20a - Glu-B1*	*Glu-B1*	55.7	4.50	-0.79	8.9
QSkw.cob-3B.1		*Xgwm285 - wPt-9310*	*Xgwm285*	10.3	3.96	0.73	7.2
QSkw.cob-6A		*Xwmc256 - wPt-3069*	*Xwmc256*	93.8	4.82	-0.79	8.9
Multiple-QTL model							37.6

† The four environments were different moisture levels during the two growing seasons: Fort Collins limited irrigation (08FD), Fort Collins full irrigation (08FW), Greeley limited irrigation (09GD), and Greeley full irrigation (09GW).

‡ Additive effect: Positive values indicate an increasing effect of Platte alleles and negative values indicate an increasing effect of CO940610 alleles.

Table 2.9. Continued.

QTL	Environment†	Marker interval	Nearest marker	Peak position	LOD	a‡	R^2 (%)
Single kernel diameter							
QSkd.cob-2B.1	08FW	*Xgwm429 - Xbarc55*	*Xgwm429*	95.0	6.35	0.05	12.2
QSkd.cob-3B.1		*Xgwm285 - wPt-9310*	*Xgwm285*	12.3	6.56	0.05	12.2
QSkd.cob-4D.1		*Xcfd71 - Xwmc720*	*Xwmc720*	7.2	2.65	0.03	4.2
QSkd.cob-6A		*wPt-3733 - wPt-8721*	*wPt-3733*	83.3	3.28	-0.03	6.8
QSkd.cob-7D.2		*Vrn-D3 - Xgwm437*	*Vrn-D3*	45.3	4.60	-0.04	10.3
Multiple-QTL model							37.6
QSkd.cob-2B.1	09GW	*wPt-3561 - Xgwm429*	*Xgwm429*	87.2	3.89	0.03	6.4
QSkd.cob-3B.1		*Xgwm285 - wPt-9310*	*Xgwm285*	10.3	10.98	0.05	17.6
QSkd.cob-6A		*Xwmc256 - wPt-3069*	*Xwmc256*	91.1	6.52	-0.04	10.6
QSkd.cob-7D.2		*Xbarc126 - Vrn-D3*	*Xbarc126*	31.4	5.79	0.03	10.4
Multiple-QTL model							39.7
QSkd.cob-1A.1	08FD	*wPt-6654 - Xbarc148*	*wPt-6654*	76.3	2.79	0.02	3.5
QSkd.cob-1B.1		*wPt-0705 - wPt-9857*	*wPt-0705*	60.6	5.68	-0.04	8.1
QSkd.cob-2B.1		*Xbarc55 - Xgwm374*	*Xbarc55*	103.7	4.10	0.03	5.6
QSkd.cob-3B.1		*Xwmc78 - Xgwm285*	*Xgwm285*	12.3	10.14	0.05	15.6
QSkd.cob-4D.1		*Xbarc98 - Xcfd71*	*Xbarc98*	0.0	2.81	0.02	3.8
QSkd.cob-6A		*Xwmc256 - wPt-3069*	*Xwmc256*	93.8	7.73	-0.04	11.1
Multiple-QTL model							58.9
QSkd.cob-1A.1	09GD	*Xwmc312 - Glu-A1*	*Glu-A1*	94.1	5.79	0.03	10.4
QSkd.cob-2B.1		*Xgwm429 - Xbarc55*	*Xbarc55*	99.0	4.02	0.03	7.2
QSkd.cob-3B.1		*Xgwm285 - wPt-9310*	*Xgwm285*	12.3	9.75	0.04	19.1
QSkd.cob-6A		*Xwmc256 - wPt-3069*	*Xwmc256*	93.8	3.29	-0.02	5.7
Multiple-QTL model							36.8

† The four environments were different moisture levels during the two growing seasons: Fort Collins limited irrigation (08FD), Fort Collins full irrigation (08FW), Greeley limited irrigation (09GD), and Greeley full irrigation (09GW).

‡ Additive effect: Positive values indicate an increasing effect of Platte alleles and negative values indicate an increasing effect of CO940610 alleles.

Table 2.9. Continued.

QTL	Environment†	Marker interval	Nearest marker	Peak position (cM)	LOD	a‡	R^2 (%)
Single kernel hardness							
QSha.cob-1D	08FW	*Glu-D3 - Xwmc336*	*Glu-D3*	0.0	2.70	1.26	5.2
QSha.cob-2B.1		*Xgwm429 - Xbarc55*	*Xgwm429*	95.0	4.27	-1.71	9.2
QSha.cob-6B.2		*wPt-7636 - wPt-0171*	*wPt-7636*	6.0	3.33	-1.79	10.0
Unlinked locus		Chromosome 5A	Xbarc319		0.0004	-1.17	6.8
Multiple-QTL model							31.6
QSha.cob-2B.1	09GW	*wPt-3561 - Xgwm429*	*wPt-3561*	81.2	6.43	-2.08	15.1
QSha.cob-6B.2		*wPt-7636 - wPt-0171*	*wPt-7636*	0.0	2.64	-1.34	5.9
QSha.cob-7A		*Xwmc83 - wPt-3393*	*Xwmc83*	31.1	3.95	1.57	8.5
QSha.cob-7D.2		*Xbarc126 - Vrn-D3*	*Vrn-D3*	35.4	5.29	1.69	9.7
Multiple-QTL model							35.5
QSha.cob-1D	08FD	*Glu-D3 - Xwmc336*	*Glu-D3*	0.0	2.64	1.05	4.9
QSha.cob-2B.1		*Xgwm374 - Xbarc349a*	*Xgwm374*	106.5	3.39	-1.21	6.3
QSha.cob-6B.2		*wPt-7636 - wPt-0171*	*wPt-7636*	0.0	2.91	-1.24	6.3
Unlinked locus		Chromosome 5A	Xbarc319		0.0005	-1.22	6.6
Multiple-QTL model							29.9
QSha.cob-2B.1	09GD	*Xgwm374 - Xbarc349a*	*Xgwm374*	106.5	3.33	-1.32	6.1
QSha.cob-6B.2		*wPt-7636 - wPt-0171*	*wPt-7636*	0.0	4.36	-1.68	9.5
QSha.cob-7D.2		*Xbarc126 - Vrn-D3*	*Vrn-D3*	33.4	3.31	1.37	6.5
Multiple-QTL model							23.2
Grain protein concentration							
QGpc.cob-1B.1	08FW	*wPt-0705 - wPt-9857*	*wPt-0705*	60.6	3.03	- 0.13	4.8
QGpc.cob-2D.1		*wPt-4413 - wPt-0638*	*wPt-4413*	56.5	3.31	-0.18	9.4
QGpc.cob-5B		*Xgwm540 - Xgwm499*	*Xgwm499*	67.2	4.53	0.17	8.0
QGpc.cob-6A		*Xwmc256 - wPt-3069*	*wPt-3069*	101.8	6.55	0.21	12.9
QGpc.cob-6B.1		*Xwmc397 - Xwmc182a*	*Xwmc397*	52.2	4.18	-0.16	7.0
QGpc.cob-7B		*wPt-7602 - Xwmc76*	*wPt-7602*	0.0	3.95	0.16	6.7
QGpc.cob-7D.2		*wPt-0789 - Xbarc126*	*wPt-0789*	18.0	3.48	-0.15	6.8
Unlinked locus		Chromosome 7B	wPt-8920		0.0004	0.17	7.6
Multiple-QTL model							54.9

† The four environments were different moisture levels during the two growing seasons: Fort Collins limited irrigation (08FD), Fort Collins full irrigation (08FW), Greeley limited irrigation (09GD), and Greeley full irrigation (09GW).

‡ Additive effect: Positive values indicate an increasing effect of Platte alleles and negative values indicate an increasing effect of CO940610 alleles.

For unlinked loci, presumed chromosome locations are provided, and in the LOD column *P*-values from SAS PROC GLM are listed.

Table 2.9. Continued.

QTL	Environment†	Marker interval	Nearest marker	Peak position (cM)	LOD	a‡	R^2 (%)
Grain protein concentration							
QGpc.cob-6A	09GW	*Xwmc256 - wPt-3069*	*wPt-3069*	95.8	2.65	0.16	5.6
QGpc.cob-7D.2		*wPt-0789 - Xbarc126*	*wPt-0789*	12.0	3.32	-1.86	7.9
Multiple-QTL model							11.3
QGpc.cob-6A	08FD	*Xwmc256 - wPt-3069*	*wPt-3069*	99.8	3.63	0.19	7.3
QGpc.cob-7B		*Xwmc76 - Xwmc182b*	*Xwmc182b*	6.6	4.75	0.22	9.2
QGpc.cob-7D.2		*wPt-4555 - wPt-0789*	*wPt-4555*	8.0	4.28	-0.23	9.5
Unlinked locus		Chromosome 7B	wPt-8920		0.0002	0.22	8.1
Multiple-QTL model							35.0
QGpc.cob-5B	09GD	*Xbarc4 - Xgwm540*	*Xgwm540*	56.5	7.77	0.25	13.6
QGpc.cob-6A		*Xwmc256 - wPt-3069*	*wPt-3069*	93.3	5.44	0.21	9.6
QGpc.cob-6B.1		*Xwmc397 - Xwmc182a*	*Xwmc397*	52.2	2.73	-0.14	4.5
QGpc.cob-7B		*wPt-7602 - Xwmc76*	*Xwmc76*	2.6	3.52	0.16	5.8
Multiple-QTL model							32.9
Grain ash							
QGac.cob-1A.1	08FW	*Xbarc148 - Xbarc83*	*Xbarc83*	81.3	4.58	0.02	9.2
QGac.cob-1B.1		*Sr24 - Glu-B3*	*Glu-B3*	3.3	6.18	-0.02	10.9
QGac.cob-4A.1		*Xgwm610 - Xwmc48*	*Xgwm610*	6.0	4.37	0.02	9.1
QGac.cob-5A		*Xwmc622 - Xcfd54a*	*Xwmc622*	0.0	3.50	0.02	6.4
QGac.cob-7B		*wPt-3873 - wPt-2994*	*wPt-3873*	27.3	2.84	0.02	5.6
Multiple-QTL model							40.6
QGac.cob-1B.1	09GW	*Sr24 - Glu-B3*	*Glu-B3*	3.3	7.04	-0.03	12.2
QGac.cob-3B.1		*Xgwm285 - wPt-9310*	*wPt-9310*	25.8	3.44	-0.02	5.4
QGac.cob-4A.1		*Xgwm610 - Xwmc48*	*Xwmc48*	8.2	3.29	0.02	5.4
QGac.cob-5A		*Xgwm443 - Xwmc713*	*Xwmc713*	5.4	2.86	0.02	4.8
QGac.cob-7B		*Xbarc278 - wPt-6498*	*Xbarc278*	21.2	2.60	0.02	4.1
Multiple-QTL model							31.9

† The four environments were different moisture levels during the two growing seasons: Fort Collins limited irrigation (08FD), Fort Collins full irrigation (08FW), Greeley limited irrigation (09GD), and Greeley full irrigation (09GW).

‡ Additive effect: Positive values indicate an increasing effect of Platte alleles and negative values indicate an increasing effect of CO940610 alleles. For unlinked loci, presumed chromosome locations are provided, and in the LOD column *P*-values from SAS PROC GLM are listed.

Table 2.9. Continued.

QTL	Environment†	Marker interval	Nearest marker	Peak position (cM)	LOD	a‡	R^2 (%)
Grain ash							
QGac.cob-1A.1	08FD	*Xwmc312 – Glu-A1*	*Glu-A1*	94.1	3.14	0.02	5.6
QGac.cob-1B.1		*Sr24 – Glu-B3*	*Glu-B3*	3.3	5.22	-0.02	9.2
QGac.cob-3D.1		*Xgwm314 – Xbarc125*	*Xgwm314*	2.0	2.62	-0.02	4.7
QGac.cob-4A.1		*Xwmc491 – Xgwm610*	*Xgwm610*	4.0	4.40	0.02	8.2
Multiple-QTL model							30.6
QGac.cob-1B.1	09GD	*wPt-1317 – wPt-3927*	*wPt-3927*	9.1	4.27	-0.02	7.3
QGac.cob-4A.1		*Xwmc48 – Xwmc420*	*Xwmc420*	9.4	3.22	0.02	5.3
QGac.cob-5A		*Xwmc622 – Xcfd54a*	*Xcfd54a*	4.0	2.60	0.02	4.2
QGac.cob-5B		*Xbarc4 – Xgwm540*	*Xgwm540*	56.5	3.44	0.02	5.7
QGac.cob-7B		*Xbarc278 – wPt-6498*	*Xbarc278*	19.2	5.97	0.03	10.9
Multiple-QTL model							29.2
Test weight							
QTwt.cob-7D.2	08FW	*Xbarc126 – Vrn-D3*	*Vrn-D3*	39.3	3.76	-0.37	8.3
Unlinked locus		Chromosome 7D	Xgwm428		0.0006	0.32	6.3
Multiple-QTL model							12.2
QTwt.cob-1B.1	09GW	*wPt-1317 – wPt-3927*	*wPt-3927*	9.1	3.07	0.32	5.9
QTwt.cob-7A		*wPt-3393 – wPt-4796*	*wPt-4796*	43.3	3.09	0.33	6.1
Multiple-QTL model							8.8
Polyphenol oxidase							
QPpo.cob-2A	08FW	*Xgwm312 – Ppo33*	*Ppo33*	133.5	51.80	-0.07	68.4
QPpo.cob-2A	09GW	*Xgwm312 – Ppo33*	*Ppo33*	133.5	35.67	-0.05	57.2
QPpo.cob-3B.1		*Xgwm285 – wPt-9310*	*Xgwm285*	10.3	3.06	0.01	3.2
Multiple-QTL model							54.9
QPpo.cob-2A	08FD	*Xgwm312 – Ppo33*	*Ppo33*	133.5	34.84	-0.06	51.9
QPpo.cob-1A.1	09GD	*wPt-2872 - wPt-6654*	*wPt-2872*	73.1	2.61	0.01	3.4
QPpo.cob-2A		*Xgwm312 - Ppo33*	*Ppo33*	133.5	28.61	-0.04	48.3
QPpo.cob-3D.1		*Xgwm314 - Xbarc125*	*Xgwm314*	10.0	6.35	0.02	8.3
QPpo.cob-5D		*Xbarc177 - wPt-0596*	*Xbarc177*	0.0	2.91	-0.01	3.5
Multiple-QTL model							55.2

† The four environments were different moisture levels during the two growing seasons: Fort Collins limited irrigation (08FD), Fort Collins full irrigation (08FW), Greeley limited irrigation (09GD), and Greeley full irrigation (09GW).

‡ Additive effect: Positive values indicate an increasing effect of Platte alleles and negative values indicate an increasing effect of CO940610 alleles. For unlinked loci, presumed chromosome locations are provided, and in the LOD column *P*-values from SAS PROC GLM are listed.

Table 2.9. Continued.

QTL	Environment†	Marker interval	Nearest marker	Peak position (cM)	LOD	a‡	R^2 (%)
Flour color L							
QFcl.cob-1D	08FW	*Xcfd48 - Glu-D1*	*Glu-D1*	103.4	2.99	0.09	5.2
QFcl.cob-2B.1		*Xgwm429 - Xbarc55*	*Xgwm429*	99.0	3.53	0.08	7.8
Multiple-QTL model							7.6
Unlinked locus	09GW	Chromosome 5A	Xbarc319		0.0001	0.07	7.8
Unlinked locus	09GD	Chromosome 5A	Xbarc319		0.0003	0.07	7.0
Flour color b							
QFcb.cob-1D	08FW	*Xgwm337 - Xbarc169*	*Xbarc169*	79.8	3.60	-0.18	5.9
QFcb.cob-3A		*Xwmc50 - Xgwm674*	*Xwmc50*	70.9	7.27	-0.29	15.7
QFcb.cob-7B		*Xwmc76 - Xwmc182b*	*Xwmc76*	6.6	3.94	-0.19	6.8
QFcb.cob-7D.2		*Xbarc126 - Vrn-D3*	*Vrn-D3*	35.4	3.07	0.17	5.2
Multiple-QTL model							26.6
QFcb.cob-1D	09GW	*Xgwm337 - Xbarc169*	*Xbarc169*	79.8	3.32	-0.15	5.2
QFcb.cob-3A		*Xwmc50 - Xgwm674*	*Xwmc50*	72.9	12.81	-0.33	24.3
QFcb.cob-7B		*Xwmc182b - Xgwm46*	*Xwmc182b*	8.5	5.70	-0.20	8.9
QFcb.cob-7D.2		*wPt-4555 - wPt-0789*	*wPt-4555*	8.0	3.72	0.19	8.3
Multiple-QTL model							45.2
QFcb.cob-1D	08FD	*Xgwm337 - Xbarc169*	*Xbarc169*	79.8	3.95	-0.17	6.2
QFcb.cob-3A		*Xwmc50 - Xgwm674*	*Xwmc50*	72.9	12.33	-0.33	23.7
QFcb.cob-7B		*Xwmc182b - Xgwm46*	*Xwmc182b*	8.5	5.23	-0.19	8.0
QFcb.cob-7D.2		*wPt-4555 - wPt-0789*	*wPt-0789*	14.0	2.87	0.16	5.5
Multiple-QTL model							36.5
QFcb.cob-1D	09GD	*Xgwm337 - Xbarc169*	*Xbarc169*	79.8	4.28	-0.16	8.1
QFcb.cob-3A		*Xwmc50 - Xgwm674*	*Xwmc50*	72.9	11.86	-0.26	21.5
QFcb.cob-7B		*Xwmc182b - Xgwm46*	*Xwmc182b*	8.5	5.65	-0.18	10.6
Multiple-QTL model							34.5

† The four environments were different moisture levels during the two growing seasons: Fort Collins limited irrigation (08FD), Fort Collins full irrigation (08FW), Greeley limited irrigation (09GD), and Greeley full irrigation (09GW).

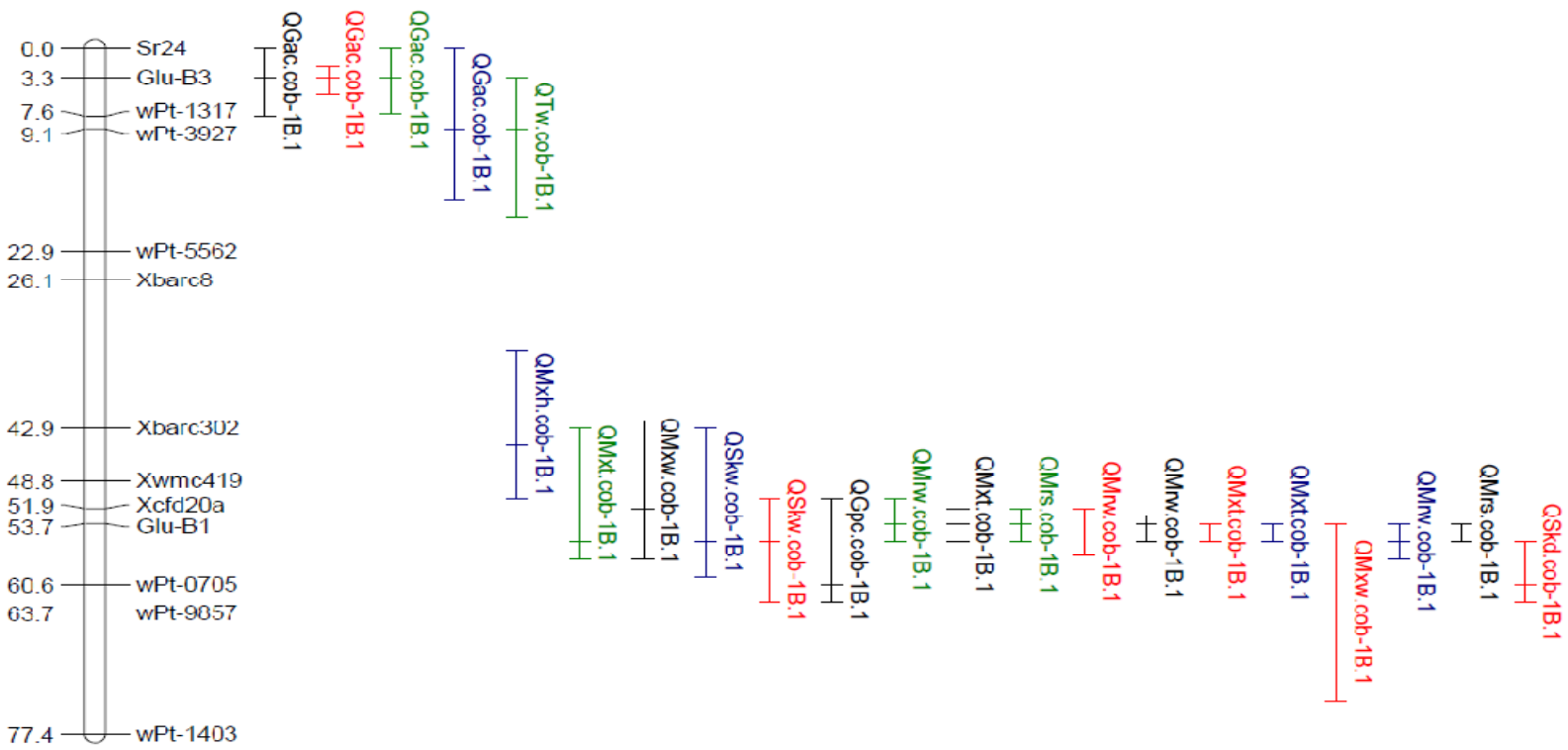
‡ Additive effect: Positive values indicate an increasing effect of Platte alleles and negative values indicate an increasing effect of CO940610 alleles. For unlinked loci, presumed chromosome locations are provided, and in the LOD column *P*-values from SAS PROC GLM are listed.

Fig. 2.3. Linkage maps showing QTL intervals associated with various quality traits in the CO940610/Platte population. Genetic distances (cM) are located to the left of the linkage group and locus names are listed to the right in different colors†. The 1-LOD support intervals for QTL locations were calculated by finding the points on either side of the estimated QTL position that corresponded to a decrease in LOD score of 1 unit.

Gac, grain ash content ; Gpc, grain protein concentration at 12% moisture content; Fcb, flour color value yellow; Fcl, flour color value whiteness; Mxt, Mixograph peak time; Mrs, Mixograph right slope; Mxh, Mixograph peak height; Mxw, Mixograph peak width; Mrw, Mixograph right width; Ppo, polyphenol oxidase activity; Skw, single kernel weight; Skw, single kernel diameter; Sha, single kernel hardness; Tw, test weight.

† Fort Collins full irrigation
Fort Collins limited irrigation
Greeley full irrigation
Greeley limited irrigation

Fig. 2.3. Continued. †



1B.1

Gac, grain ash content ; Gpc, grain protein concentration at 12% moisture content; Fcb, flour color value yellow; Fcl, flour color value whiteness; Mxt Mixograph peak time; Mrs, Mixograph right slope; Mxh, Mixograph peak height; Mxw, Mixograph peak width; Mrw, Mixograph right width Ppo, polyphenol oxidase activity; Skw, single kernel weight; Skw, single kernel diameter; Sha, single kernel hardness; Tw, test weight.

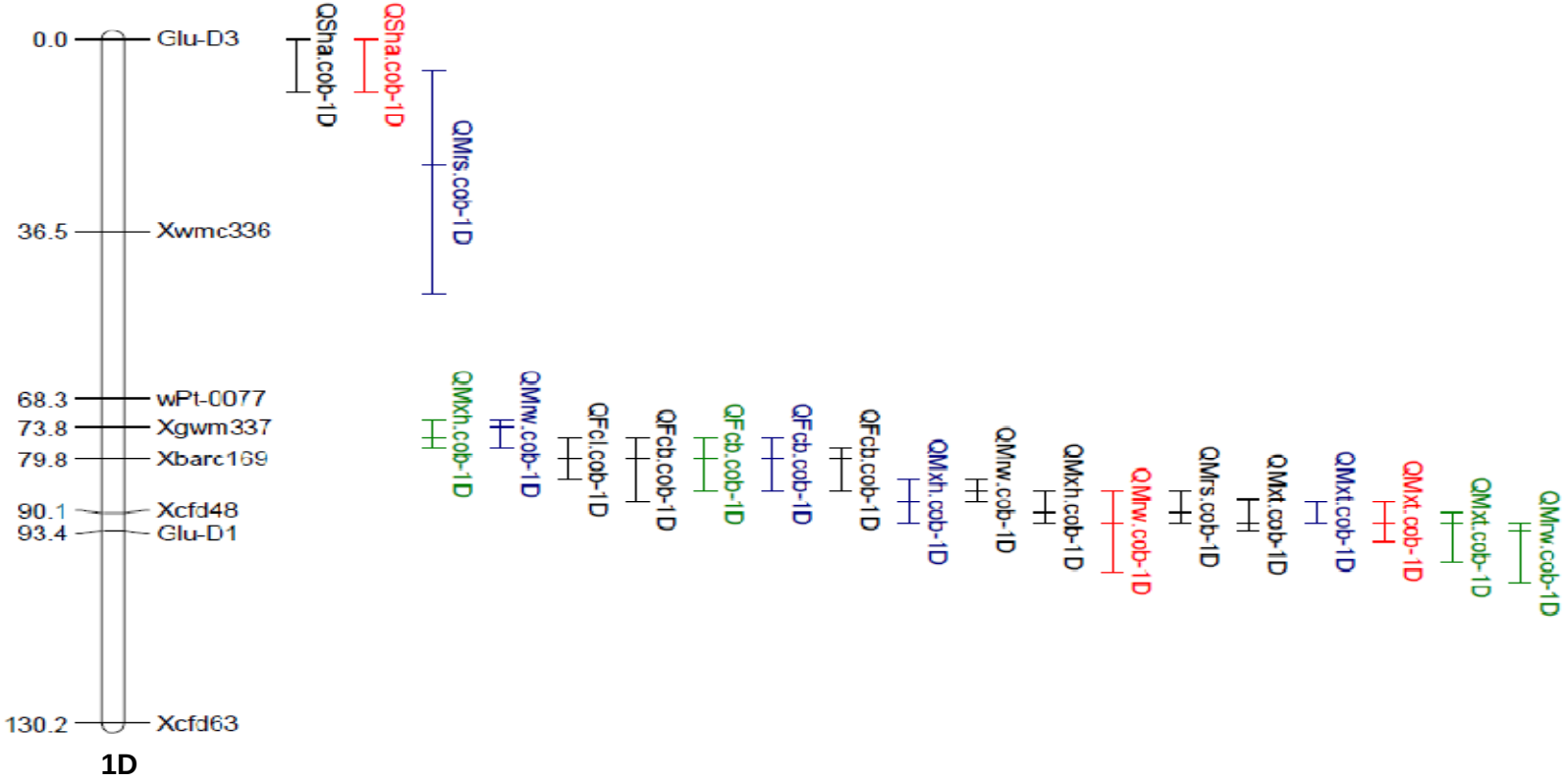
† Fort Collins full irrigation

Fort Collins limited irrigation

Greeley full irrigation

Greeley limited irrigation

Fig. 2.3. Continued. †



Gac, grain ash content ; Gpc, grain protein concentration at 12% moisture content; Fcb, flour color value yellow; Fcl, flour color value whiteness; Mxt Mixograph peak time; Mrs, Mixograph right slope; Mxh, Mixograph peak height; Mxw, Mixograph peak width; Mrw, Mixograph right width Ppo, polyphenol oxidase activity; Skw, single kernel weight; Skw, single kernel diameter; Sha, single kernel hardness; Tw, test weight.

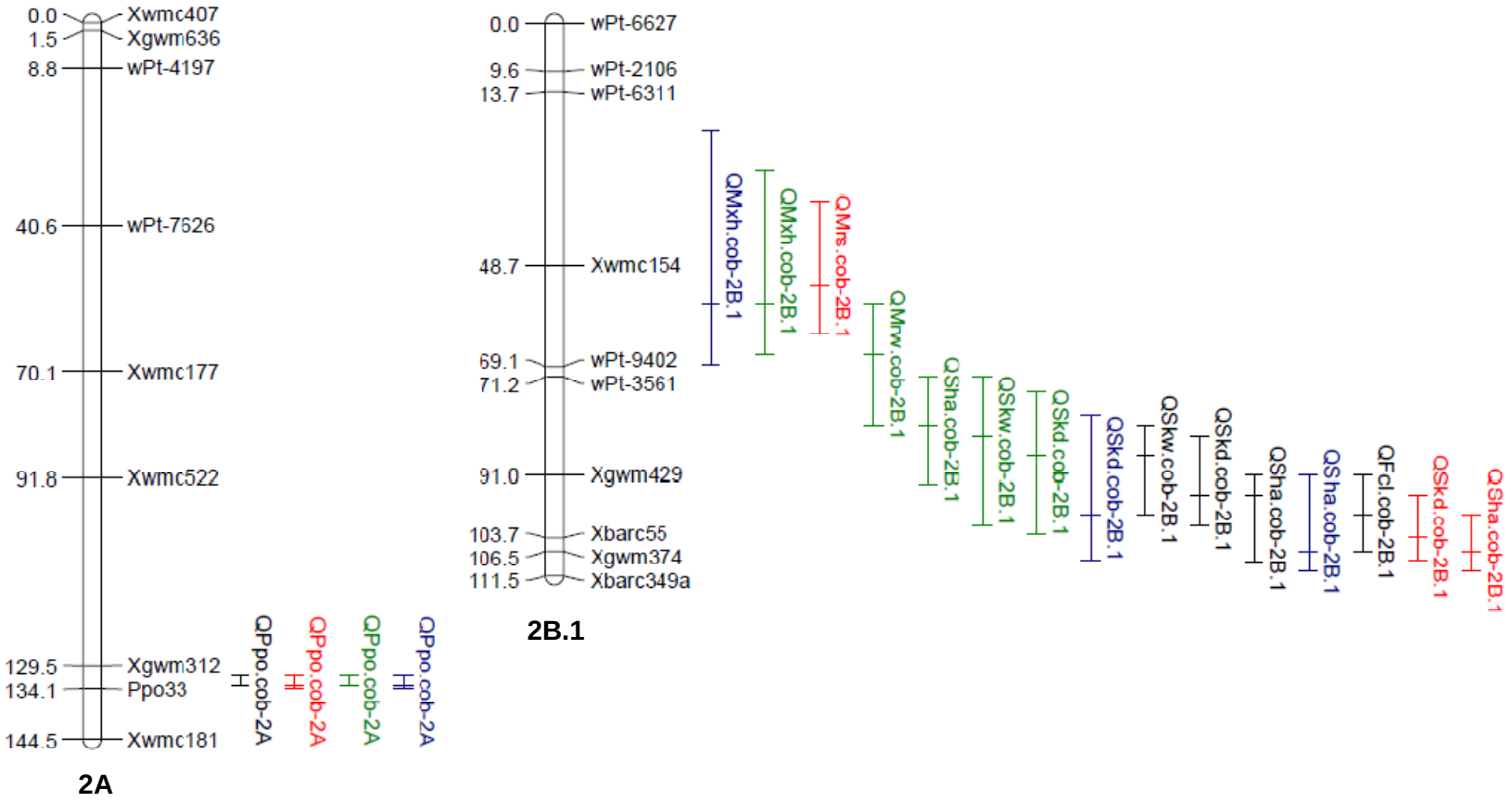
† Fort Collins full irrigation

Fort Collins limited irrigation

Greeley full irrigation

Greeley limited irrigation

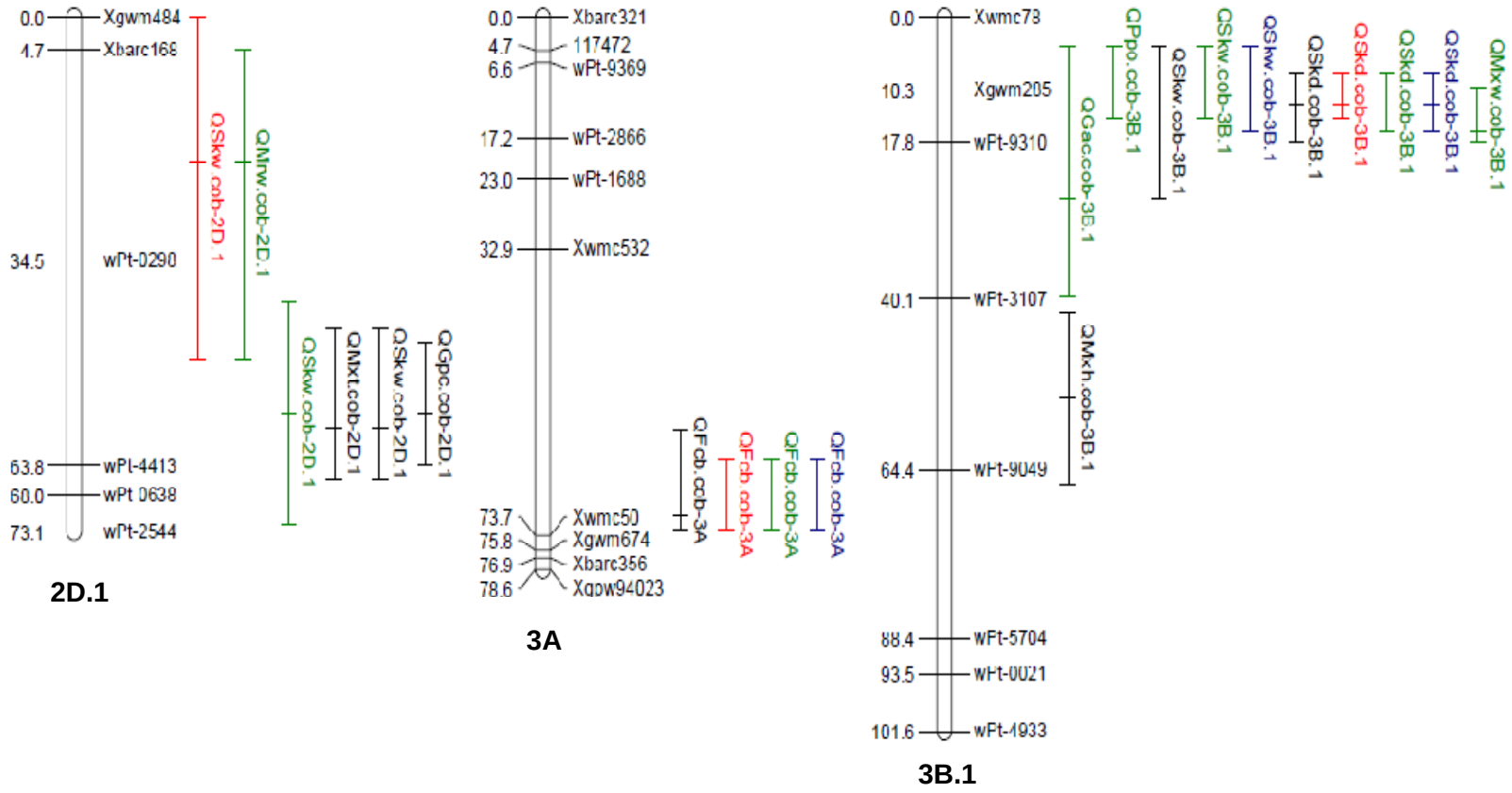
Fig. 2.3. Continued. †



Gac, grain ash content ; Gpc, grain protein concentration at 12% moisture content; Fcb, flour color value yellow; Fcl, flour color value whiteness; Mxt Mixograph peak time; Mrs, Mixograph right slope; Mxh, Mixograph peak height; Mxw, Mixograph peak width; Mrw, Mixograph right width Ppo, polyphenol oxidase activity; Skw, single kernel weight; Skw, single kernel diameter; Sha, single kernel hardness; Tw, test weight.

† Fort Collins full irrigation
Fort Collins limited irrigation
Greeley full irrigation
Greeley limited irrigation

Fig. 2.3. Continued. †



Gac, grain ash content ; Gpc, grain protein concentration at 12% moisture content; Fcb, flour color value yellow; Fcl, flour color value whiteness; Mxt Mixograph peak time; Mrs, Mixograph right slope; Mxh, Mixograph peak height; Mxw, Mixograph peak width; Mrw, Mixograph right width Ppo, polyphenol oxidase activity; Skw, single kernel weight; Skw, single kernel diameter; Sha, single kernel hardness; Tw, test weight.

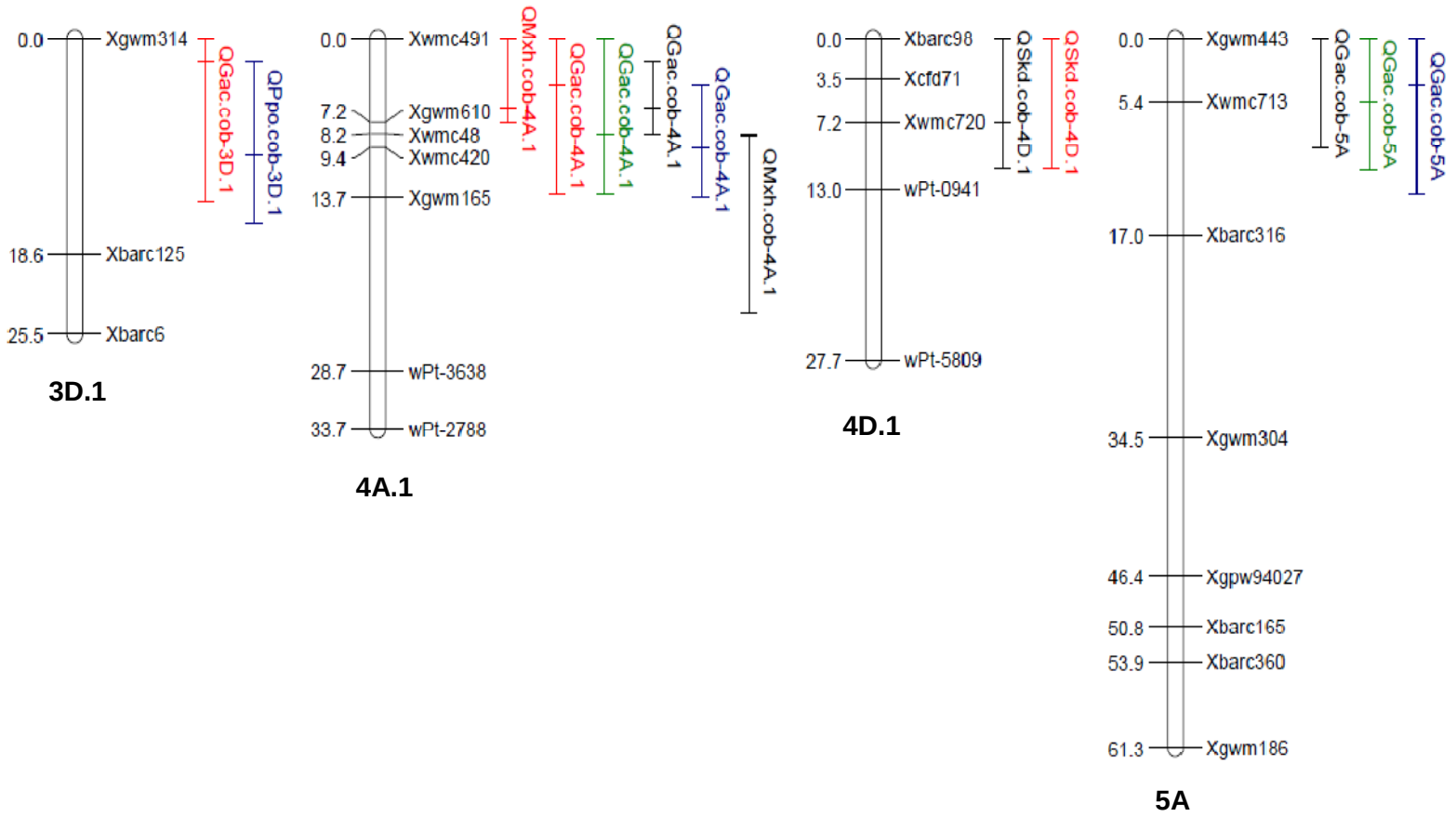
† Fort Collins full irrigation

Fort Collins limited irrigation

Greeley full irrigation

Greeley limited irrigation

Fig. 2.3. Continued. †



Gac, grain ash content ; Gpc, grain protein concentration at 12% moisture content; Fcb, flour color value yellow; Fcl, flour color value whiteness; Mxt Mixograph peak time; Mrs, Mixograph right slope; Mxh, Mixograph peak height; Mxw, Mixograph peak width; Mrw, Mixograph right width Ppo, polyphenol oxidase activity; Skw, single kernel weight; Skw, single kernel diameter; Sha, single kernel hardness; Tw, test weight.

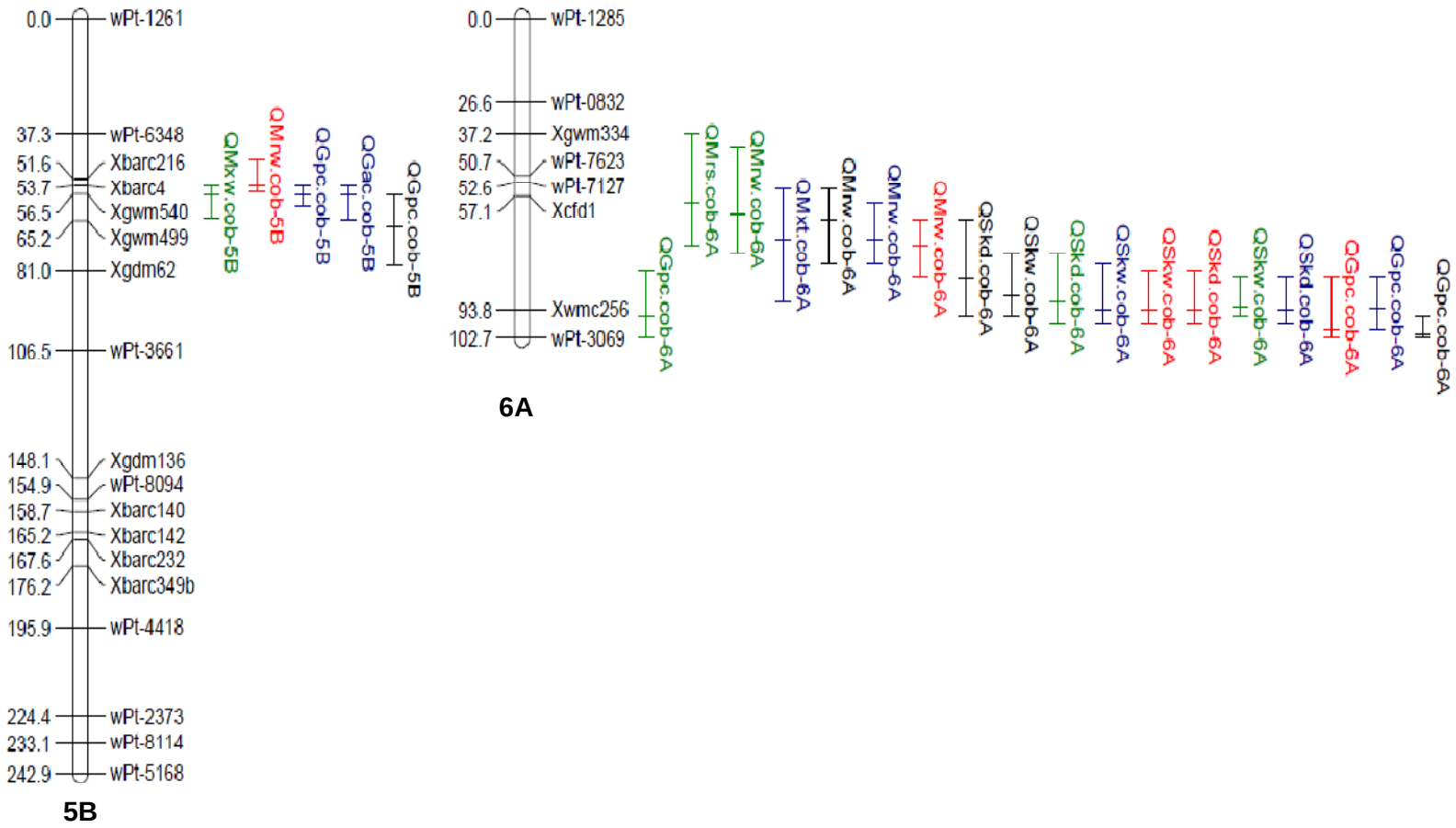
† Fort Collins full irrigation

Fort Collins limited irrigation

Greeley full irrigation

Greeley limited irrigation

Fig. 2.3. Continued. †



Gac, grain ash content ; Gpc, grain protein concentration at 12% moisture content; Fcb, flour color value yellow; Fcl, flour color value whiteness; Mxt Mixograph peak time; Mrs, Mixograph right slope; Mxh, Mixograph peak height; Mxw, Mixograph peak width; Mrw, Mixograph right width Ppo, polyphenol oxidase activity; Skw, single kernel weight; Skw, single kernel diameter; Sha, single kernel hardness; Tw, test weight.

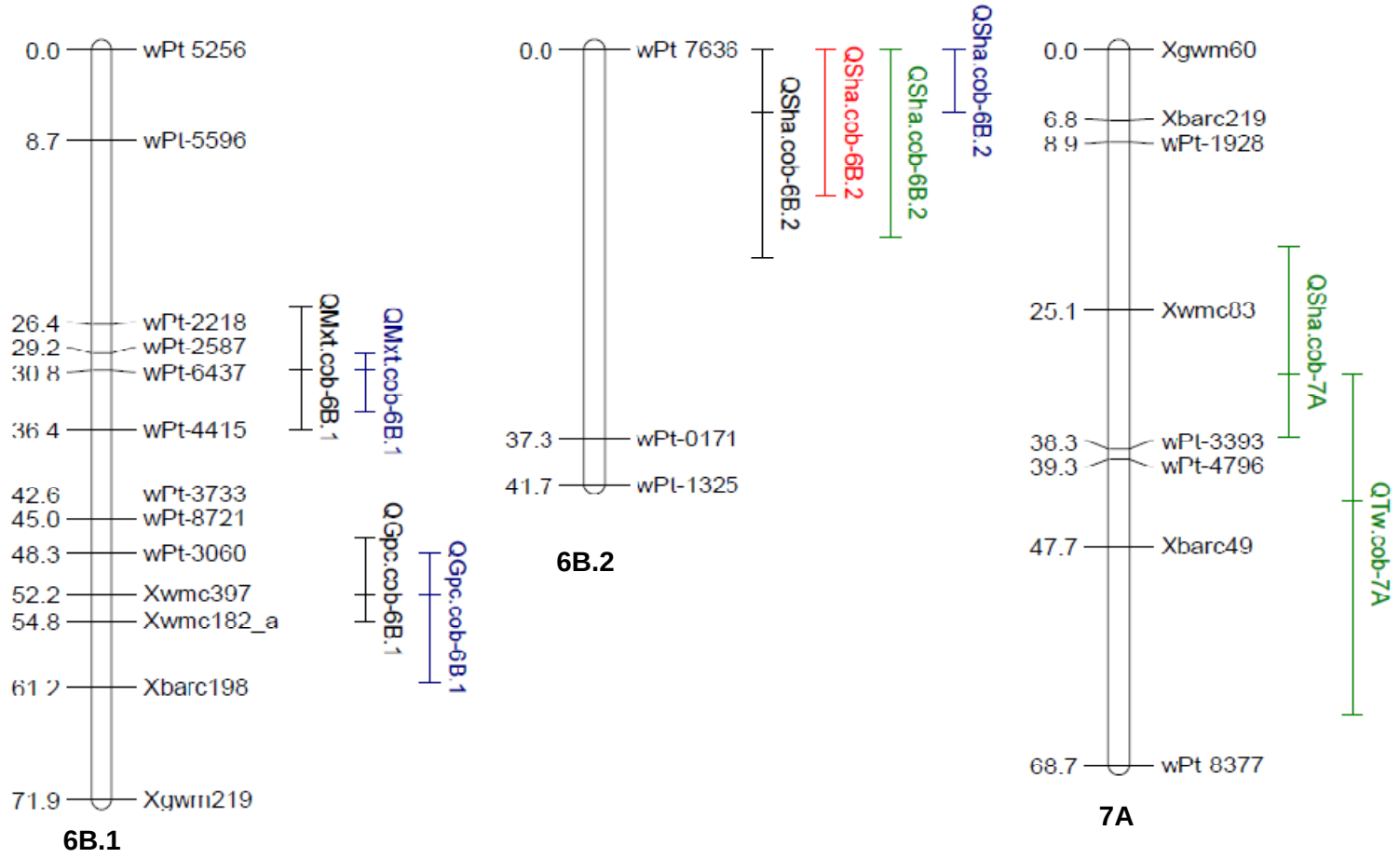
† Fort Collins full irrigation

Fort Collins limited irrigation

Greeley full irrigation

Greeley limited irrigation

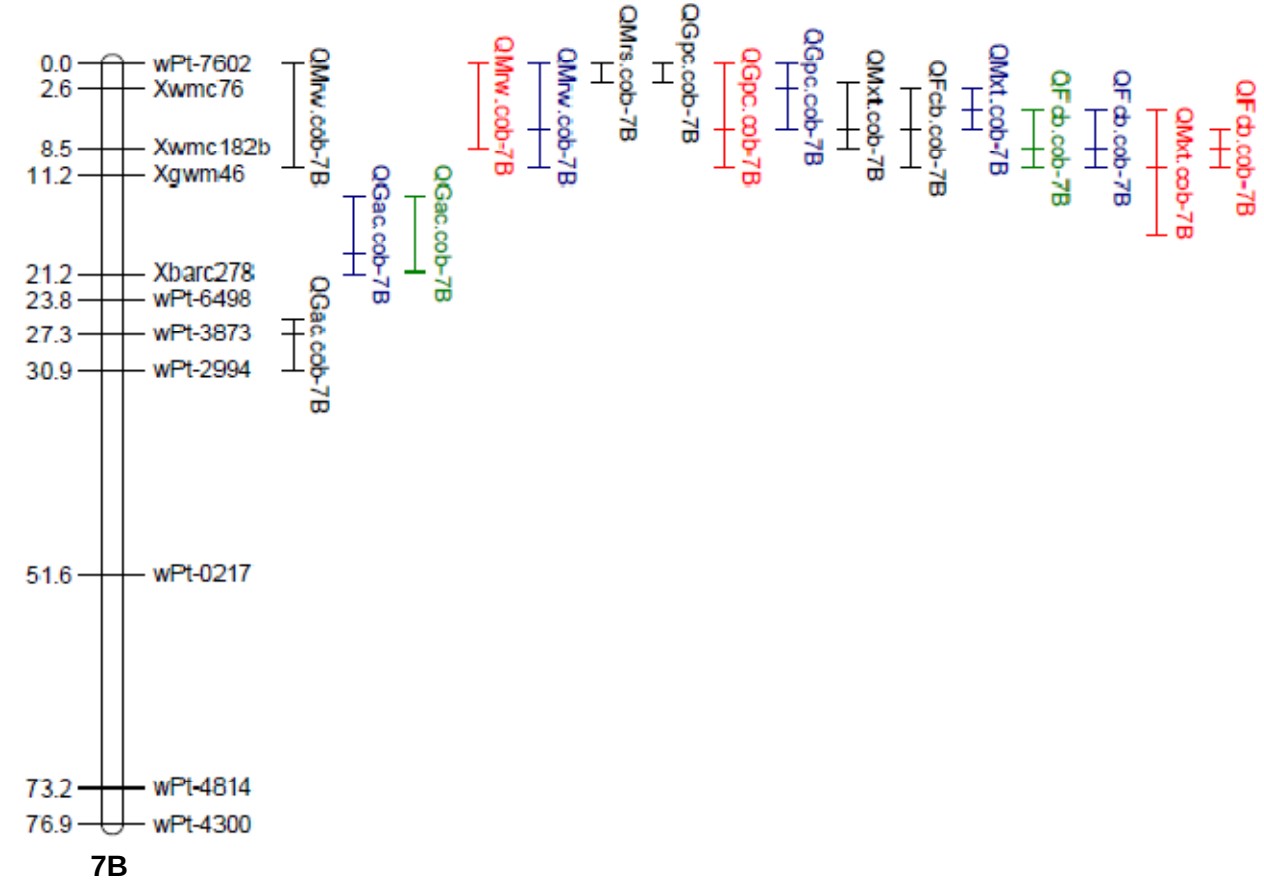
Fig. 2.3. Continued. †



Gac, grain ash content ; Gpc, grain protein concentration at 12% moisture content; Fcb, flour color value yellow; Fcl, flour color value whiteness; Mxt Mixograph peak time; Mrs, Mixograph right slope; Mxh, Mixograph peak height; Mxw, Mixograph peak width; Mrw, Mixograph right width Ppo, polyphenol oxidase activity; Skw, single kernel weight; Skw, single kernel diameter; Sha, single kernel hardness; Tw, test weight.

† Fort Collins full irrigation
Fort Collins limited irrigation
Greeley full irrigation
Greeley limited irrigation

Fig. 2.3. Continued. †



Gac, grain ash content ; Gpc, grain protein concentration at 12% moisture content; Fcb, flour color value yellow; Fcl, flour color value whiteness; Mxt Mixograph peak time; Mrs, Mixograph right slope; Mxh, Mixograph peak height; Mxw, Mixograph peak width; Mrw, Mixograph right width Ppo, polyphenol oxidase activity; Skw, single kernel weight; Skw, single kernel diameter; Sha, single kernel hardness; Tw, test weight.

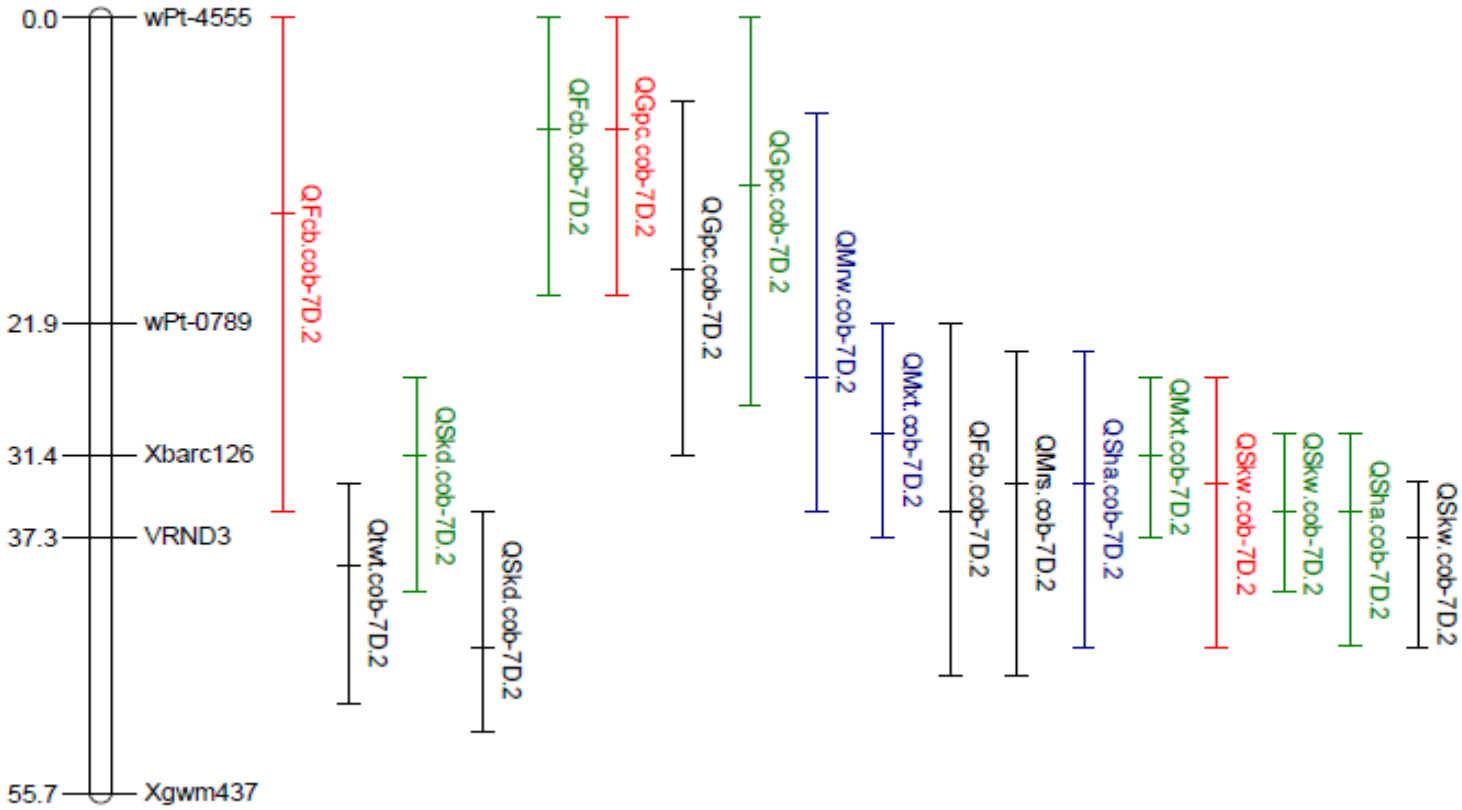
† Fort Collins full irrigation

Fort Collins limited irrigation

Greeley full irrigation

Greeley limited irrigation

Fig. 2.3. Continued. †



7D.2

Gac, grain ash content ; Gpc, grain protein concentration at 12% moisture content; Fcb, flour color value yellow; Fcl, flour color value whiteness; Mxt Mixograph peak time; Mrs, Mixograph right slope; Mxh, Mixograph peak height; Mxw, Mixograph peak width; Mrw, Mixograph right width Ppo, polyphenol oxidase activity; Skw, single kernel weight; Skw, single kernel diameter; Sha, single kernel hardness; Tw, test weight.

†
Fort Collins full irrigation
Fort Collins limited irrigation
Greeley full irrigation
Greeley limited irrigation

When the markers nearest those QTL were analyzed in multiple-locus models, most markers remained significant at *P*<0.05 and the models explained 7.6 to 73.8% of the phenotypic variation. Eight unlinked markers were significant by *P*<0.001 associated with at least one trait in a single marker analysis and retained significance in the multiple-locus models (Table 2.9).

2.2.6.1. Mixograph parameters

For the five mixograph parameters measured in this population, 48 QTL were detected with both major and minor effects (Table 2.9, Fig. 2.3). Marker intervals *Xwmc312-GLU-A1* (1A.1), *Xcfd20a-Glu-B1* (1B.1), *Glu-D3-Xwmc336* (1D), *Xcfd48 - Glu-D1* (1D), and *wPt-0789 - Xbarc126* (7D.2) were significantly associated with several mixograph traits (Figs. 2.4). All the QTL for mixograph parameters on chromosomes 1A.1, 1D, and 7D.2 were detected with a positive additive effect, indicating the association of the Platte allele with increasing trait values. This is consistent with Platts overall superior values for mixograph parameters compared to CO940610 (Fig. 2.5). However, all QTL for mixograph parameters on chromosome 1B.1 were detected with negative additive effects, indicating the association of the CO940610 allele with increasing trait values at those QTL.

2.2.6.1.1. Mixograph peak time (Mxt)

Mxt gave the highest number of significant QTL (14) among mixograph parameters (Table 2.9 and Fig. 2.3). Marker interval *Xcfd20a-Glu-B1* on chromosome 1B.1, designated *QMxt.cob-1B.1,* was significantly associated with Mxt in all environments. The percent phenotypic variation explained by this QTL ranged from 22.1 to 26.3%, with LOD scores ranging from 12.8 to 25.4. Another prominent marker interval, *GLU-D1-Xcfd48* on chromosome 1D, was designated *QMxt.cob-1D* and was significantly associated with Mxt in all environments. The percent phenotypic variation ranged from 25.8 to 29.3% and the LOD score ranged from 21.1 to 26.3. Less

consistent or environment-specific chromosome regions associated with Mxt were identified on linkage groups 2D.1, 6A, 6B.1, 7B, and 7D.2.

2.2.6.1.2. Mixograph peak height (Mxh)

Eleven QTL for Mxh were detected, individually explaining 4.7 to 21.3% of the phenotypic variation. The most significant of the 11 QTL, designated *QMxh.cob-1A.1,* was identified on chromosome 1A.1, and was consistent over all environments. Platte contributed the allele at that QTL that had a positive effect on *Mxh* in all environments. The amount of phenotypic variation explained by that QTL was 6.6 to 21.3%. Another QTL, designated *QMxh.cob-1D*, was identified in three environments (08FW, 09GW, and 08GD), but its position and effect were inconsistent (Table 2.9 and Fig. 2.3). Platte contributed the allele for increased Mxh at the QTL on chromosomes 1A.1, 1D, 2B.1, 3B.1, and 4A.1, while CO940610 contributed the allele for increased Mxh at the QTL on chromosomes 1B.1, 1B.2, and 1D in all environments.

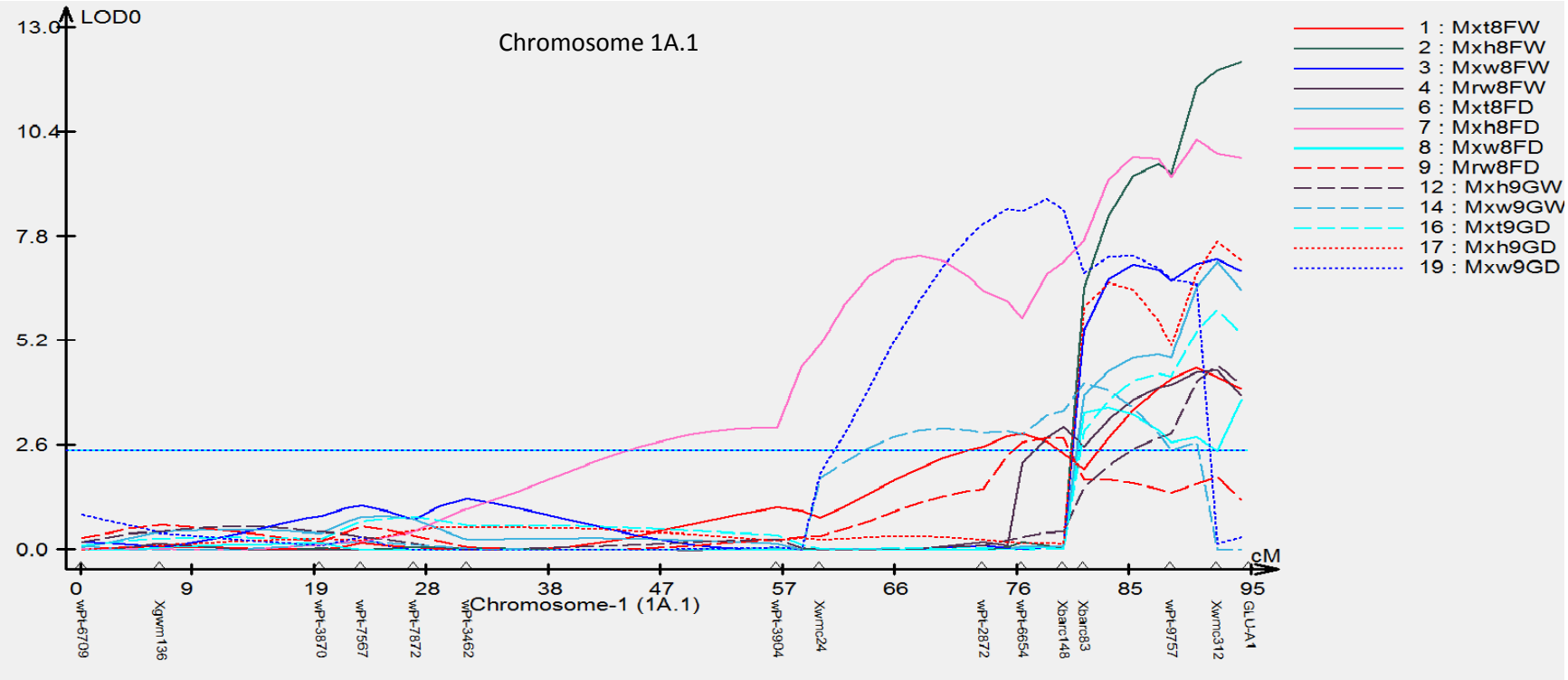
2.2.6.1.3. Mixograph peak width (Mxw)

Five QTL for Mxw explained 5.7 to 18.2% of the phenotypic variation. A significant QTL, designated *QMxw.cob-1A.1,* was detected on chromosome 1A.1 in all environments (Table 2.9, Fig. 2.3). In 09GW and 08FD, the marker interval was *Xbarc148-Xbarc83*, in 08FW it was flanked by *Xwmc312 -GLU-A1*, while in 09GD it was flanked by *wPt-6654-Xbarc148* (Table 2.9, Fig. 2.3). *QMxw.cob-1A.1* explained 7.9 to 14.3% of the phenotypic variation, and Platte contributed the favorable allele. Less consistent or environment-specific chromosomes regions associated with Mxw were identified on linkage groups 1B.1, 3B.1, and 5B.

2.2.6.1.4. Mixograph right width (Mrw)

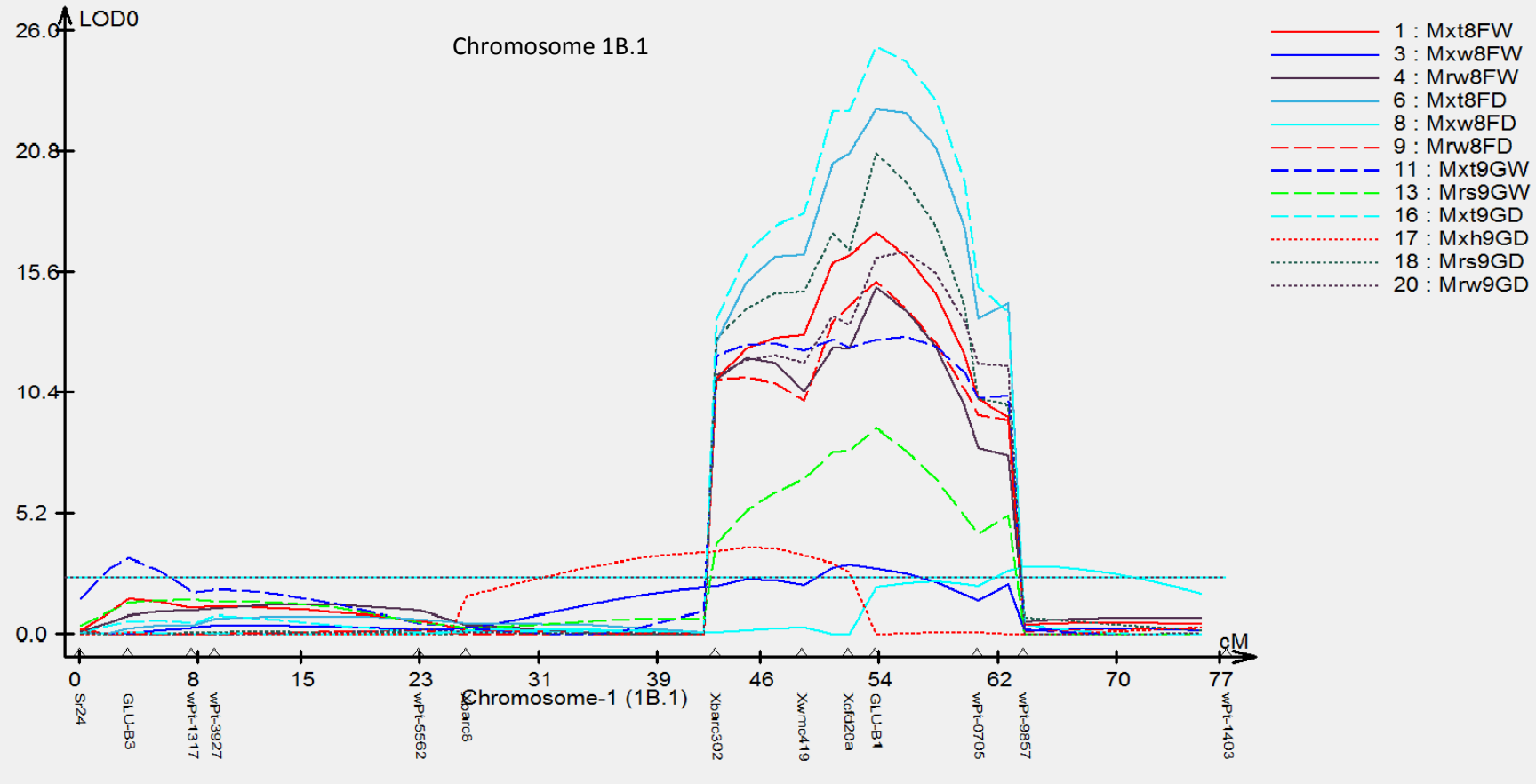
Thirteen QTL were detected under different moisture levels and explained 3.4 to 26.6% of the phenotypic variation (Table 2.9, Fig. 2.3). A major QTL, designated *QMrw.cob-1B.1,* was detected on chromosome 1B.1 in all environments.

Fig. 2.4. QTL Cartographer output for mixograph traits of the CO940610/Platte population under two irrigation levels in the 2007-08 and 2008-09 growing seasons.†



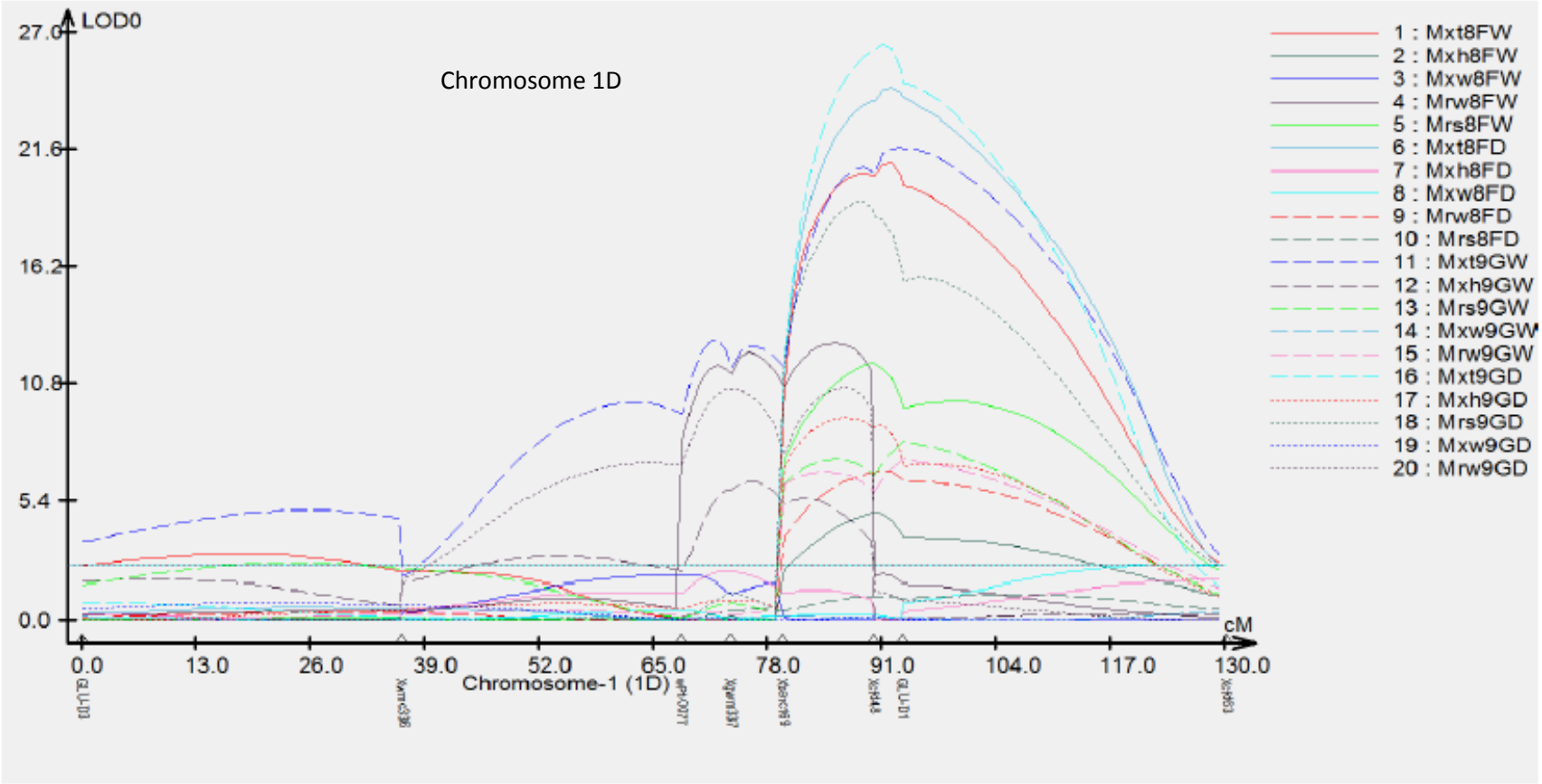
† The first three letters of each LOD curve label indicate trait name: Mxt, mixograph peak time; Mxh, mixograph peak height; Mxw, mixograph peak width; Mrw, mixograph right width; Mrs, mixograph right slope. The last portion of the label indicates environment: 8FD, Fort Collins Dry, 2008; 8FW, Fort Collins Wet, 2008; 9GD, Greleey Dry, 2009; 9GW, Greleey Wet 2009.

Fig. 2.4. Continued. †



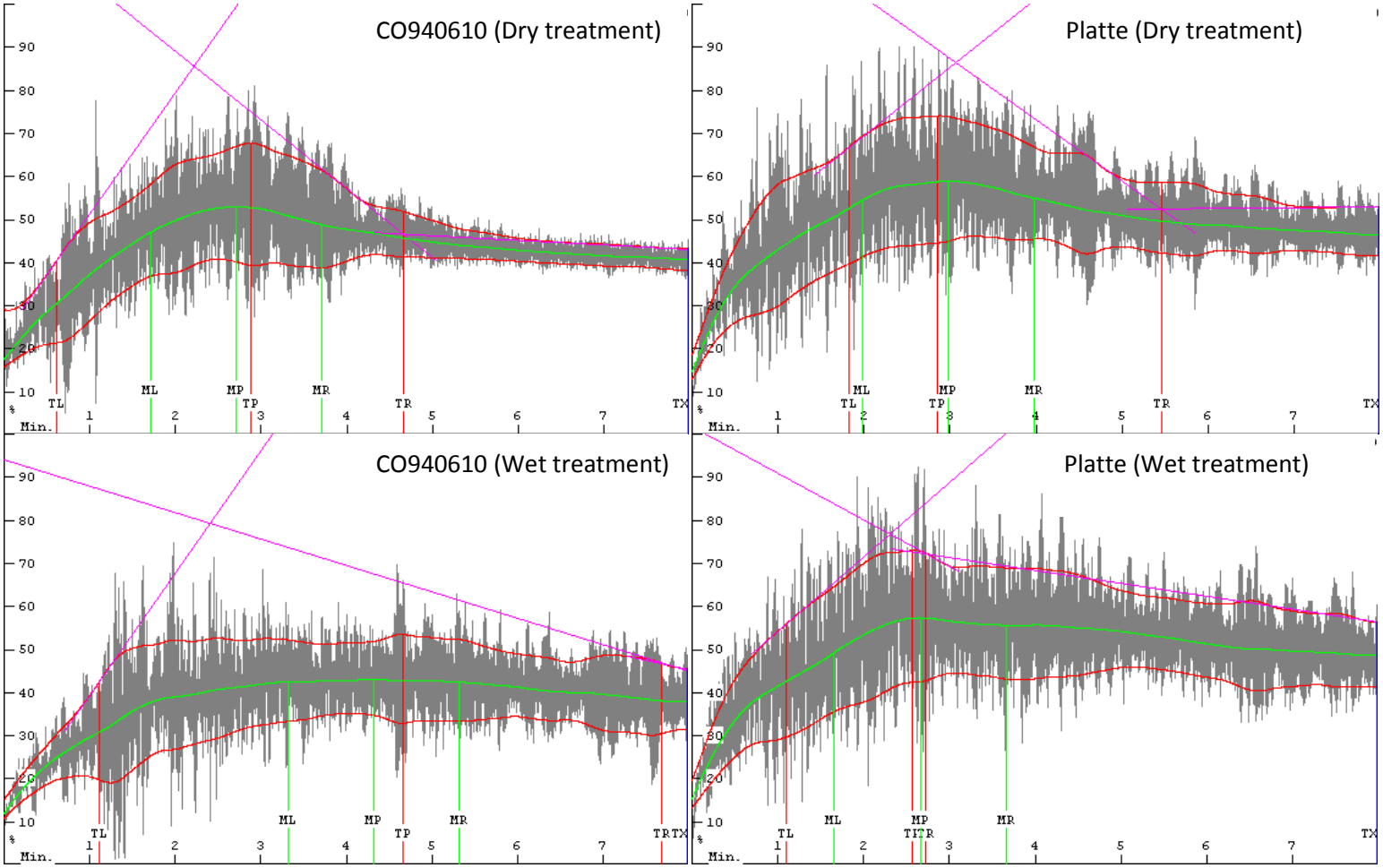
† The first three letters of each LOD curve label indicate trait name: Mxt, mixograph peak time; Mxh, mixograph peak height; Mxw, mixograph peak width; Mrw, mixograph right width; Mrs, mixograph right slope. The last portion of the label indicates environment: 8FD, Fort Collins Dry, 2008; 8FW, Fort Collins Wet, 2008; 9GD, Greleey Dry, 2009; 9GW, Greleey Wet 2009.

Fig. 2.4. Continued. †



† The first three letters of each LOD curve label indicate trait name: Mxt, mixograph peak time; Mxh, mixograph peak height; Mxw, mixograph peak width; Mrw, mixograph right width; Mrs, mixograph right slope. The last portion of the label indicates environment: 8FD, Fort Collins Dry, 2008; 8FW, Fort Collins Wet, 2008; 9GD, Greleey Dry, 2009; 9GW, Greleey Wet 2009.

Fig 2.5. Sample mixograms of CO940610 and Platte under two moisture treatments at Greeley in the 2008-09 growing season



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This QTL was located within the interval flanked by the markers *Xcfd20a and Glu-B1* and accounted for 10.1 to 26.6% of the phenotypic variation. CO94610 contributed the allele at *QMrw.cob-1B.1* with a positive effect on Mrw. Another prominent QTL, *QMrw.cob-6A,* was consistent for the same trait over all environments. It was located within the interval flanked by the markers *Xcfd1* and *Xwmc256* and accounted for 10.1 to 26.6% of the phenotypic variation. Platte contributed the allele at *QMrw.cob-6A that* had a positive effect on Mrw*.* Less consistent or environment-specific chromosomes regions associated with Mrw were identified on linkage groups 1B.1, 1D, 2B.1, 2D.1, 5B, 7B, and 7D.2.

2.2.6.1.5. Mixograph right slope (Mrs)

Composite interval mapping revealed five QTL influencing Mrs, but only in the full irrigation treatments (08FW and 09GW). A consistent Mrs QTL was identified on chromosome 1B.1 and designated *QMrs.cob-1B.1* (Table 2.9 and Fig. 2.3). The percent phenotypic variation explained by this QTL was 26.5% in 08FW and 14.7% in 09GW. A QTL designated *QMrs.cob-1D* in 08FW and 09GW explained 2.6 to 11.8% of the phenotypic variation.

2.2.6.2. Single kernel characteristics

Three single kernel characteristics were measured in this population: single kernel weight (Skw), single kernel diameter (Skd), and single kernel hardness (Sha). Thirty-three QTL were detected for single kernel characteristics with major and minor effects in the four environments (Table 2.9, Fig. 2.3). Clusters of single kernel characteristics were found on linkage groups 1A.1, 1B.1, 2B.1, 6A, and 7D.2*.* Marker interval *Xbarc126-Vrn-D3* on chromosome *7D.2* was significantly associated with all kernel characteristics under the two moisture levels. Another cluster of significant QTL was identified on chromosome 3B.1 within the interval flanked by the markers *Xgwm285-wPt-9310*, and influenced all kernel parameters but was inconsistent among

environments. Most had moderate effects, with LOD values ranging from 2.9 to 10.9 (Table 2.9).

2.2.6.2.1. Single kernel weight (Skw)

Skw had the highest number of significant QTL among single kernel characteristics. Fifteen QTL were detected with minor to moderate effects under different moisture levels and explained 4.2 to 17.8% of the phenotypic variation (Table 2.9, Fig. 2.3). A prominent QTL, designated *QSkw.cob-6A,* was detected on chromosome 6A in all environments. This QTL was located within the interval flanked by the markers *Xwmc256* and *wPt-3069* and accounted for 8.9 to 12.1% of the phenotypic variation. CO94610 contributed the allele at *QSkw.cob-6A* that had the positive effect on Skw. Another QTL was detected on chromosome 7D.2 within the interval flanked by *Xbarc126-Vrn-D3*; individually it explained 4.8 to 8.1% of the phenotypic variation, but was only detected in three environments (08FW, 08FD, and 09GW). CO94610 contributed the allele that had the positive effect at Skw on that QTL. Other QTL were detected on other linkage groups but were inconsistent among environments with LOD scores ranging from 2.6 to 9.2.

2.2.6.2.2. Single kernel diameter (Skd)

Eleven QTL with minor to intermediate effects were detected under different moisture levels and explained 3.5 to 17.6% of the phenotypic variation (Table 2.9, Fig. 2.3). Two significant QTL, designated *QSkd.cob-3B.1* and *QSkd.cob-6A,* were identified on chromosomes 2B.1 and 6A and were consistent over all environments. Platte contributed the alleles that had the positive effect on Skd at the 3B.1 QTL, while CO940610 contributed the alleles that had the positive effect at the 6A QTL. Another moderate QTL effect on chromosome 2B.1 was detected in all environments but with different flanking markers. The percent phenotypic variation explained by this QTL ranged from 15.6 to 12.2%. Other QTL were detected on other linkage groups (1A.1,

4D.1, and 7D.2), but were inconsistent among environments with LOD values ranging from 2.7 to 5.8.

2.2.6.2.3. Single kernel hardness (Sha)

Seven QTL were detected with minor to intermediate effects under different moisture levels and explained 4.9 to 15.1% of the phenotypic variation (Table 2.9, Fig. 2.3). Only one QTL was detected over the four environments; it was designated *QSha.cob-2B.1* on chromosome 2B.1 and explained 6.1 to 15.1% of the phenotypic variation. The other QTL where distributed on various linkage groups with minor to intermediate effects (R^2 values of 4.9 to 10.0%).

2.2.6.3. Grain protein concentration (Gpc)

Thirteen QTL were detected with minor to intermediate effects under different moisture levels (Table 2.9, Fig. 2.3). Marker interval *Xwmc256-wPt-3069* on chromosome 6A, designated *QGpc.cob-6A,* was significantly associated with Gpc in all environments. The percent of phenotypic variation explained by this QTL ranged from 5.6 to 13.6%. Another marker interval *wPt-0789-Xbarc126* on chromosome 7D.2, designated *QGpc.cob-7D.2,* was significantly associated with Gpc in two environments (08FW and 09GW), explaining 6.8 to 7.9% of the phenotypic variation, respectively. Less consistent or environment-specific chromosomes regions associated with Gpc were identified on linkage groups 1B.1, 2D.1, 5B, 6B.1, and 7B.

2.2.6.4. Grain ash concentration (Gac)

Thirteen QTL were detected under different moisture levels in various chromosomal positions and explained 4.1 to 12.2% of the phenotypic variation (Table 2.9, Fig. 2.3). Two significant QTL, designated *QGac.cob-1B.1* and *QGac.cob-4A.1,* were identified on chromosomes 1B.1 and 4A.1 and were consistent over all environments. CO940610 contributed the favorable allele at *QGac.cob-1B.1,* while Platte contributed the favorable allele at *QGac.cob-4A.1.* Another significant QTL effect on

chromosome 7B was detected in 08FW, 09GW, and 09GD environments, but with different flanking markers. The percent phenotypic variation explained by this QTL ranged from 4.1 to 10.9%, with LOD scores ranging from 2.5 to 5.9. Other QTL were detected on other linkage groups (1A.1, 3B.1, 3D.1, and 5A), but were inconsistent among environments with LOD values ranging from 2.5 to 4.4.

2.2.6.5. Test weight (Tw)

Three minor QTL, designated *QTw.cob-1B.1*, *QTw.cob-7A,* and *QTw.cob-7D.2,* were detected on chromosomes 1B.1, 7A, and 7D.2, respectively, and were only detected in the full irrigation treatment (Table 2.9, Fig. 2.3). These QTL explained from 5.9 to 8.3% of the phenotypic variation.

2.2.6.6. Polyphenol oxidase activity (Ppo)

Five QTL were detected under different moisture levels in various chromosomal positions and explained 3.2 to 68.4% of the phenotypic variation (Table 2.9, Fig. 2.3). A major QTL, designated *QPpo.cob-2A,* was detected in all environments on chromosome 2A. This QTL was located within the interval flanking Xgwm312 and Ppo33 and accounted for 48.7 to 68.4% of the phenotypic variation. CO940610 contributed the favorable allele for Ppo at 2A. In addition, four significant QTL were detected on chromosomes 1A.1, 3B.1, 3D.1, and 5D in different environments.

2.2.6.7. Flour color

2.2.6.7.1. Flour color L (Fcl)

Only two minor QTL were detected in 08FW, designated *QFcl.cob-1D* and *QFcl.cob-2B.1.* Platte contributed the favorable allele for *Fcl* at both QTL.

2.2.6.7.2. Flour color b (Fcb)

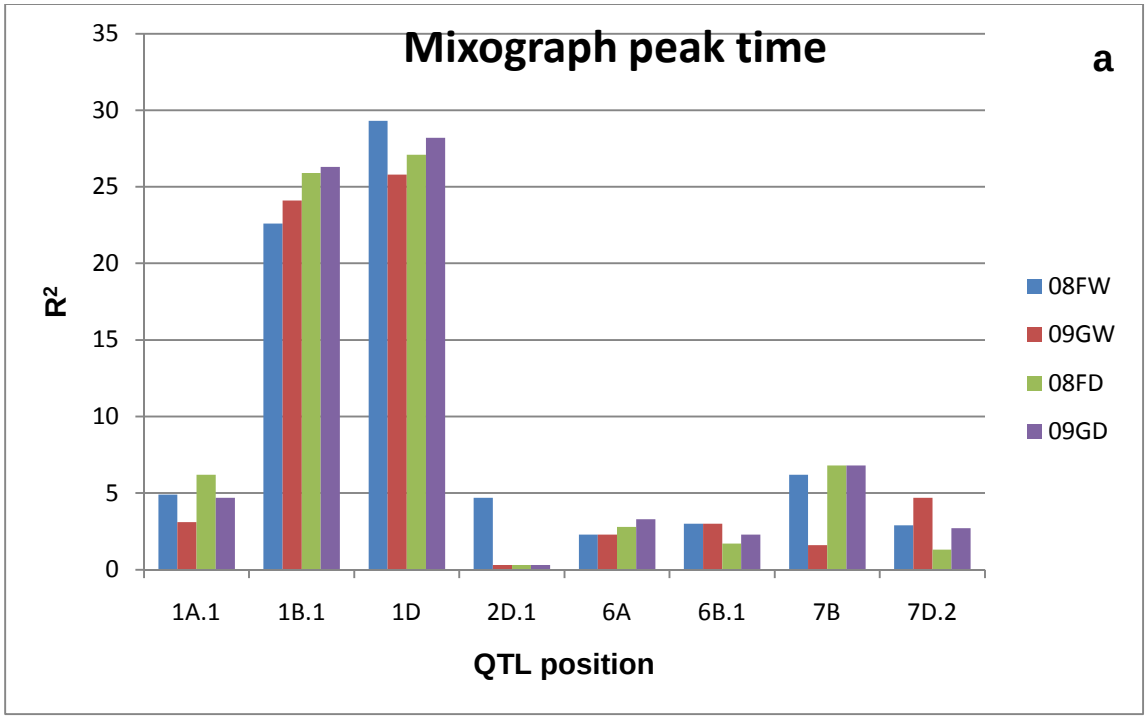
Unlike flour color L, six QTL were detected with intermediate to major effects, explaining 5.5 to 23.7% of the phenotypic variation. A major QTL, designated *QFcb.cob-3A,* was detected on chromosome 3A in all environments (Table 2.9, Fig. 2.3). This QTL

was located within the interval flanked by the markers *Xwmc50* and *Xgwm674* and accounted for 15.7 to 24.3% of the phenotypic variation. CO940610 contributed the favorable allele at *QFcb.cob-3A*. In addition, three significant QTL, designated QFcb.cob-*1D*, *QFcb.cob-7B*, and *QFcb.cob-7D.2* were consistent in all environments.

2.2.7. Stability of QTL across environments

In general, most of the intermediate and major QTL were consistent across environments and with approximately the same magnitude, with some exceptions. We selected five quality traits as examples for a graphical comparison of the presence and size of QTL across environments (Fig. 2.6). Two major QTL for Mxt designated *QMxt.cob-1B.1* and *QMxt.cob-1D* were consistent in all environments (Fig. 2.6a). Two QTL designated *QMxt.cob-1A.1* and *QMxt.cob-7B* were consistent in 08FW, 08FD, and 09GD. Only one QTL was consistently detected in all environments for Mxh (*QMxh.cob-1A.1*). Other QTL designated *QMxh.cob-2B.1* and *QMxh.cob-4A.1* were identified in both treatments in Greeley and Fort Collins, respectively (Fig. 2.6b). Three consistent QTL for single kernel diameter designated *QSkd.cob-2B.1, QSkd.cob-3B.1,* and *QSkd.cob-6A.1* were detected in all environments (Fig.2.6c). For grain protein concentration only one consistent QTL (*QGpc.cob-6A*) was detected across environments, but with different magnitude (Fig. 2.6d). The QTL on chromosome 7B was detected in three environments, except 09GW. Three consistent QTL were detected for flour color b designated *QFcb.cob-1D, QFcb.cob-3A,* and *QFcb.cob-7B* (Fig. 2.6e). The size of the QTL were about the same in each environment.

Fig 2.6. Comparison of presence and size of QTL for four quality traits across environments



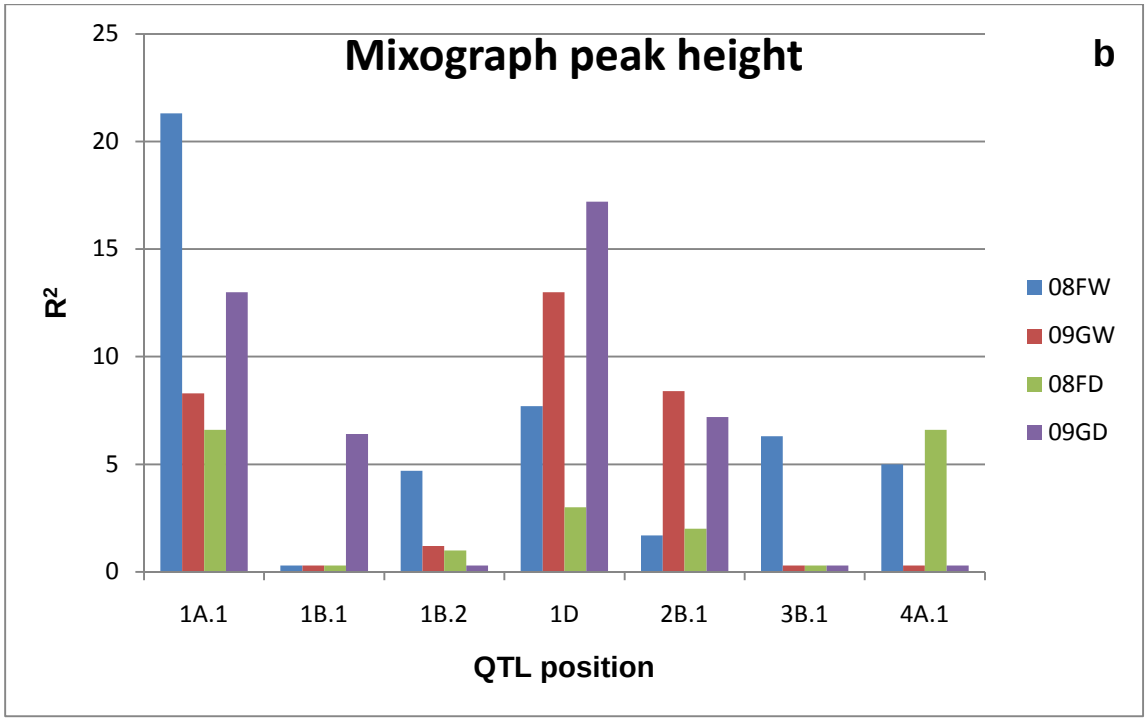
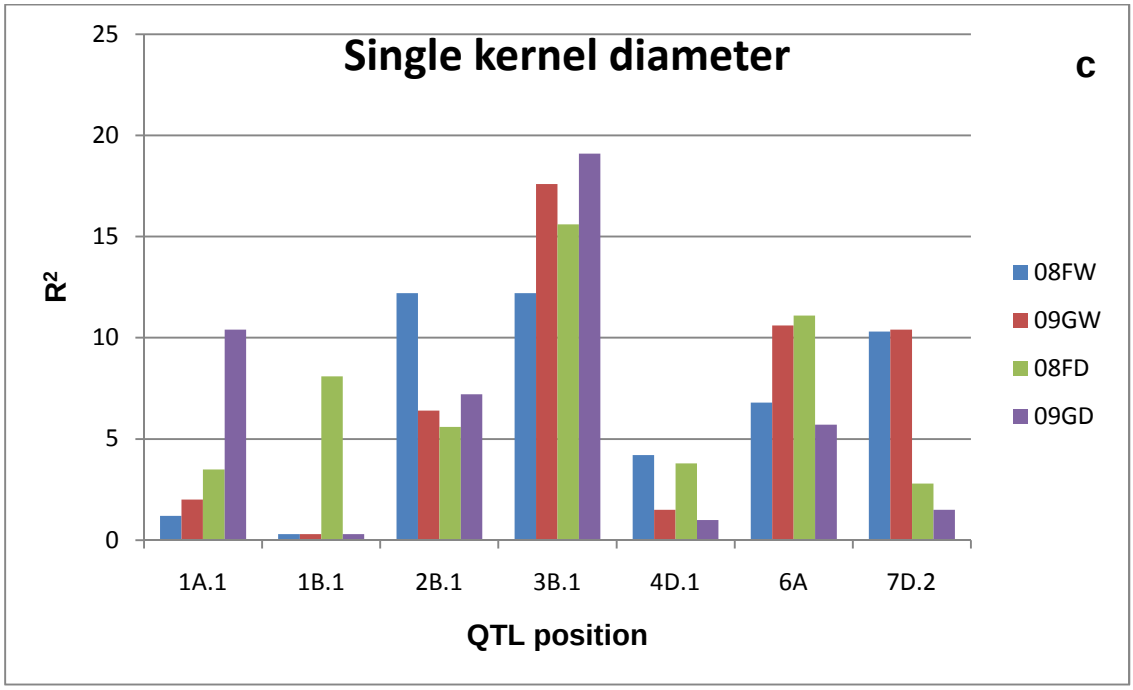


Fig 2.6. Continued



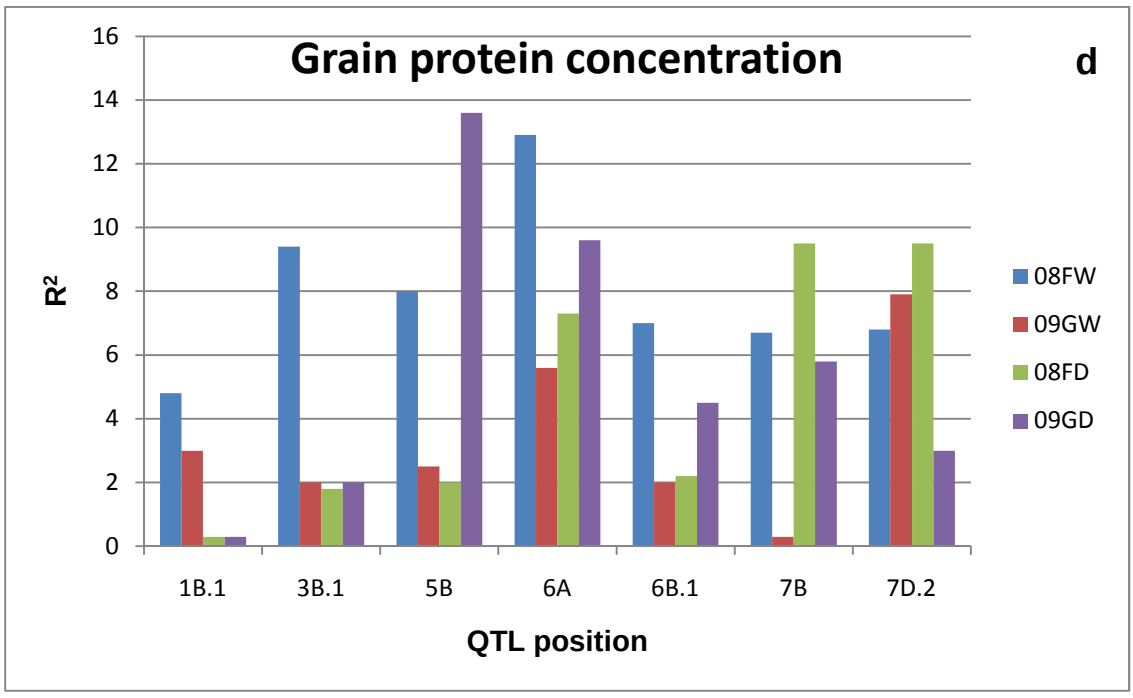
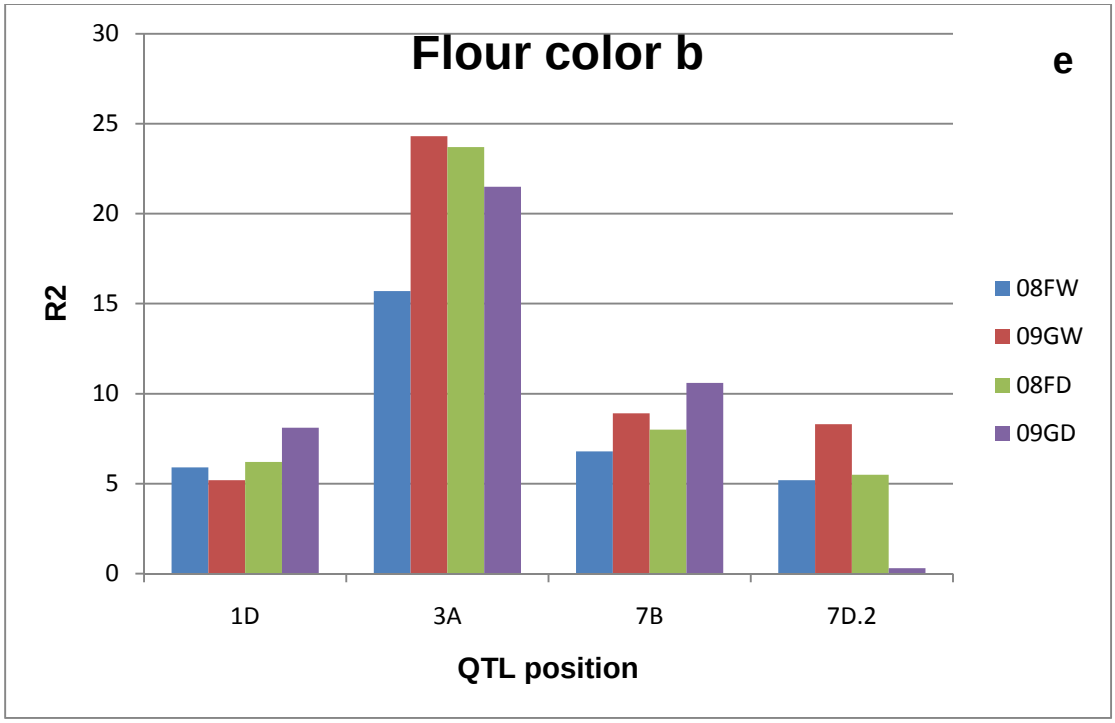


Fig 2.6. Continued



2.3 DISCUSSION

2.3.1. Marker analysis and genetic map construction

Adequate marker coverage of the wheat genome is important for QTL detection studies. Due to wheat's genome size and low rate of genetic polymorphism among improved germplasm, it has been difficult to construct complete genome maps with uniform marker coverage. In several published studies, maps used for QTL detection contained 100 to 250 markers and did not cover all chromosomes (Groos et al., 2003; Huang et al., 2006; Zanetti et al., 2001). Recently, Li et al. (2009), Patil et al. (2009), Sun et al. (2010), and Zhang et al. (2009) constructed wheat genetic maps using different marker types. Their maps spanned a total map length of 3,324, 2,328, 2,203, and 1,682 cM, respectively. The map length reported in the present study (2,083 cM) is within that range and similar to the lengths of two of those maps. The CO940610/Platte map was considerably shorter than the SSR consensus map (Somers et al., 2004), which spanned 2,569 cM. This was due to incomplete coverage of some chromosomes, especially chromosomes 4B, 4D, and 5D.

In general, marker density of the A genome was higher than that of the B and D genomes. These results are consistent with the study by Breseghello et al. (2005). Despite poor marker coverage on some chromosomes, a linkage map of the CO940610/Platte population was useful for understanding the genetic control of multiple wheat quality traits and identifying molecular markers associated with variation in those traits. The marker loci were subjected to a Chi-square test at $P<0.01$ and 26 of 221 loci (11.7%) were found to deviate from expectations of 1:1 segregation (Table A2, Fig. 2.4). The distorted loci were distributed on 17 linkage groups and several were clustered on linkage groups 4A.1 and 5B. Clusters of distorted markers suggest a biological basis for the distortion (e.g., loci in the distorted region at which alleles from one of the parents reduce viability of gametes or result in poorer performance in tissue culture) rather than

a technical problem with marker evaluation or scoring. Framework maps with skewed markers have been constructed in wheat by Blanco et al. (1998), Suenaga et al. (2005) and Nachit et al. (2001). Loci with segregation distortion were previously reported to be clustered on chromosomes 1A, 4B, 4D, 5A, 6A, 6B, and 6D in a DH bread wheat population (Suenaga et al., 2005). Quarrie et al. (2005) reported 17 of 567 markers (3.0%) distorted in a DH mapping population on chromosomes 1AL, 3BS, 4AL, 4AS, 4DS/L, 5AS, 6AS and 7BL. In contrast, 27% of the markers mapped by Cadalen et al. (1997) deviated significantly from the 1:1 ratio in their DH mapping population.

2.3.2. Trait means, correlation, and heritability estimates

Grain protein concentration is known to be influenced by genetic factors and environmental conditions, including drought, temperature, and nitrogen nutrition (Daniel and Triboi, 2002; Prasad et al., 2003; Zheng et al., 2009). This was also found to be true for the CO940610/Platte population. The mean grain protein concentration under limited irrigation in both years of the study was significantly higher than in the full irrigation treatment. This is consistent with the fact that protein concentration increases in response to drought (Weightman et al., 2008). Drought limits green leaf area and the plant's ability to fix dry matter during the grain filling period. Therefore, less starch is accumulated in the grain, resulting in higher final grain protein concentration (Foulkes et al., 2002). Due to the higher protein levels, the lower moisture treatment produced significantly higher mean values for all mixograph traits except mixograph right width.

Furthermore, all single kernel characteristics and test weight in both years had higher mean values (P<0.05) under limited irrigation compared to the full irrigation treatments. This finding agrees with many studies (e.g., Weightman et al., 2008; Suprayogi et al., 2009). In all environments, normal or approximately normal phenotypic distributions of DH line means for most traits were observed. Transgressive segregation was observed for all traits, with a wide range of variation among the DH lines (Fig. A1).

Transgressive segregation indicates that alleles from both parents influenced end use quality. Such segregants for various quality traits were previously reported for grain protein concentration (Dholakia et al., 2001; Huang et al., 2006), seed size and shape (Ammiraju et al., 2001) and mixograph traits (Huang et al., 2006). Platte, which is known for its excellent bread making quality had higher values than CO940610 for mixograph traits and grain protein concentration under different moisture levels (Fig. 2.5 and Fig. A1).

Correlations between pairs of quality traits were analyzed for all environments (Table 2.5 and 2.6). Most of the mixograph traits in this study were positively correlated with each other in each trial with a few exceptions. This finding agrees with many studies (e.g., Campbell et al., 2001; Nelson et al., 2006). Test weight was significantly correlated ($P<0.05$) with single kernel weight and kernel diameter in the four environments, suggesting that DH lines with higher test weight tended to have heavier and larger kernels, in agreement with Sun et al. (2010) and Weightman et al. (2008). Simultaneous improvement in grain yield and grain protein concentration has been limited by the generally negative relationship between those traits (Simmonds, 1995). In the CO940610/Platte population under all environments grain protein concentration was negatively correlated with grain yield with a range from -0.36 to -0.66 ($P<0.01$).

Heritability estimates varied considerably from trait to trait. Compared to other quality traits, grain protein concentration was estimated to have relatively low heritability (0.523 to 0.609) while flour color b had the highest heritability estimates among the measured traits (0.872 to 0.927) (Table 2.7). In our study, the estimated heritability of most quality traits was high, indicating that a large part of the expression of these traits was genetically controlled, making it easier to make progress from selection in a breeding program. High heritability estimates also reflect the relative uniformity of field and laboratory conditions and repeatability of phenotypic evaluations, thus reducing

environmental variation. High heritability estimates for quality traits, especially for mixograph parameters, single kernel characteristics, and flour color in this study agree with results of Mann et al. (2009). The lower heritability estimates for grain protein concentration indicated that environmental or measurement factors had more influence on this trait compared to other quality traits. Heritability estimates based on combined data for the four environments increased when compared to individual environments (Table 2.8). When combining data over multiple environments, the heritability estimates are expected to rise with an increasing number of environments when the genotype by environment interaction is large (Hill et al., 1998, p.127). This is because the effect of the σ^2_{GE} term in the denominator of the heritability calculation is divided by the number of environments, thus reducing the overall value of the denominator term (see p. 53 of this dissertation).

2.3.3. QTL mapping

The main objective of this study was to locate QTL associated with multiple wheat quality traits under different moisture treatments. CIM analysis produced a total of 123 major and minor QTL for quality traits (Table 2.9, Fig. 2.2). The 123 QTL were distributed over 19 wheat chromosomes, with only chromosomes 4B and 5D not represented. Distribution of QTL was relatively balanced between irrigation levels and many of the most important QTL were detected in both irrigation treatments. This indicates that the same set of genes controls these traits regardless of the degree of moisture. This finding is convenient for wheat breeders, who do not need to modify their selection schemes based on the moisture stress of target environments, at least over the range of moisture sampled in this study. Several QTL were mapped to eight major QTL clusters on chromosomes 1A.1, 1B.1, 1D, 2B.1, 3B.1, 6A, 7B, and 7D.2, while the remaining QTL mapped to other regions of the genome. The QTL clusters could be the result of two or more linked genes or a single gene with pleiotropic effects. Many QTL for

quality traits (mixograph parameters, single kernel characteristics, grain protein concentration, and flour color) are co-localized on different positions on chromosomes 1A.1, 1B.1, 1D, 2B.1, 3B.1, 6A, 7B, and 7D.2, in both irrigation treatments. The comparison of QTL map locations highlights the complex relationships among quality traits in this population. As expected, the traits with higher heritability generally had more phenotypic variation explained by the detected QTL.

2.3.3.1. QTL for mixograph traits

Five mixograph parameters were measured in CO940610/Platte population: mixograph right slope (Mrs), mixograph peak time (Mxt), mixograph peak height (Mxh), mixograph peak width (Mxw), and mixograph right width (Mrw). Most of the large-effect QTL detected for mixograph parameters were mainly on chromosomes 1A.1, 1B.1, and 1D, in the vicinity of *Glu-A1*, *Glu-B1, Glu-D1,* and *Glu-D3* (Table 2.9, Fig. 2.3, and Fig. 2.4). This study confirmed previous studies on the importance of glutenin loci on mixograph parameters (Huang et al., 2006; Li et al., 2010; Mann et al., 2009; McCartney et al., 2006; Payne et al., 1987; Zhang et al., 2009c; Zheng et al., 2009).

In our population, the *Glu-A1b* allele (subunit 2*) from Platte was always associated with higher value of mixograph parameters than the *Glu-A1c* (null) allele from CO940610 (Table 2.8). This result is in agreement with the studies by Moonen et al. (1983) and Zheng et al. (2009). Marker interval *Xwmc312-Glu-A1* (1A.1) was associated with many mixograph traits (Mxt, Mxh, Mxw, and Mrw) under both moisture treatments in both years. These results are in agreement with previous reports for Mxt (Zhang et al., 2009c; Zheng et al., 2009), Mxh (Campbell et al., 2001; Mann et al., 2009; Zheng et al., 2009), Mxw (Patil et al., 2009), and Mrw (Zhang et al., 2009d).

The *Glu-B1b* allele (subunit 7+8) from CO940610 was associated with higher values for all mixograph traits in all environments than *Glu-B1e* (subunit 20x+20y) from Platte. This agrees with results from Eagles et al. (2004) and Zheng et al. (2009).

Marker interval *Xcfd20a-Glu-B1* (1B.1) was associated with all mixograph traits. QTL for Mxt and Mrw designated *QMxt.cob-1B.1* and *QMrw.cob-1B.1,* respectively, were consistent over all environments. The CO940610 allele at *QMxt.cob-1B.1,* increased Mxt by 0.29 to 0.39 min**.** Our results are in agreement with several previous studies (Table 1.2).

The *Glu-D1d* allele (subunit 5+10) from Platte always gave higher values of mixograph parameters than the *Glu-D1a* allele (subunit 2+12) from CO940610 (Table 2.8). The results for CO940610/Platte confirmed the important effects of *Glu-D1d* on breadmaking quality, as shown in previous studies (Eagles et al., 2004; Zheng et al., 2009). Marker interval *Xcfd48-Glu-D1* (1D) was associated with Mxt, Mxh, and Mrw. Two QTL, designated *QMrs.cob-1D* and *QMxt.cob-1D,* were mapped to the short arm of chromosome 1D, suggesting the importance of *Glu-D3,* a LMW-GS locus. Platte contributed the favorable allele at both QTL on chromosome 1D.

Another QTL cluster for mixograph traits was located on the short arm of chromosome 6A (Fig. 2.2). Several QTL for Mrw, Mxt, and Mrs were detected near or within the X*cfd1– Xwmc256* marker interval, which is located near the *Gli-A2* locus on 6AS (Blanco et al., 2002). This result suggests the importance of gliadin proteins on dough properties (Salentijn et al., 2009).

Seven QTL for mixograph traits were identified under different moisture levels on the short arm of chromosome 7B. These QTL individually explained 4.0 to 8.8% of the phenotypic variation, with the poor quality parent CO940610 contributing the favorable allele for all traits. Most of these traits were identified within the *wPt-7602–Xwmc76* marker interval. A few studies have reported QTL for mixograph traits on chromosome 7B but in different locations (Mann et al., 2009; Patil et al., 2009). The 7BS QTL region near DArT marker *wPt-7602* may reflect a novel quality locus or loci (Fig. 2.2). Storlie et

al. (2009) reported that the 7BS chromosome arm may contain a transcription factor that affects expression of the high molecular weight glutenin loci

In summary, most of QTL for the mixograph traits were consistent over environments, especially the large-effect QTL associated with the HMW-GS (Table 2.9, Fig. 2.2). Consistency of HMW-GS allelic effects across soil moisture levels in Colorado was previously reported by Zheng et al. (2009). This consistency simplifies selection strategies in breeding programs because the same suite of alleles will have relatively similar effects in a broad range of soil moisture conditions.

2.3.3.2. QTL for Single kernel characteristics

The end use quality of wheat is greatly influenced by seed characteristics, including kernel weight (Skw), kernel diameter (Skd), and kernel hardness (Sha) (Breseghello et al., 2007; Campbell et al., 1999; Dholakia et al., 2003; Li et al., 2009; Pshenichnikova et al., 2008; Sun et al., 2010). Identifying molecular markers linked to QTL controlling seed characteristics could help to improve end use quality in wheat (Huang et al., 2006; Weightman et al., 2008). Thirty-three QTL were detected for SKCS traits with major and minor effects mainly on chromosomes 1A.1, 1B.1, 2B.1, 6A, and 7D.2 (Table 2.9, Fig. 2.2). This study confirmed previous reports that QTL influencing kernel characteristics are distributed across the wheat genome (Sun et al., 2010).

In this study, Skw QTL were distributed on seven linkage groups (1A.1, 1B.1, 2B.1, 2D.1, 3B.1, 6A, and 7D.2) over both moisture treatments. This agreed with results that Skw QTL were distributed with various effects on different chromosomes (Campbell et al., 1999; Galande et al., 2001; Dholakia et al., 2003; Groos et al., 2003; Huang et al., 2006). CO940610 contributed the favorable allele for most of the Skw QTL, which helps explain the higher mean value for grain yield for CO940610 compared to Platte (Table 2.3). In general, limited irrigation QTL did not differ from those detected in the full irrigation treatment, and most of the QTL were detected in both years. QTL designated

QSkw.cob.1A.1, *QSkw.cob.1B.1,* and *QSkw.cob.6A,* may indicate the effects of *Glu-A1*, *Glu-B1,* and *Gli-A2,* respectively. Of the detected QTL, those on chromosomes 1B and 6A have been reported in other studies of wheat kernel weight (Sun et al., 2010). However, we could not confirm whether the QTL were the same as in the present study. Dholakia et al. (2003) identified QTL for Skw on chromosome 2BL, near the QTL designated *QSkw.cob.2B.1*.

QTL analysis for Skd revealed 11 QTL with percent phenotypic variation explained ranging from 3.5 to 19.1%. The QTL were located on seven linkage groups, namely 1A.1, 1B.1, 2B.1, 3B.1, 4D.1, 6A, and 7D.2, Sun et al. (2009) identified QTL for the same trait on chromosomes 4AL, 5AL, 5AS, and 6AS, which explained 42 to 71% of the phenotypic variation. Sun et al. (2010) reported a Skd QTL on chromosome 6A, comparable to our QTL location on the same chromosome, but the other detected QTL were different. Platte contributed the favorable allele for most Skd QTL. A major QTL, designated *QSkd.cob-3B.1,* was consistent across environments and explained 12.2 to 19.1% of the phenotypic variation. The region on chromosome 2B.1 was also consistent across environments and was similar to the QTL reported by Campbell et al. (1999) on the same chromosome. To my knowledge, the QTL on on chromosomes 1B and 3B have not been previously reported for Skd. Their co-localization with QTL for mixograph traits and Skw suggests that the QTL may be due to pleiotropic effects.

The *Ha* locus on chromosome 5D is considered the main determinant of grain texture in hexaploid wheat (Weightman et al., 2008; Li et al., 2009; Sun et al., 2010). However, the results of this study, as well as those from other reports (e.g., Zanetti et al., 2001, Narasimhamoorthy et al., 2006; Sourdille et al., 2003; Li et al., 2009; Mann et al., 2009; Sun et al., 2010), indicate that kernel hardness is influenced by more loci than *Ha.* QTL analysis in CO940610/Platte revealed seven QTL distributed on chromosomes 1D, 2B.1, 6B.2, 7A, and 7D.2. Two QTL, designated *QSha.cob-2B.1* and *QSha.cob-6B.2,*

were consistent over environments and explained 5.9 to 15.1% of the phenotypic variation. CO940610 contributed the favorable alleles for the 2B.1 and 6B.2 QTL which increased the hardness index by 1.21 to 2.08. Groos et al. (2004) also identified QTL for kernel hardness on chromosomes 2B and 6B, in addition to chromosomes 1A, 1B, 2A, 2D, 3A, 3B, 4A, 5A, 5B, 5D, 6A, and 6D. Other genetic analyses have shown the influence of chromosomes 2A, 2D, 3A, 4A, 4B, 5A, 5B, 6D and 7A on hardness (Campbell et al., 1999; Sourdille et al., 1996). We did not detect the major hardness locus *Ha* on chromosome 5D in our population, possibly because the hardness allele is fixed in elite hard winter wheat germplasm. Another potential explanation is the poor marker coverage of chromosome 5D; only three markers mapped to that linkage group, covering 7.8 cM.

2.3.3.3. Grain protein and ash concentration

Grain protein concentration (Gpc) is considered a quantitative trait controlled by several genes distributed across the wheat genome (Groos et al., 2004; Huang et al., 2006; Prasad et al., 2003; Mann et al., 2009; Parasad et al., 2003; Suprayogi et al., 2009; Weightman et al., 2008). The increase in Gpc, as observed in the present study, is a recognized response to drought in wheat (Table 2.1 and 2.2). Generally, there is a negative relationship between Gpc and grain yield components in wheat, and it has also been observed that drought stress increased Gpc compared to optimum conditions (Weightman et al., 2008). Platte had higher Gpc than CO940610 under both moisture levels, but transgressive segregants were observed for that trait (Fig. A1) and alleles for both parents were found to increase values of the trait. QTL analysis for Gpc revealed 13 QTL with the percent phenotypic variation explained ranging from 4.8 to 13.6%. The QTL were located on seven chromosomes, namely 1B.1, 2D.1, 5B, 6A, 6B.1, 7B and 7D.2. These positions agree well with previous reports for this trait (Table 1.2). Two QTL, designated *QGpc.cob-6A* and *QGpc.cob-6B.1,* were detected on the short arm on

chromosomes 6A and 6B, near gliadin loci. This is consistent with previously published QTL for Gpc using other populations (Perretant et al., 2000; Prasad et al., 2003; Salentijn et al., 2009). A region on 5B influencing Gpc in our study is in a position consistent with loci identified in Suprayogi et al. (2009). Although the regions on 7B and 7D.2 influencing Gpc in our study were previously identified by Suprayogi et al. (2009) and Weightman et al. (2008), respectively, we were not able to confirm if they are the same loci because common markers were not identified.

To the best of my knowledge, there are no published studies on QTL for grain ash concentration (Gac). In this study Gac QTL were distributed on eight linkage groups with percent phenotypic variation explained ranging from 4.1 to 12.2 %. Platte contributed the favorable allele at most of these QTL, and had higher mean values under both moisture levels. Two significant QTL, designated *QGac.cob-1B.1* and *QGac.cob-4A.1*, were identified on chromosomes *1B.1* and *4A.1* and were consistent over all environments. Gac QTL were consistently localized with QTL for some mixograph parameters on linkage groups 1A.1, 3B.1, 4A.1, and 7B (Table 2.8 and Fig. 2.2).

2.3.3.4. Test weight

Test weight (Tw) is often positively correlated with grain yield and kernel weight (Huang et al. 2006; Mclntyre et al., 2010). In our study also, it was correlated with grain yield (r = 0.21 to 0.43, P<0.05) and kernel weight (r = 0.18 to 0.39, P<0.05). Three QTL were detected on chromosomes 1B.1, 7A, and 7D.2, under the full moisture treatment, with percent phenotypic variation explained ranging from 5.9 to 8.3%. The QTL designated QTw.cob-7A, was located in a similar position to QTL for Tw identified by Elouafi and Nachit (2004) and Huang et al. (2006). Tw had the lowest number of QTL in this study, possibly because of the high amount of error in estimating this trait due to different people conducting this test.

2.3.3.5. Polyphenol oxidase activity (Ppo)

Many reports indicate that the *Ppo* genes on homoeologous group 2 chromosomes are responsible for grain Ppo activity, especially those on chromosomes 2A and 2D (Jimenez and Dubcovsky, 1999; Anderson and Morris, 2001; Sun et al., 2005; He et al., 2007; Raman et al., 2007; Watanabe et al., 2004 and 2006). In the CO940610/Platte population we identified a major QTL, designated *QPpo-cob-2A*, within the *Xgwm312–Ppo33* interval on the long arm of chromosome 2A; percent phenotypic variation explained was 48.3 to 68.4%. The allele for higher Ppo activity was from CO940610. Raman et al. (2005) identified a major locus controlling Ppo activity on 2AL within *Xgwm312-Xgwm294b* marker interval.

2.3.3.6. Flour color

Improvement of flour color is an important quality objective for many wheat end product studies (Raman et al., 2009). Three QTL were identified for flour color b, designated *QFcb.cob-1D*, *QFcb.cob-3A*, and *QFcb.cob-7B*, which were consistent across environments. *QFcb.cob-3A* explained up to 24.2% of the phenotypic variation (Table 2.8), indicating that this is a major QTL that could be manipulated in wheat breading programs. CO940610 had higher mean values for flour color b than Platte (Table 2.3), and contributed the favorable allele at all three QTL. Heritability estimates for flour color b were high (0.94 to 0.96) in individual environments, consistent with estimate by Zhang et al. (2009b).

2.3.4. Stability of QTL across environments

Distribution of QTL was relatively balanced between the two irrigation treatments, with 67 QTL (54.7%) detected under full irrigation and 56 QTL (45.5%) detected in the limited irrigation treatment. In most cases especially for the consistent QTL the size of those QTL were the same across environments. In some cases the absence of QTL for one trait affects the presence of QTL for another trait. As an example, the absence of

QTL for Gpc on chromosome 7B in the full irrigation treatment in Greeley may be responsible for the absence of QTL for Mxt in that region (Fig. 2.6a and d).

In summary, a population of 185 DH hard white winter wheat derived from a cross between CO940610 and 'Platte' was evaluated in field experiments under well watered and moderate soil moisture stress conditions to identify QTL for end use quality traits, including mixograph parameters, single kernel characteristics, grain protein concentration, polyphenol oxidase activity, and flour color. All quality traits showed a wide range of trait mean values under both irrigation treatment with higher mean values for most traits under the limited irrigation treatment. A total of 123 QTL was detected in four environments with approximately equal numbers of QTL detected in the full and the limited irrigation treatment. Many QTL for correlated traits were mapped in the same genomic regions, forming QTL clusters. Many of the detected QTL were located on linkage group 1A.1, 1B.1, and 1D; most likely they reflect the effects of the high molecular weight glutenin loci *Glu-A1*, *Glu-B1*, and *Glu-D1*. Other QTL clusters were located on linkage groups 2B.1 and 7D.2, these QTL may be due to the photoperiod response gene *Ppd-B1* and vernalization locus *Vrn-D3*.

In conclusion, most of the QTL for most of quality traits were detected in both soil moisture levels. This indicates that the same set of genes controls these traits regardless of the degree of moisture. This finding is convenient for wheat breeders, who do not need to modify their selection schemes based on the moisture stress of target environments. This study confirms previous reports on the importance of high and low molecular weight glutenin loci and the effects of specific alleles at those loci on breadmaking quality traits. Also in agreement with previous studies, the relative effects of these alleles did not vary greatly with moisture stress over the range evaluated in these trials. The effects of the developmental genes *Ppd-B1* and *Vrn-D3* on quality traits

had not been well documented previously. This study suggests that these genes have major effects on multiple quality traits, most likely through their effects on maturity.

CHAPTER 3

Mapping quantitative trait loci for agronomic traits in winter wheat under different soil moisture levels

ABSTRACT

The identification of quantitative trait loci (QTL) for agronomic traits is the first step to dissecting their complex genetic nature so that they can be manipulated more effectively in breeding programs. Water deficit is the main environmental factor limiting wheat (*Triticum aestivum* L.) productivity in many parts of the world. Identification of QTL affecting yield and other agronomic traits under drought stress will facilitate the development of drought tolerant cultivars. The objectives of this study were to identify QTL for phenological parameters, morphological parameters, yield and yield components, normalized difference vegetation index (Ndvi), and drought susceptibility index (Dsi). Field evaluation of a population of 185 doubled haploid (DH) hard white winter bread wheat derived from a cross between CO940610 and 'Platte' were carried out at Fort Collins and Greeley, Colorado, USA in 2007-08 and 2008-09, respectively. One trial was grown under moderate moisture stress ("dry") and one under fully irrigated ("wet") conditions, for a total of four environments. A genetic map of 31 linkage groups covering the 21 chromosomes was constructed based on 221 marker loci, consisting of 108 SSR, 105 DArT, 3 STS, and 5 protein markers, and spanning 2,083 cM. Frequency distributions for all agronomic traits demonstrated transgressive segregation, indicating that alleles from both parents influenced the traits. In general, DH lines from the fully irrigated treatment had higher mean values (P<0.05) of agronomic traits than those from the limited irrigation treatment. A total of 128 QTL was detected in the four

environments. They were distributed on 19 chromosomes and explained from 3.7 to 42.6% of the total phenotypic variation. Approximately equal numbers of QTL were detected in the full and limited irrigation treatment. For all categories of traits, QTL frequency was highest in the B genome with 62 QTL (48.4%); another 30 (23.4%) and 36 (28.1%) QTL were found in the A and D genomes, respectively. In general, QTL for phenological parameters (days to heading and days to physiological maturity) were consistently identified in the four environments on chromosomes 1B.1, 2B.1, and 7D.2. Multiple-locus models explained 49.5 to 64.8% of the variation for days to heading in the four environments. Many QTL for correlated traits were mapped in the same genomic regions, forming QTL clusters. A cluster of QTL for 12 traits that were generally consistent across environments was found on chromosome 2B.1. This QTL cluster was observed within the *wPt-3561–Xgwm429* interval and seems likely to be coincidental with the photoperiod response gene *Ppd-B1*. Generally, CO940610 contributed favorable alleles for most QTL identified on chromosome 2B.1. Another QTL cluster was detected on chromosome 7D near the vernalization response gene *Vrn-D3* and had the largest effect on agronomic traits. Platte contributed the favorable allele for most of the QTL detected at this position. A QTL was identified on chromosomes 5B and 7B for drought susceptibility index in Greeley. CO94610 contributed the favorable allele effects for this trait. The most significant QTL for grain yield in the current study was located on chromosome 5A (*QGY.cob-5A*), with $\%R^2$ ranging from 7.7 to 11.3. This QTL was consistent across environments. After validation, the QTL identified in this study, particularly those that were consistent across environments may have applications for marker assisted breeding strategies in winter wheat breeding programs.

3.0 INTRODUCTION

Wheat is one of the most world's important food crops. Because wheat is grown in many arid and semi-arid regions, drought stress is the major environmental factor limiting its productivity in those areas (Weightman et al., 2008; Peleg et al., 2009). Improving yield and yield components, especially under drought stress, is difficult, as they are complex traits controlled by many genes and highly influenced by environmental factors.

Wheat is a hexaploid species (2n=6x=42; genome AABBDD) with a large genome (15.960 Mb) (Arumuganathan and Earle, 1991), which makes it one of the most complex crops for genetic analysis. However, with the advent of molecular markers, a new approach to dissect complex traits using quantitative trait locus (QTL) analysis became available (Doerge, 2002). Microsatellites, also known as simple sequence repeats (SSR), are an advantageous marker class for QTL detection in wheat. These markers detect a high level of polymorphism because they target highly variable regions of the genome. Detailed SSR genetic maps are available for wheat (Roder et al., 1998; Pestsova et al., 2000; Somers et al., 2004), and SSR have been widely used in wheat for QTL detection (McIntyre et al., 2010). Another important marker class, Diversity Array Technology (DArTs), can detect and type DNA variation at several thousand genomic loci without relying on sequence information (Wenzl et al., 2004). The technology has recently been used in QTL studies in wheat (Crossa et al., 2007; Griffiths et al., 2009; Raman et al., 2009).

Doubled haploid (DH) wheat populations have been used in several mapping studies (e.g., Huang et al., 2006; Chu et al., 2008; Raman et al., 2009). DH populations allow for the rapid development of homozygous lines that can be planted in replicated trials across different locations and years.

The presence of QTL clusters for yield and yield component traits on many chromosomes has been reported by many authors (Shah et al., 1999; Araki et al., 1999; Kato et al., 2000; Borner et al., 2002; Campbell et al., 2003; Groos et al., 2003; Quarrie et al., 2005; Marza et al., 2006; Maccaferri et al., 2008; McIntyre et al., 2010). For example, Quarrie et al. (2005) identified 17 clusters of yield QTL under a wide range of moisture stress conditions: two on group 1 chromosomes, one each on group 2 and group 3, five on group 4, four on group 5, one on group 6 and three on group 7 chromosomes. Yield QTL clusters coincided with major genes regulating plant height (*Rht-B1* on 4BS), vernalization (*Vrn-A1* and *Vrn-D1* on chromosomes 5AL and 5DL, respectively), and photoperiod sensitivity, on chromosomes 2BS (*Ppd-B1*) and 2DS (*Ppd-D1*).

A number of genes are known to affect flowering time in wheat and thus are important in determining yield. Flowering time is controlled by three major groups of genes, vernalization response genes (*Vrn*), photoperiod response genes (*Ppd*), and developmental rate genes ('earliness per se', *Eps*) (Lin et al., 2008). There are five wheat vernalization loci: *Vrn-A1* on chromosome 5AL (Galiba et al., 1995), *Vrn-B1* on chromosome 5BL (Iwaki et al., 2002), *Vrn-D1* on chromosome 5DL (Nelson et al., 1995), *Vrn-B3* on chromosome 7BS (Yan et al., 2006), and *Vrn-D3* on chromosome 7DS (Wang et al., 2009). The major genes affecting photoperiod response in wheat, *Ppd-A1*, *Ppd-B1*, and *Ppd-D1*, were mapped to homoeologous positions on the short arms of group 2 chromosomes (Scarth and Law, 1983). Chromosomes that carry *Eps* genes include 2BL (Scarth and Law, 1983), 3A, 4B, 4D, and 6B (Hoogendoorn, 1985).

Our objectives were (1) to evaluate a DH mapping population for multiple agronomic and drought tolerance traits in environments differing in moisture stress; (2) to develop a genome-wide molecular marker linkage map for the population; (3) and to

conduct QTL analysis to determine the location and size of QTL and their stability across environments.

3.1 MATERIAL AND METHODS

Population development, trial design, marker evaluation, linkage map construction, and statistical analysis are described in detail in Chapter 2.

Agronomic traits were measured or calculated either from the whole plot or from a 1-m strip, as described in Tables 3.1 and 3.2 and in sections 3.1.1-3.1.3.

Table 3.1. Summary of agronomic traits measured in whole plots of the CO940610/Platte mapping population in the 2007-08 and 2008-09 growing seasons.

Trait	Method of Measurement
Plant height (Ht), cm	Measured from the ground to the tip of the spike, excluding awns, approximately two weeks before harvest.
Leaf length (Ll), cm	Recorded from 5 flag leaves/plot, measured from the leaf colar to the tip.
Leaf width (Lw), cm	Recorded from 5 flag leaves/plot, measured on the widest part of the leaf.
Spike length (Sl), cm	Averaged from 5 random spikes/plot excluding awns
Days to heading (Dth)	The numbers of days from January 1st until 50% of the plants in a plot had heads fully emerged above the flag leaf collar.
Flag leaf senescence (Fls)	The numbers of days from January 1st until 50% of the flag leaves in a plot had turned yellow.
Days to physiological maturity (Dpm)	The numbers of days from January 1st until 50% of plants in a plot had a yellow peduncle, indicating the end of the grain filling period.
Grain filling duration (Gfd)	Calculated by subtracting days to heading from days to physiological maturity .
Grain filling rate (Gfr), g d^{-1}	Calculated by dividing 1-m grain weight by Gfd.
Grain yield (Gy)	The total grain yield from the plot based on combine harvest plus 1-m grain weight from the biomass sample

Table 3.2. Agronomic traits measured from 1-m strips of the CO940610/Platte mapping population in the 2007-08 and 2008-09 growing seasons.

Trait	Method of Measurement
Above ground biomass (Agb), g	Just before harvest, a 1-m strip of one row was sickled at ground level for each plot, collected in a paper bag, and weighed
One meter grain weight (1mg), g	Grain weight was recorded in grams obtained after threshing the 1-m biomass sample
Harvest index (Hi)	Estimated as Agb/1mg
Kernel weight (Kw), mg	From the 1-mg sample we counted 200 seeds using a seed counter (International Marketing and Design Corp Model 900-2), recorded the weight in grams, and divided by 200

3.1.1. Pre-harvest sprouting

The pre-harvest sprouting (Phs) test was conducted following the method of Mares et al. (2005). Five heads per plot were harvested just as they entered physiological maturity, i.e., when the peduncle had begun to turn yellow. The heads were stored at room temperature for 5 days and then transferred to a freezer at -2 C° until the time of the experiment. For each plot the five spikes were carefully threshed and the seeds bulked. For each plot, 50 well-filled grains free from obvious defects were incubated on uniformly moist filter paper, but with no excess water in a Petri dish. Distilled water was used to minimize mold growth during incubation. The covered Petri dishes were placed in a growth chamber at 20 C° with a photoperiod of 12 hours light and 12 hours dark. Each day the dishes were examined to insure they contained a thin layer of water in the bottom to maintain humidity. Seeds were counted as 'germinated' when the white radicle had protruded and there was a visible tear in the seed germ.

Germinated grains were counted at daily intervals for 7 days starting from the day after starting the test, and expressed as a weighted germination index (Walker-Simmons, 1988). This index gives maximum weight to grains that germinate rapidly and is calculated from the following formula: Germination index (GI) = (7 x N_1 + 6 x N_2 +…1 x N_7)/ (total days of test x total grains), where N_1, N_2, N_3, ..., N_7 are the number of grains that had germinated on day 1, day 2,…., day 7. The maximum index is 1.0 if all grains germinate by day 1, while lower indices are indicative of increasing levels of grain dormancy or reduced germinability.

3.1.2. Normalized difference vegetation index (Ndvi)

This trait was only measured in 2008-09 in Greeley during early grain filling to evalaute vegetation cover and biomass production using a GreenSeeker (RT200) NTech industries, Ukiah, CA (Aparicio et al., 2000). The instrument sensor had an angle of 19 degrees on the walking direction, so that only the two rows were in the field of the sensor. Previous tests have shown good agreement between the 90 degree and the 19 degree angles (Aparicio et a., 2000). The Ndvi was calculated as (R_{900} - R_{680})/(R_{900} + R_{680}) according to Penuelas et al. (1997). *Rn* is the reflectance at the indicated wavelength (in nm).

3.1.3. Drought susceptibility index (Dsi)

The drought susceptibility index (Dsi) was calculated from mean grain yield following the method of Fischer and Maurer, (1978). They defined Dsi as (1-Y_d/Y_w)/D where Y_d = mean yield of an entry under drought, Y_w = mean yield of an entry under well-watered conditions, and D = environmental stress intensity = 1- (mean yield of all genotypes under drought/mean yield of all genotypes under well-watered conditions).

3.1.4. Other drought tolerance evaluations

Cooler crop canopies are an indication of a plant's access to water and have been used routinely in CIMMYT's drought tolerance selection program (Reynolds et al.,

2005). By using a portable infared thermometer, this trait can be measured quickly and is therefore suitable for large field trails. We attempted to use a Mikron MI-N15+ infared thermometer (www.mikroninfrared.com/) for this purpose. However, atmospheric conditions at our field sites are almost always windy, and the use of this instrument requires still conditions. Therefore, we were not able to obtain reliable readings on canopy temperature.

Similarly, we obtained a leaf porometer (model SC-1, Decagon Instruments, www.decagon.com) to measure stomatal conductance, an indication of the degree of opening of the stomata of the sampled leaf area. We found the readings to be highly variable, requiring 25 or more readings per plot to obtain a reliable estimate. Given the 768 plots/year in our study, it was not feasible to use this instrument on all the plots.

3.2 RESULTS

3.2.1. Trait means

The agronomic traits were classified into six categories for ease of discussion: phenological parameters, morphological parameters, yield parameters, pre-harvest sprouting, normalized difference vegetation index (Ndvi), and drought susceptibility index. Analysis of variance with Proc Mixed revealed highly significant differences (P<0.01) in trait means among DH lines (data not shown) and between treatments within locations (Tables 3.3 and 3.4) for most traits. When frequency distributions of BLUPs were analyzed, most traits were normally or approximately normally distributed, and transgressive segregation was common for all traits (Appendix Fig. A1).

In general, the fully irrigated treatment had higher mean values (P<0.05) for agronomic traits than the limited irrigation treatment. Exceptions were flag leaf senescence and spike length in 2007-08 (Table 3.3) and kernel weight and Ndvi in 2008-09 (Table 3.4). DH lines grown under the fully irrigated treatment had higher grain yield than those grown under limited irrigation (3719.7 kg ha^{-1} vs. 2923.9 kg ha^{-1} in 2008, and 3760.9 vs. 3056.9 kg ha^{-1} in 2009). The percent reduction in grain yield between the two treatments was 21.4% and 18.7% in 2008 and 2009, respectively. Therefore, the degree of moisture stress experienced by the dry treatment was moderate rather than severe. Pre-harvest sprouting was only measured under full irrigation, with an overall mean index for the population of 0.65 in 2008 and 0.46 in 2009, with higher values indicating more sprouting.

There were significant variations among DH lines for most traits. Grain yield varied over ranges of 2261.3 to 3839.5 kg ha^{-1}, and plant height varied over a range of 16 to 29 cm even though neither of the common semi-dwarfing genes segregated in this population.

Table 3.3. Means, standard errors, and ranges for agronomic traits of the CO940610/Platte population (n=185) under two irrigation treatments at Fort Collins in the 2007-08 growing season.

Treatment	Full irrigation (08FW)				Limited irrigation (08FD)				P for difference between treatments
Variable†	Mean	Std Error	Min	Max	Mean	Std Error	Min	Max	
Dth (d)	156.3	0.31	151.0	164.7	152.5	0.16	149.5	157.9	<0.001
Dpm (d)	191.2	0.30	189.53	195.53	186.72	0.5	185.3	189.0	<0.001
Gfd (d)	34.8	0.32	30.9	38.6	33.9	0.38	31.1	37.1	<0.001
Gfr (g d^{-1})	4.39	0.09	3.44	5.17	3.20	0.20	2.66	3.81	<0.001
Fls (d)	186.8	0.27	185.9	187.6	181.2	0.21	179.3	186.6	<0.052
Ht (cm)	79.4	0.81	64.9	90.8	67.9	2.29	52.2	79.3	<0.001
Ll (cm)	13.9	0.29	11.1	16.6	10.7	0.39	9.4	12.3	<0.001
Lw (cm)	1.24	0.01	1.09	1.67	1.08	0.02	0.93	1.27	<0.001
Sl (cm)	8.6	0.08	7.0	10.4	8.6	0.10	7.2	9.8	<0.488
Agb (g)	366.3	9.73	343.6	690.6	296.9	22.74	278.3	321.8	<0.001
1mg (g)	152.7	4.26	126.6	172.4	109.7	8.51	93.9	128.6	<0.001
Hi	0.42	0.01	0.39	0.48	0.37	0.01	0.31	0.44	<0.001
Kw (mg)	35.7	0.093	26.7	52.7	36.3	0.07	25.7	46.4	<0.001
Gy (kg ha^{-1})	3719.7	22.10	2091.9	4609.6	2923.9	40.82	1571.6	3832.9	<0.001
Phs	0.65	0.01	0.31	0.81					

† Dth, days to heading; Dpm, days to physiological maturity; Gfd, grain filling duration; Gfr, grain filling rate; Fls, flag leaf senescence; Ht, plant height; Ll, leaf length; Lw, leaf width; Sl, spike length; Agb, above ground biomass, 1mg, one meter grain weight; Hi, harvest index; kw, kernel weight; Gy, grain yield; Phs, pre-harvest sprouting.

Table 3.4. Means, standard errors, and ranges of the CO940610/Platte population (n=185) under two irrigation treatments at Greeley in the 2008-09 growing season.

Treatment	Full irrigation (09GW)				Limited irrigation (09GD)				P for difference between treatments
Variable†	Mean	Std Error	Min	Max	Mean	Std Error	Min	Max	
Dth (d)	144.7	0.23	139.5	154.5	143.2	0.19	138.7	152.4	<0.032
Dpm (d)	184.2	0.38	180.1	190.9	181.5	0.31	178.9	189.9	<0.012
Gfd (d)	39.4	0.35	37.4	41.7	38.2	0.22	36.3	41.3	<0.033
Gfr (g d^{-1})	4.25	0.09	2.79	4.85	3.51	0.10	1.90	4.37	<0.001
Ht (cm)	91.1	0.72	74.9	104.3	74.6	0.75	65.7	82.1	<0.001
Ll (cm)	17.3	0.30	16.2	18.2	16.1	0.23	14.3	17.5	<0.001
Lw (cm)	1.42	0.020	1.32	1.53	1.29	0.03	1.12	1.44	<0.001
Sl (cm)	9.4	0.08	8.1	11.2	9.7	0.13	8.7	10.8	<0.001
Agb (g)	463.5	12.66	394.6	507.0	401.5	13.0	319.3	470.9	<0.001
1mg (g)	167.5	3.94	105.8	191.9	134.6	4.35	77.2	163.8	<0.001
Hi	0.36	0.01	0.19	0.43	0.34	0.01	0.18	0.46	<0.001
Kw (mg)	35.7	0.06	23.0	42.2	36.2	0.05	25.6	42.2	<0.112
Gy (kg ha^{-1})	3760.9	14.16	837.1	4676.6	3056.9	13.30	823.9	4040.1	<0.001
Phs	0.46	0.02	0.33	0.56					
Ndvi	0.71	0.01	0.66	0.73	0.71	0.02	0.67	0.73	<0.128

† Dth, days to heading; Dpm, days to physiological maturity; Gfd, grain filling duration; Gfr, grain filling rate; Ht, plant height; Ll, leaf length; Lw, leaf width; Sl, spike length; Agb, above ground biomass, 1mg, one meter grain weight; Hi, harvest index; Kw, kernel weight; Gy, grain yield; Phs, pre-harvest sprouting; Ndvi, normalized difference vegetation index.

All phenological parameters (days to heading, days to physiological maturity, grain filling duration, and grain filling rate) had higher values under fully irrigated conditions compared to limited irrigation.

Both parents had higher trait values for most of the agronomic traits under full irrigation compared to the limited irrigation conditions (Table 3.5). CO940610 had a higher grain yield in all environments, with a range of 3308.6 to 4223.9 Kg ha^{-1}, compared to Platte, which yielded from 2830.4 to 3720.3 Kg ha^{-1}. Furthermore, CO940610 had taller plants in all environments (range of 73.3 to 94.6 cm), compared to Platte (range of 67.1 to 88.3 cm). On the other hand, Platte had the higher trait values for leaf length, leaf width, and spike length in both treatments in both locations.

3.2.2. Correlation among traits

Phenotypic correlation coefficients among traits were calculated using the BLUPs of 185 DH lines for each treatment. Significant correlations among many characteristics were observed (Tables 3.6 and 3.7). Phenological parameters were highly correlated ($P<0.01$) with each other under different moisture levels over the two locations of study. Days to heading was positively correlated with days to physiological maturity ($0.62<r<0.73$, $P<0.001$), and negatively correlated with grain filling duration ($-0.92<r<-0.52$, $P<0.001$). In all environments, yield was negatively correlated with days to heading ($-0.37<r<-0.18$, $P<0.05$), positively correlated with plant height ($0.19<r<0.35$, $P<0.05$), and positively correlated with kernel weight ($0.19<r<0.39$, $P<0.05$). Plant height was positively correlated with above ground biomass at all locations ($0.27<r<0.45$, $P<0.001$). Harvest index was positively correlated with grain yield ($0.21<r<0.48$, $P<0.01$) at all locations, but was negatively correlated with plant height at two locations ($-0.19<r<-0.11$, $P<0.05$). Drought susceptibility index in Fort Collins and Greeley was negatively correlated with grain yield under limited irrigation ($-0.51<r<-0.63$, $P<0.01$),

Table 3.5. Means for agronomic characteristics of the two parents, CO940610 and Platte, under two irrigation levels in the 2007-08 and 2008-09 growing seasons.

Env‡ / Variable†	08FD		08FW		09GD		09GW	
	CO960610	Platte	CO960610	Platte	CO960610	Platte	CO960610	Platte
Dth (d)	151.0	152.2**	153.9	156.8**	142.0	143.7**	143.2	145.1**
Dpm (d)	186.4	186.6	190.8	190.7	181.3	181.0	183.6	184.2
Gfd (d)	34.7	34.0	36.9**	34.2	38.9	37.4	40.0	39.3
Gfr (g d^{-1})	3.2	3.2	4.5	4.4	4.0	3.3	4.2	4.0
Ht (cm)	73.3**	67.1	84.7**	77.7	77.6	72.0	94.6**	88.3
Fls (d)	181.5	180.9	187.7	186.8				
Ll (cm)	10.4	11.0	13.1	14.5*	17.3	17.4	15.8	16.4
Lw (cm)	1.00	1.15**	1.19	1.32*	1.36	1.48	1.23	1.47**
Sl (cm)	7.8	9.0**	8.2	9.3**	9.5	9.9	9.1	9.9**
Agb (g)	300.9	295.3	374.1	364.5	452.2**	386.6	472.3	436.8
1mg (g)	109.2	109.4	159.1	151.0	152.5	127.7	166.6	153.8
Hi	0.42	0.33	0.44	0.40	0.33	0.32	0.46	0.33
Kw (mg)	39.0**	35.0	40.0**	34.5	37.0	35.5	38.5**	35.5
Gy (kg ha^{-1})	3308.6*	2830.4	4200.5	3720.3	3651.3**	2960.9	4223.9**	3697.5
Phs			0.63	0.79			0.50	0.69
Ndvi					0.7	0.7	0.7	0.7

*, ** The parental mean with asterisks is significantly higher than the other parental mean at the 0.05 and 0.01 levels of probability, respectively for each environment.

† The four environments were obtained from two moisture treatments in each of two growing seasons: Fort Collins limited irrigation (08FD), Fort Collins full irrigation (08FW), Greeley limited irrigation (09GD), and Greeley full irrigation (09GW).

‡ Dth, days to heading; Dpm, days to physiological maturity; Gfd, grain filling duration; Gfr, grain filling rate; Ht, plant height; Ll, leaf length; Lw, leaf width; Sl, spike length; Agb, above ground biomass, 1mg, one meter grain weight; Hi, harvest index; kw, kernel weight; Gy, grain yield; Fls, flag leaf senescence; Phs, pre-harvest sprouting; Ndvi, normalized difference vegetation index.

Table 3.6. Pearson correlation coefficients among agronomic characteristics of the CO940610/Platte population (n=185) under two irrigation treatments at Fort Collins in the 2007-08 growing season.†

Env		Full irrigation														
Limited irrigation	**Variable‡**	**Dth**	**Dpm**	**Gfd**	**Gfr**	**Ht**	**Ll**	**Lw**	**Sl**	**Agb**	**1mg**	**GY**	**Kw**	**Fls**	**Hi**	**Phs**
	Dth		0.72**	-0.92**	-0.29**	0.46**	0.38**	0.35**	0.38**	0.07	0.94**	-0.26*	-0.50**	0.46**	-0.16*	-0.12
	Dpm	0.62**		-0.39**	-0.04	0.17**	0.30**	0.28**	0.38**	-0.16*	-0.21**	-0.19**	-0.39**	0.51**	-0.19**	0.22**
	Gfd	-0.85**	-0.26**		-0.41**	-0.49**	-0.33**	-0.32**	-0.29**	-0.18**	-0.09	-0.14*	0.45**	-0.13*	0.11	0.07
	Gfr	-0.25**	-0.26**	-0.23**		0.40**	0.21**	0.14	0.23**	0.79**	0.94**	0.59**	-0.01	0.15*	0.39**	-0.12
	Ht	0.48**	0.24**	-0.49**	0.29**		0.29**	0.13	0.32**	0.37**	0.26**	0.35**	0.01	0.26**	-0.11*	-0.09
	Ll	-0.13	-0.09	0.19**	0.09	-0.06		0.32**	0.47**	0.15*	0.11	0.13	-0.08	0.25**	-0.08	0.08
	Lw	0.12	0.13	-0.07	0.12	-0.03	0.32**		0.29**	0.09	0.05	0.37	0.01	0.21**	-0.07	0.19**
	Sl	0.07	0.11	-0.01	0.03	0.13	0.33**	0.11		0.15*	0.14	0.12	-0.12	0.22**	-0.06	0.13
	Agb	0.08	0.01	-0.08	0.84**	0.27**	0.21**	0.06	0.03		0.82**	0.52**	0.12	0.08	-0.08	-0.06
	1mg	-0.05	0.06	-0.02	0.95**	0.19**	0.14	0.10	0.02	0.84**		0.59**	0.19*	0.07	0.46**	-0.10
	Gy	-0.18**	-0.12*	-0.14*	-0.14*	0.33**	0.08	0.07	0.09	0.40**	0.51**		0.19*	-0.04	0.21**	-0.07
	Kw	-0.27**	-0.17*	0.24**	0.09	0.23**	0.14*	0.21**	0.11	0.15*	0.15*	0.22**		-0.19**	0.11	-0.06
	Fls	0.48**	0.05**	-0.35**	-0.35**	0.33**	-0.06	0.03	0.07	0.02	0.01	-0.15*	0.03		-0.05	0.21**
	Hi	0.06	0.03	-0.01	-0.01	0.04	-0.05	0.08	0.05	0.04	0.48**	0.36**	0.05	-0.09		-0.08

*, ** significant at the 0.05 and 0.01 levels of probability, respectively

† The upper right half of the table is the correleation of traits from the irrigated treatment; the lower left half is the correlation of traits from the limited irrigation treatment.

‡ Dth, days to heading; Dpm, days to physiological maturity; Gfd, grain filling duration; Gfr, grain filling rate; Ht, plant height; Ll, leaf length; Lw, leaf width; Sl, spike length; Agb, above ground biomass, 1mg, one meter grain weight; Gy, grain yield; Kw, kernel weight; Hi, harvest index; Phs, pre-harvest sprouting index.

Table 3.7. Pearson correlation coefficients among agronomic characteristics of the CO940610/Platte population (n=185) under two irrigation treatments at Greeley in the 2008-09 growing season.†

Env		Full irrigation														
Limited irrigation	**Variable‡**	**Dth**	**Dpm**	**Gfd**	**Gfr**	**Ht**	**Ll**	**Lw**	**Sl**	**Agb**	**1mg**	**GY**	**Kw**	**Hi**	**NDVI**	**Phs**
	Dth		0.72**	-0.52**	-0.14*	0.35**	-0.06	0.21**	0.25**	-0.01	-0.28**	-0.37**	-0.39**	-0.42**	-0.26**	-0.08
	Dpm	0.73**		0.11	-0.21**	0.19**	-0.02	0.13	0.22**	0.02	-0.18**	-0.29**	-0.39**	-0.30**	-0.22**	-0.04
	Gfd	-0.67**	-0.01		-0.08	-0.25**	0.10	-0.10	-0.09	0.04	0.19**	0.15*	0.12	0.20**	0.16*	0.05
	Gfr	-0.15*	-0.39**	-0.24**		0.21**	0.04	0.03	-0.05	0.77**	0.96**	0.59**	0.23**	0.39**	0.42**	-0.01
	Ht	0.19**	0.13	-0.12	0.24**		-0.11	-0.01	0.09	0.45**	0.14	0.19*	0.25**	-0.19**	0.18**	-0.07
	Ll	-0.14*	-0.13	0.08	0.13	0.03		0.31**	0.41**	0.02	0.07	0.07	0.01	0.01	0.25**	0.02
	Lw	0.23**	0.05	-0.27**	0.09	-0.03	0.17*		0.29**	-0.04	-0.01	0.04	0.14*	0.01	0.06	0.14
	Sl	0.24**	0.17*	-0.16*	0.02	0.01	0.16*	0.20**		0.03	-0.08	-0.08	-0.11	-0.16*	0.17*	0.11
	Agb	0.13	0.02	-0.16*	0.75**	0.39**	0.15*	0.12	0.12		0.77**	0.49**	0.16*	0.14*	0.45**	-0.04
	1mg	-0.13*	-0.31**	-0.09	0.98**	0.22**	0.15*	0.06	-0.01	0.75**		0.63**	0.26**	0.43**	0.45**	0.01
	Gy	-0.11*	-0.29**	-0.16*	0.71**	0.25**	0.05	0.05	0.02	0.54**	0.58**		0.39**	0.44**	0.48**	0.01
	Kw	-0.38**	-0.31**	0.19**	0.31**	0.12	0.08	0.05	0.04	0.28**	0.36*	0.21**		0.17*	0.32**	0.15*
	Hi	-0.43**	-0.53**	0.05	0.63**	-0.14	0.06	-0.04	-0.13	0.02	0.65**	0.48**	0.27**		0.26**	0.02
	Ndvi	0.08	-0.18**	-0.09	0.20**	0.01	0.05	0.03	0.09	0.20**	0.18**	0.29**	0.15*	0.12		0.05

*, ** significant at the 0.05 and 0.01 levels of probability, respectively

† The upper right half of the table is the correleation of traits from the irrigated treatment; the lower left half is the correlation of traits from the limited irrigation treatment.

‡ Dth, days to heading; Dpm, days to physiological maturity; Gfd, grain filling duration; Gfr, grain filling rate; Ht, plant height; Ll, leaf length; Lw, leaf width; Sl, spike length; Agb, above ground biomass, 1mg, one meter grain weight; Gy, grain yield; Kw, kernel weight; Hi, harvest index; Phs, pre-harvest sprouting; Ndvi, normalized vegetation index

indicating that low yielding lines in dry conditions had lower grain reductions under drought. DSI was positively correlated with grain yield only in Fort Collins under the full irrigation treatment (r =0.37, P<0.01), showing the reverse relationship between drought susceptibility index and grain yield under the dry conditions.

3.2.3. Heritability estimates

Heritability estimates of agronomic traits ranged from 0.115 for above ground biomass (09GW) to 0.938 for days to heading (09GD) (Table 3.8). Days to heading had the highest heritability estimate of all traits in the four environments (0.869 to 0.938) with an overall estimate of 0.957. For combined environment data, plant height had a high heritability estimate (0.819), while the estimate for grain yield was moderate (0.629). For traits measured in all four environments, above ground biomass and leaf length had the lowest heritability estimates (0.425 and 0.601, respectively). Pre-harvest sprouting and Ndvi, evaluated in just two environments, had very low estimates (0.298 and 0.287, respectively).

3.2.4. QTL mapping

Composite interval mapping produced a total of 128 putative major and minor QTL for agronomic traits (Table 3.9, Fig. 3.1). When the markers nearest those QTL were analyzed in multiple-locus models, most markers retained significance at P<0.05 and the models explained 8.4 to 64.8% of the phenotypic variance (Table 3.1). For all categories of traits, QTL frequency was highest in the B genome with 62 QTL (48.4%); another 30 (23.4%) and 36 (28.1%) of QTL were found in the A and D genomes, respectively. Distribution of QTL was balanced between the full and limited irrigation treatments: 64 (50.0%) were detected under full irrigation and 62 (48.4%) under the limited irrigation treatment. In addition, two QTL were detected for Dsi between

Table 3.8. Heritability estimates for agronomic characteristics of the CO940610/Platte population at four Colorado environments in the 2007-08 and 2008-09 growing seasons.†

Environment / Variable‡	08FD	09GD	08FW	09GW	Four environments (90% confidence interval)*
Dth	0.905	0.938	0.869	0.910	0.957 (0.964 – 0.977)
Dpm	0.746	0.680	0.711	0.765	0.778 (0.605 – 0.794)
Gfd	0.642	0.713	0.840	0.668	0.843 (0.808 – 0.877)
Gfr	0.492	0.507	0.415	0.385	0.603 (0.514 – 0.673)
Ht	0.731	0.766	0.786	0.795	0.819 (0.778 – 0.850)
Ll	0.247	0.209	0.353	0.300	0.601 (0.511 – 0.671)
Lw	0.382	0.446	0.400	0.403	0.739 (0.681 – 0.785)
Sl	0.648	0.539	0.772	0.778	0.842 (0.807 – 0.870)
Agb	0.142	0.297	0.214	0.115	0.425 (0.295 – 0.526)
1mg	0.222	0.449	0.303	0.315	0.534 (0.428 – 0.615)
Hi	0.526	0.663	0.670	0.762	0.621 (0.535 – 0.687)
Kw	0.713	0.832	0.758	0.823	0.898 (0.875 – 0.916)
Gy	0.671	0.689	0.607	0.617	0.629 (0.568 – 0.676)
Phs			0.545	0.331	0.298 (0.138 – 0.421)
Ndvi		0.394		0.350	0.287 (0.126 – 0.412)

† The four environments obtained from different moisture levels during the two growing seasons: Fort Collins limited irrigation (08FD), Fort Collins full irrigation (08FW), Greeley limited irrigation (09GD), and Greeley full irrigation (09GW).

‡ Dth, days to heading; Dpm, days to physiological maturity; Gfd, grain filling duration; Gfr, grain filling rate; Ht, plant height; Ll, leaf length; Lw, leaf width; Sl, spike length; Agb, above ground biomass, 1mg, one meter grain weight; Hi, harvest index; Kw, kernel weight; Gy, grain yield; Phs, pre-harvest sprouting; Ndvi, Normalized difference vegetation index.

* Knapp et al. (1985).

Table 3.9. QTL detected for agronomic characteristics of the CO940610/Platte population in four environments of the 2007-08 and 2008-09 growing seasons.

QTL	Environment†	Marker interval	Nearest marker	Peak position (cM)	LOD	a‡	R^2 (%)
Days to heading							
QDth.cob-1B.1	08FW	*Glu-B3 - wPt-1317*	*Glu-B3*	5.3	5.75	0.64	6.7
QDth.cob-2B.1		*wPt-3561 - Xgwm429*	*wPt-3561*	83.2	14.11	-1.14	21.5
QDth.cob-3A		*Xwmc532 - Xwmc50*	*Xwmc50*	56.9	2.84	-0.55	5.1
QDth.cob-7D.2		*Xbarc126 - Vrn-D3*	*Vrn-D3*	37.3	23.06	1.41	32.1
Multiple-QTL model							49.5
QDth.cob-1B.1	09GW	*wPt-1317 - wPt-3927*	*wPt-1317*	7.3	2.60	0.40	3.7
QDth.cob-2A		*Xgwm312 - Ppo33*	*Xgwm312*	123.8	3.56	0.53	4.7
QDth.cob-2B.1		*wPt-3561 - Xgwm429*	*Xgwm429*	85.4	15.28	-1.12	21.5
QDth.cob-7D.2		*Xbarc126 - Vrn-D3*	*Vrn-D3*	35.4	26.84	1.51	39.3
Multiple-QTL model							55.9
QDth.cob-1B.1	08FD	*Glu-B3 - wPt-1317*	*Glu-B3*	5.3	3.77	0.36	4.4
QDth.cob-2A		*Xgwm312 - Ppo33*	*Xgwm312*	121.8	2.63	0.33	3.7
QDth.cob-2B.1		*wPt-3561 - Xgwm429*	*Xgwm429*	85.2	16.81	-0.85	24.7
QDth.cob-3A		*Xwmc50 - Xgwm674*	*Xwmc50*	66.9	3.37	-0.34	4.6
QDth.cob-7D.2		*Xbarc126 - Vrn-D3*	*Vrn-D3*	39.3	23.88	1.03	35.9
Multiple-QTL model							64.8
QDth.cob-1B.1	09GD	*wPt-1317 - wPt-3927*	*wPt-1317*	7.6	3.49	0.40	3.7
QDth.cob-2B.1		*Xgwm429 - Xbarc55*	*Xbarc55*	99.0	15.02	-0.97	20.6
QDth.cob-7D.2		*Xbarc126 - Vrn-D3*	*Vrn-D3*	35.4	28.88	1.38	42.6
Multiple-QTL model							54.1
Days to physiological maturity							
QDpm.cob-2B.1	08FW	*wPt-3561 - Xgwm429*	*Xgwm429*	87.2	7.24	-0.32	15.6
QDpm.cob-7D.2		*Xbarc126 - Vrn-D3*	*Vrn-D3*	37.3	6.79	0.29	12.7
Multiple-QTL model							23.9

† The four environments obtained from different moisture levels during the two growing seasons: Fort Collins limited irrigation (08FD), Fort Collins full irrigation (08FW), Greeley limited irrigation (09GD), and Greeley full irrigation (09GW).
‡ Average additive effect: Positive values indicate an increasing effect of Platte alleles and negative values indicate an increasing effect of CO940610 alleles.

Table 3.9. Continued.

QTL	Environment†	Marker interval	Nearest marker	Peak position (cM)	LOD	a‡	R^2 (%)
Days to physiological maturity							
QDpm.cob-1B.1	09GW	*wPt-1317 - wPt-3927*	*wPt-1317*	7.6	4.48	0.44	7.0
QDpm.cob-2B.1		*wPt-3561 - Xgwm429*	*Xgwm429*	83.2	9.14	-0.65	18.0
QDpm.cob-7B		*Xwmc182b - Xgwm46*	*Xwmc182b*	8.5	4.65	-0.41	7.2
QDpm.cob-7D.2		*Xbarc126 - Vrn-D3*	*Vrn-D3*	35.4	12.32	0.74	21.7
Multiple-QTL model							37.5
QDpm.cob-2B.1	08FD	*wPt-3561 - Xgwm429*	*Xgwm429*	81.2	6.65	-0.26	15.2
QDpm.cob-2B.2		*wPt-3632 - wPt-2397*	*wPt-3632*	16.3	3.16	0.17	6.5
QDpm.cob-3A		*Xbarc356 - Xgpw94023*	*Xbarc356*	76.9	4.3	-0.19	9.1
QDpm.cob-7D.2		*Xbarc126 - Vrn-D3*	*Vrn-D3*	39.3	3.44	0.17	6.8
Multiple-QTL model							32.2
QDpm.cob-7D.2	09GD	*Xbarc126 - Vrn-D3*	*Vrn-D3*	35.4	9.18	0.52	16.7
Grain filling duration							
QGfd.cob-1B.1	08FW	*wPt-1317 - wPt-3927*	*wPt-3927*	9.0	4.33	-0.39	5.1
QGfd.cob-2B.1		*wPt-3561 - Xgwm429*	*Xgwm429*	87.2	9.65	0.66	14.4
QGfd.cob-7D.2		*Xbarc126 - Vrn-D3*	*Vrn-D3*	39.3	23.18	-1.05	37.3
Multiple-QTL model							51.9
QGfd.cob-7B	09GW	*Xwmc76 - Xwmc182b*	*Xwmc76*	4.6	3.13	-0.21	5.8
QGfd.cob-7D.2		*Xbarc126 - Vrn-D3*	*Vrn-D3*	41.3	9.05	-0.34	17.6
Multiple-QTL model							20.9
QGfd.cob-1B.1	08FD	*Glu-B3 - wPt-1317*	*Glu-B3*	5.3	4.09	-0.32	7.1
QGfd.cob-2B.1		*wPt-3561 - Xgwm429*	*Xgwm429*	85.2	9.48	0.47	15.7
QGfd.cob-7D.2		*Xbarc126 - Vrn-D3*	*Vrn-D3*	35.4	16.69	-0.66	31.2
Multiple-QTL model							50.9

† The four environments obtained from different moisture levels during the two growing seasons: Fort Collins limited irrigation (08FD), Fort Collins full irrigation (08FW), Greeley limited irrigation (09GD), and Greeley full irrigation (09GW).
‡ Average additive effect: Positive values indicate an increasing effect of Platte alleles and negative values indicate an increasing effect of CO940610 alleles.

Table 3.9. Continued.

QTL	Environment†	Marker interval	Nearest marker	Peak position (cM)	LOD	a‡	R^2 (%)
Grain filling duration							
QGfd.cob-2B.1	09GD	*wPt-3561 - Xgwm429*	*wPt-3561*	79.2	5.39	0.37	12.8
QGfd.cob-7D.2		*Xbarc126 - Vrn-D3*	*Vrn-D3*	41.3	6.27	-0.45	15.5
Multiple-QTL model							25.6
Grain filling rate							
QGfr.cob-5A	08FW	*Xbarc165 - Xbarc360*	*Xbarc360*	53.9	3.54	0.08	7.2
QGfr.cob-7D.2		*wPt-0789 - Xbarc126*	*wPt-0789*	21.9	4.26	0.09	8.9
Multiple-QTL model							15.1
QGfr.cob-7B	09GW	*wPt-0217 - wPt-4814*	*wPt-0217*	51.6	2.63	0.07	6.0
QGfr.cob-7D.2	08FD	*wPt-2551 - wPt-0303*	*wPt-0303*	31.7	2.65	0.05	6.1
QGfr.cob-2D.1	09GD	*wPt-0638 - wPt-2544*	*wPt-2544*	72.0	4.43	-0.13	9.6
QGfr.cob-5B		*Xbarc4 - Xgwm540*	*Xgwm540*	56.5	3.53	-0.11	6.7
QGfr.cob-7B		*Xbarc278 - wPt-6498*	*Xbarc278*	21.2	3.32	-0.11	6.3
Multiple-QTL model							20.3
Flag leaf senescence							
QFls.cob-2B.1	08FW	*wPt-3561 - Xgwm429*	*wPt-3561*	79.2	3.73	-0.11	9.5
QFls.cob-7D.2		*Xbarc126 - Vrn-D3*	*Vrn-D3*	37.3	3.29	0.09	7.1
Multiple-QTL model							12.3
QFls.cob-2B.1	08FD	*wPt-3561 - Xgwm429*	*wPt-3561*	81.2	2.89	-0.22	6.5
QFls.cob-3A		*Xbarc356 - Xgpw94023*	*Xbarc356*	76.9	5.60	-0.29	11.5
QFls.cob-7D.2		*Xbarc126 - Vrn-D3*	*Vrn-D3*	37.3	2.96	0.21	6.0
Multiple-QTL model							20.9
Plant height							
QHt.cob-3A	08FW	*Xgwm674 - Xbarc356*	*Xgwm674*	75.8	8.82	-1.75	12.9
QHt.cob-3B.1		*wPt-3107 - wPt-9049*	*wPt-3107*	52.1	2.86	-1.09	5.1

† The four environments obtained from different moisture levels during the two growing seasons: Fort Collins limited irrigation (08FD), Fort Collins full irrigation (08FW), Greeley limited irrigation (09GD), and Greeley full irrigation (09GW).
‡ Average additive effect: Positive values indicate an increasing effect of Platte alleles and negative values indicate an increasing effect of CO940610 alleles.

Table 3.9. Continued.

QTL	Environment†	Marker interval	Nearest marker	Peak position (cM)	LOD	a‡	R^2 (%)
Plant height							
QHt.cob-5B	08FW	*Xgwm499 - Xgdm62*	*Xgwm499*	75.2	3.57	-1.16	5.5
QHt.cob-6A		*Xwmc256 - wPt-3069*	*Xwmc256*	93.1	9.11	-1.83	14.1
QHt.cob-7D.2		*Xbarc126 - Vrn-D3*	*Xbarc126*	33.4	10.09	1.98	16.4
Multiple-QTL model							46.3
QHt.cob-3A	09GW	*Xgwm674 - Xbarc356*	*Xgwm674*	75.8	7.01	-1.69	9.9
QHt.cob-4D.1		*Xwmc720 - wPt-0941*	*Xwmc720*	13.0	3.48	-1.18	4.8
QHt.cob-5B		*Xgwm540 - Xgwm499*	*Xgwm540*	71.2	2.71	-1.14	4.1
QHt.cob-6A		*Xwmc256 - wPt-3069*	*Xwmc256*	95.8	15.34	-2.76	26.1
QHt.cob-7D.2		*Vrn-D3 - Xgwm437*	*Vrn-D3*	43.3	10.08	2.19	16.6
Multiple-QTL model							50.6
QHt.cob-2B.1	08FD	*Xwmc154 - wPt-9402*	*Xwmc154*	52.7	3.09	-0.94	4.6
QHt.cob-3A		*Xgwm674 - Xbarc356*	*Xgwm674*	75.8	5.57	-1.23	7.6
QHt.cob-5B		*Xgdm62 - wPt-3661*	*Xgdm62*	87.0	5.72	-1.37	9.2
QHt.cob-6A		*Xwmc256 - wPt-3069*	*Xwmc256*	95.8	8.67	-1.65	13.6
QHt.cob-7D.2		*Vrn-D3 - Xgwm437*	*Vrn-D3*	41.3	11.98	2.04	20.6
Multiple-QTL model							50.2
QHt.cob-3A	09GD	*Xgwm674 - Xbarc356*	*Xbarc356*	76.9	2.88	-0.68	4.9
QHt.cob-5A		*Xgwm443 - Xwmc713*	*Xwmc713*	5.4	4.83	-0.89	8.4
QHt.cob-6A		*Xwmc256 - wPt-3069*	*Xwmc256*	85.1	3.17	-0.83	7.2
QHt.cob-7D.2		*wPt-0789 - Xbarc126*	*wPt-0789*	23.9	6.22	1.06	11.8
Multiple-QTL model							28.9
Spike length							
QSl.cob-1A.1	08FW	*Xbarc148 - Xbarc83*	*Xbarc83*	83.3	7.73	0.24	15.5
QSl.cob-1D		*Xcfd48 - Glu-D1*	*Glu-D1*	103.4	2.89	0.15	6.3

† The four environments obtained from different moisture levels during the two growing seasons: Fort Collins limited irrigation (08FD), Fort Collins full irrigation (08FW), Greeley limited irrigation (09GD), and Greeley full irrigation (09GW).
‡ Average additive effect: Positive values indicate an increasing effect of Platte alleles and negative values indicate an increasing effect of CO940610 alleles.

Table 3.9. Continued.

QTL	Environment†	Marker interval	Nearest marker	Peak position (cM)	LOD	a‡	R^2 (%)
Spike length							
QSl.cob-2B.1	08FW	*Xgwm429 - Xbarc55*	*Xgwm429*	97.0	5.82	-0.20	11.3
QSl.cob-3B.2		*Xgwm533 - Xgwm493*	*Xgwm533*	0.0	2.79	-0.13	4.4
QSl.cob-5B		*wPt-8114 - wPt-5168*	*wPt-8114*	241.1	2.68	0.14	5.3
QSl.cob-6B.1		*Xwmc397 - Xwmc182a*	*Xwmc182a*	54.8	2.87	0.13	4.8
QSl.cob-7A		*Xgwm60 - Xgwm219*	*Xgwm60*	0.0	2.74	0.13	4.4
QSl.cob-7D.2		*Xbarc126 - Vrn-D3*	*Vrn-D3*	31.4	5.41	0.17	8.3
Multiple-QTL model							46.3
QSl.cob-1A.1	09GW	*Xwmc312 - Glu-A1*	*Xwmc312*	94.4	2.77	0.14	5.7
QSl.cob-1D		*Xgwm337 - Xbarc169*	*Xgwm337*	73.8	3.44	0.17	7.6
QSl.cob-3D.1		*Xgwm314 - Xbarc125*	*Xgwm314*	10.0	4.72	-0.19	10.4
QSl.cob-7A		*Xwmc83 - wPt-3393*	*Xwmc83*	29.1	5.95	0.21	12.4
Unlinked locus		Chromosome 5D	Xgwm174		0.0007	0.15	6.2
Multiple-QTL model							28.0
QSl.cob-1A.1	08FD	*Xbarc148 - Xbarc83*	*Xbarc83*	81.3	6.69	0.16	12.5
QSl.cob-1D		*Xgwm337 - Xbarc169*	*Xgwm337*	73.8	2.82	0.10	5.1
Multiple-QTL model							26.1
QSl.cob-1A.1	09GD	*Xwmc312 - Glu-A1*	*Xwmc312*	92.1	3.05	0.09	5.6
QSl.cob-2B.1		*wPt-3561 - Xgwm429*	*Xgwm429*	85.2	5.19	-0.14	12.0
QSl.cob-4D.2		*Xwmc622 - Xcfd54a*	*Xwmc622*	0.0	3.28	0.10	5.6
QSl.cob-6B.1		*Xwmc397 - Xwmc182a*	*Xwmc182a*	54.8	3.15	0.10	5.8
QSl.cob-7A		*wPt-4796 - Xbarc49*	*Xbarc49*	47.3	2.67	0.01	4.7
QSl.cob-7B		*Xbarc278 - wPt-6498*	*wPt-6498*	23.8	4.41	0.13	8.4
Multiple-QTL model							38.7
Leaf length							
QLl.cob-2B.1	08FW	*Xwmc154 - wPt-9402*	*Xwmc154*	52.7	4.36	-0.27	9.6

† The four environments obtained from different moisture levels during the two growing seasons: Fort Collins limited irrigation (08FD), Fort Collins full irrigation (08FW), Greeley limited irrigation (09GD), and Greeley full irrigation (09GW).

‡ Average additive effect: Positive values indicate an increasing effect of Platte alleles and negative values indicate an increasing effect of CO940610 alleles. For unlinked loci, presumed chromosome locations are provided, and in the LOD column *P*-values from SAS PROC GLM are listed.

Table 3.9 Continued.

QTL	Environment†	Marker interval	Nearest marker	Peak position (cM)	LOD	a‡	R^2 (%)
Leaf length							
QLl.cob-6B.1	08FW	*wPt-2587 - wPt-6437*	*wPt-2587*	29.2	3.03	0.22	6.1
QLl.cob-7D.2		*Vrn-D3 - Xgwm437*	*Vrn-D3*	45.3	2.61	0.21	6.1
Multiple-QTL model							20.4
QLl.cob-1B.1	09GW	*Sr24 - Glu-B3*	*Sr24*	2.0	4.13	-0.15	8.8
QLl.cob-2B.1		*Xbarc55 - Xgwm374*	*Xgwm374*	105.7	2.78	-0.12	5.2
Multiple-QTL model							12.2
QLl.cob-1B.1	08FD	*Sr24 - Glu-B3*	*Sr24*	2.0	3.68	-0.15	7.1
QLl.cob-6B.1		*wPt-5596 - wPt-2218*	*wPt-2218*	22.7	3.88	0.16	8.4
Multiple-QTL model							20.7
QLl.cob-1B.1	09GD	*Sr24 - Glu-B3*	*Sr24*	0.0	5.45	-0.12	11.0
QLl.cob-2A		*Xwmc522 - Xgwm312*	*Xwmc522*	109.8	2.80	-0.11	8.8
Multiple-QTL model							12.2
Leaf width							
QLw.cob-2D.2	08FW	*Xgwm261 - Xgwm455*	*Xgwm261*	2.0	3.42	-0.02	7.4
QLw.cob-5B		*Xbarc216 - Xbarc4*	*Xbarc216*	51.6	2.64	0.02	5.5
Unlinked locus		Chromosome 5A	Xbarc319		0.0001	0.02	8.1
Multiple-QTL model							18.8
QLw.cob-1A.2	09GW	*wPt-7215 - wPt-6005*	*wPt-6005*	40.4	2.67	0.01	5.9
QLw.cob-1B.1		*Xcfd20a - Glu-B1*	*Gu-B1*	55.7	4.12	-0.02	9.2
QLw.cob-7D.2		*Xbarc126 - Vrn-D3*	*Vrn-D3*	55.7	2.55	0.01	5.1
Unlinked locus		Chromosome 5A	Xbarc319		0.0001	0.02	8.9
Multiple-QTL model							19.3
QLw.cob-1B.1	08FD	*Xbarc8 - Xbarc302*	*Xbarc302*	36.1	2.90	-0.02	7.1
QLw.cob-2D.2		*Xgwm261 - Xgwm455*	*Xgwm261*	0.0	4.59	-0.02	9.5
QLw.cob-4A.1		*Xgwm610 - Xwmc48*	*Xwmc48*	8.2	4.09	0.02	7.6
Unlinked locus		Chromosome 5A	Xbarc319		0.0001	0.02	8.9
Multiple-QTL model							31.6

† The four environments obtained from different moisture levels during the two growing seasons: Fort Collins limited irrigation (08FD), Fort Collins full irrigation (08FW), Greeley limited irrigation (09GD), and Greeley full irrigation (09GW).
‡ Average additive effect: Positive values indicate an increasing effect of Platte alleles and negative values indicate an increasing effect of CO940610 alleles.
For unlinked loci, presumed chromosome locations are provided, and in the LOD column *P*-values from SAS PROC GLM are listed.

Table 3.9. Continued.

QTL	Environment†	Marker interval	Nearest marker	Peak position (cM)	LOD	a‡	R^2 (%)
Kernel weight							
QKw.cob-1B.1	08FW	*Sr24 - Glu-B3*	*Sr24*	0.0	4.46	-0.17	6.7
QKw.cob-2B.1		*Xgwm429 - Xbarc55*	*Xgwm429*	95.0	7.46	0.25	13.9
QKw.cob-2D.1		*wPt-0298 - wPt-4413*	*wPt-4413*	52.5	4.23	-0.21	10.0
QKw.cob-6A		*Xwmc256 - wPt-3069*	*Xwmc256*	93.8	5.42	-0.19	9.2
QKw.cob-7D.2		*Xbarc126 - Vrn-D3*	*Vrn-D3*	39.3	6.01	-0.22	11.1
Multiple-QTL model							42.6
QKw.cob-1A.1	09GW	*wPt-2872 - wPt-6654*	*wPt-2872*	71.9	3.84	0.16	8.0
QKw.cob-1D		*Xgwm337 - Xbarc169*	*Xgwm337*	73.8	2.70	0.12	4.2
QKw.cob-2B.1		*wPt-3561 - Xgwm429*	*wPt-3561*	85.2	4.56	0.18	8.9
QKw.cob-2D.1		*wPt-4413 - wPt-0638*	*wPt-4413*	56.5	3.41	-0.16	7.3
QKw.cob-6A		*Xwmc256 - wPt-3069*	*Xwmc256*	91.1	8.29	-0.24	16.0
QKw.cob-6B.1		*wPt-8721 - wPt-3060*	*wPt-8721*	83.3	5.17	0.16	9.6
Multiple-QTL model							35.2
QKw.cob-2B.1	08FD	*wPt-0705 - wPt-9857*	*wPt-0705*	60.6	6.97	0.19	11.5
QKw.cob-2D.1		*wPt-0298 - wPt-4413*	*wPt-0298*	46.5	2.77	-0.14	6.1
QKw.cob-2D.2		*Xgdm35 - Xbarc95*	*Xgdm35*	8.1	2.89	-0.12	4.5
QKw.cob-3B.1		*wPt-9310 - wPt-3107*	*wPt-9310*	23.8	5.57	0.19	11.0
QKw.cob-6A		*Xwmc256 - wPt-3069*	*Xwmc256*	93.8	7.58	-0.19	12.5
Multiple-QTL model							40.6
QKw.cob-1A.1	09GD	*Xbarc148 - Xbarc83*	*Xbarc148*	83.3	5.17	0.16	9.6
QKw.cob-1B.1		*Glu-B1 - wPt-0705*	*wPt-0705*	57.7	4.25	-0.14	7.8
QKw.cob-2B.1		*Xbarc55 - Xgwm374*	*Xgwm374*	106.5	4.55	0.10	3.9
QKw.cob-3B.1		*Xgwm285 - wPt-9310*	*Xgwm285*	10.3	5.52	0.15	9.5
QKw.cob-6A		*Xwmc256 - wPt-3069*	*Xwmc256*	93.8	5.61	-0.16	9.6
Multiple-QTL model							39.6

† The four environments obtained from different moisture levels during the two growing seasons: Fort Collins limited irrigation (08FD), Fort Collins full irrigation (08FW), Greeley limited irrigation (09GD), and Greeley full irrigation (09GW).
‡ Average additive effect: Positive values indicate an increasing effect of Platte alleles and negative values indicate an increasing effect of CO940610 alleles.

Table 3.9. Continued.

QTL	Environment†	Marker interval	Nearest marker	Peak position (cM)	LOD	a‡	R^2 (%)
Above ground biomass							
QAgb.cob-2D.1	08FW	*wPt-4413 - wPt-0638*	*wPt-4413*	63.8	3.18	-2.34	6.8
QAgb.cob-5A		*Xbarc165 - Xbarc360*	*Xbarc360*	53.9	3.25	2.29	6.5
QAgb.cob-7D.2		*wPt-4555 - wPt-0789*	*wPt-0789*	16.0	3.46	2.57	8.2
Unlinked locus		Chromosome 6D	wPt-6661		0.0008	-2.55	6.7
Multiple-QTL model							23.4
QAgb.cob-1A.1	09GW	*wPt-7872 - wPt-3462*	*wPt-3462*	31.0	2.62	-3.96	5.6
QAgb.cob-6A		*Xwmc256 - wPt-3069*	*Xwmc256*	93.8	3.26	-4.35	6.7
Multiple-QTL model							12.8
QAgb.cob-4D.2	08FD	*Xwmc622- Xcfd54a*	*Xcfd54a*	63.8	3.11	-2.05	6.6
QAgb.cob-2D.1	09GD	*wPt-0638 - wPt-2544*	*wPt-0638*	72.0	3.59	-7.83	8.2
QAgb.cob-5B		*Xgwm499 - Xgdm62*	*Xgdm62*	81.0	3.07	-6.78	6.2
Multiple-QTL model							12.5
Harvest index							
QHi.cob-2D.2	08FW	*Xgdm35 - Xbarc95*	*Xgdm35*	8.1	3.07	-0.02	6.3
QHi.cob-6B.1		*wPt-7623 - wPt-7127*	*wPt-7623*	29.2	3.39	0.02	7.4
Multiple-QTL model							8.4
QHi.cob-2D.2	08FD	*Xgwm261 - Xgwm455*	*Xgwm261*	0.0	2.98	-0.01	6.5
QHi.cob-1A.1	09GD	*Xwmc312 - Glu-A1*	*Glu-A1*	94.1	3.28	-0.01	6.7
QHi.cob-1B.1		*Xcfd20a - Glu-B1*	*Glu-B1*	53.7	2.79	-0.01	5.1
QHi.cob-2B.1		*Xgwm374 - Xbarc349a*	*Xbarc349a*	110.5	4.16	0.01	8.7
QHi.cob-2B.2		*wPt-3632 - wPt-2397*	*wPt-2397*	18.3	2.79	-0.01	6.1
QHi.cob-3A		*Xwmc532 - Xwmc50*	*Xwmc532*	52.9	2.96	0.01	7.9
Multiple-QTL model							25.6

† The four environments obtained from different moisture levels during the two growing seasons: Fort Collins limited irrigation (08FD), Fort Collins full irrigation (08FW), Greeley limited irrigation (09GD), and Greeley full irrigation (09GW).
‡ Average additive effect: Positive values indicate an increasing effect of Platte alleles and negative values indicate an increasing effect of CO940610 alleles. For unlinked loci, presumed chromosome locations are provided, and in the LOD column *P*-values from SAS PROC GLM are listed.

Table 3.9. Continued.

QTL	Environment†	Marker interval	Nearest marker	Peak position (cM)	LOD	a‡	R^2 (%)
One-meter grain weight							
Q1mg.cob-5A	08FW	*Xbarc165 - Xbarc360*	*Xbarc360*	53.9	3.83	2.06	8.2
Q1mg.cob-2B.1	09GW	*wPt-9402 - wPt-3561*	*wPt-3561*	73.2	3.30	3.19	7.8
Q1mg.cob-4D.2	08FD	*Xcfd54a - Xgwm194*	*Xgwm194*	10.2	2.76	-1.48	6.6
Q1mg.cob-2B.1	09GD	*Xgwm374 - Xbarc349a*	*Xbarc349a*	110.5	2.91	3.48	5.5
Q1mg.cob-2D.1		*wPt-0638 - wPt-2544*	*wPt-2544*	72.0	4.27	-4.35	9.1
Q1mg.cob-5B		*Xbarc4 - Xgwm540*	*Xgwm540*	56.5	3.50	-3.72	6.5
Q1mg.cob-7B		*Xbarc278 - wPt-6498*	*Xbarc278*	21.2	3.88	-3.90	7.3
Multiple-QTL model							21.6
Grain yield							
QGy.cob-5A	08FW	*Xbarc165 - Xbarc360*	*Xbarc360*	52.8	3.56	109.92	8.0
Unlinked locus		Chromosome 7B	wPt-8920		0.0001	-128.50	9.6
Multiple-QTL model							17.4
QGy.cob-5A	09GW	*Xbarc165 - Xbarc360*	*Xbarc360*	52.8	5.32	157.81	11.3
QGy.cob-2D.1	08FD	*wPt-0638 - wPt-2544*	*wPt-2544*	72.0	3.84	-100.39	8.8
QGy.cob-5A		*Xbarc165 - Xbarc360*	*Xbarc360*	52.8	3.54	93.72	7.7
Unlinked locus		Chromosome 7B	wPt-8920		0.0005	-332.51	9.0
Multiple-QTL model							24.4
QGy.cob-5A	09GD	*Xbarc165 - Xbarc360*	*Xbarc360*	52.8	4.52	166.23	8.2
QGy.cob-5B		*Xbarc4 - Xgwm540*	*Xgwm540*	56.5	6.60	-174.23	12.1
QGy.cob-7B		*wPt-7602 - Xwmc76*	*Xwmc76*	2.01	4.70	-156.99	9.8
Unlinked locus		Chromosome 7B	wPt-8920		0.0001	-142.92	7.3
Multiple-QTL model							31.3
Pre-harvest sprouting							
QPhs.cob-4A.1	08FW	*Xwmc420 - Xgwm165*	*Xgwm165*	17.7	5.73	0.03	13.3
QPhs.cob-4D.1		*wPt-0941 - wPt-5809*	*wPt-5809*	25.0	4.53	0.03	12.2
Unlinked locus		Chromosome 5B or 7A	Xcfd20b		0.001	0.02	4.0
Multiple-QTL model							22.8
QPhs.cob-2B.1	09GW	*Xgwm374 - Xbarc349a*	*Xbarc349a*	110.5	3.34	0.01	6.5

† The four environments obtained from different moisture levels during the two growing seasons: Fort Collins limited irrigation (08FD), Fort Collins full irrigation (08FW), Greeley limited irrigation (09GD), and Greeley full irrigation (09GW).

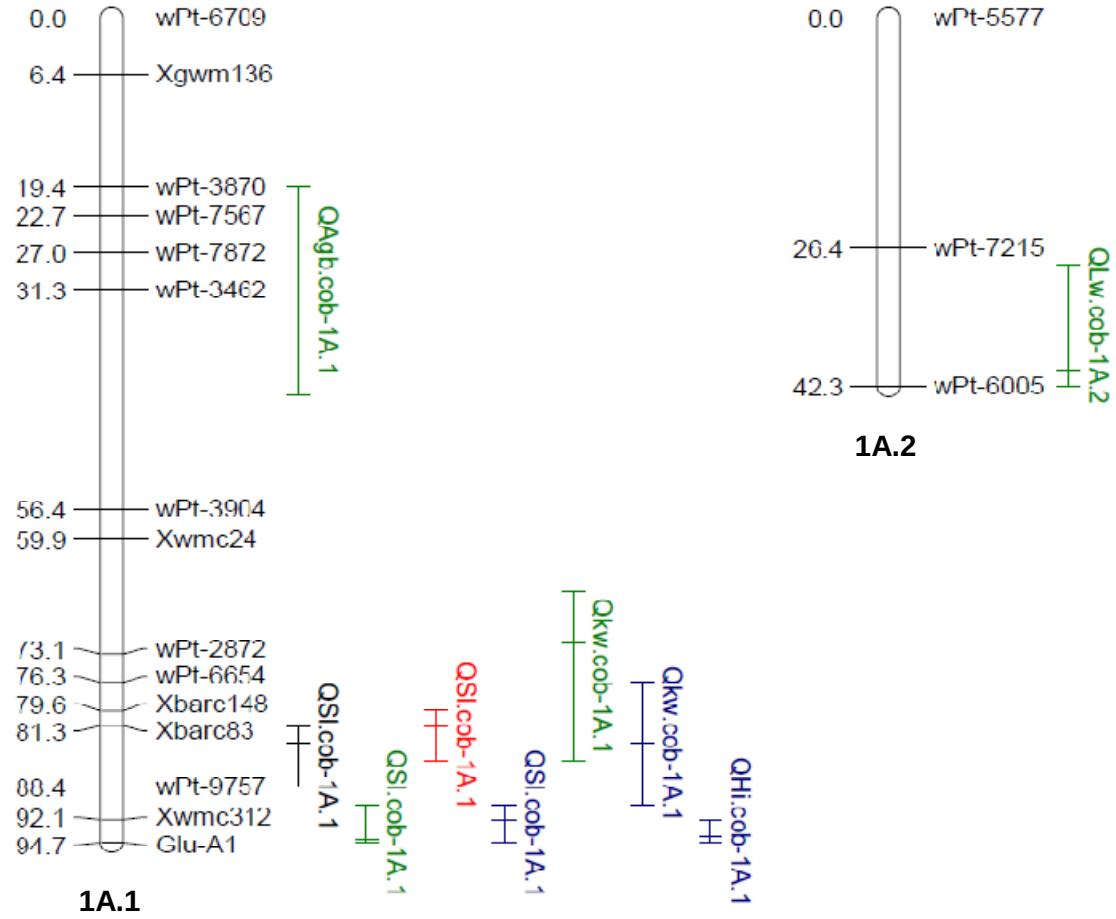
‡ Average additive effect: Positive values indicate an increasing effect of Platte alleles and negative values indicate an increasing effect of CO940610 alleles. For unlinked loci, presumed chromosome locations are provided, and in the LOD column *P*-values from SAS PROC GLM are listed.

Table 3.9. Continued.

QTL	Environment†	Marker interval	Nearest marker	Peak position (cM)	LOD	a‡	R^2 (%)
Normalized Difference Vegetation Index							
QNdvi.cob-3A	09GW	*wPt-2866 - wPt-1688*	*wPt-1688*	23.0	2.78	0.01	5.4
QNdvi.cob-6A		*Xwmc256 - wPt-3069*	*Xwmc256*	91.1	3.16	-0.01	7.3
Multiple-QTL model							13.9
QNdvi.cob-4B	09GD	*Xcfd71 - Xwmc720*	*Xwmc720*	39.4	2.69	0.02	5.6
Drought susceptibility index							
QDsi.cob-5B	09 GD-GW	*Xbarc4 - Xgwm540*	*Xgwm540*	50.5	5.95	0.17	11.0
QDsi.cob-7B	09 GD-GW	*wPt-7602 - Xwmc76*	*wPt-7602*	2.60	4.38	0.15	9.8
Multiple-QTL model							21.9

† The four environments obtained from different moisture levels during the two growing seasons: Fort Collins limited irrigation (08FD), Fort Collins full irrigation (08FW), Greeley limited irrigation (09GD), and Greeley full irrigation (09GW).
‡ Average additive effect: Positive values indicate an increasing effect of Platte alleles and negative values indicate an increasing effect of CO940610 alleles.

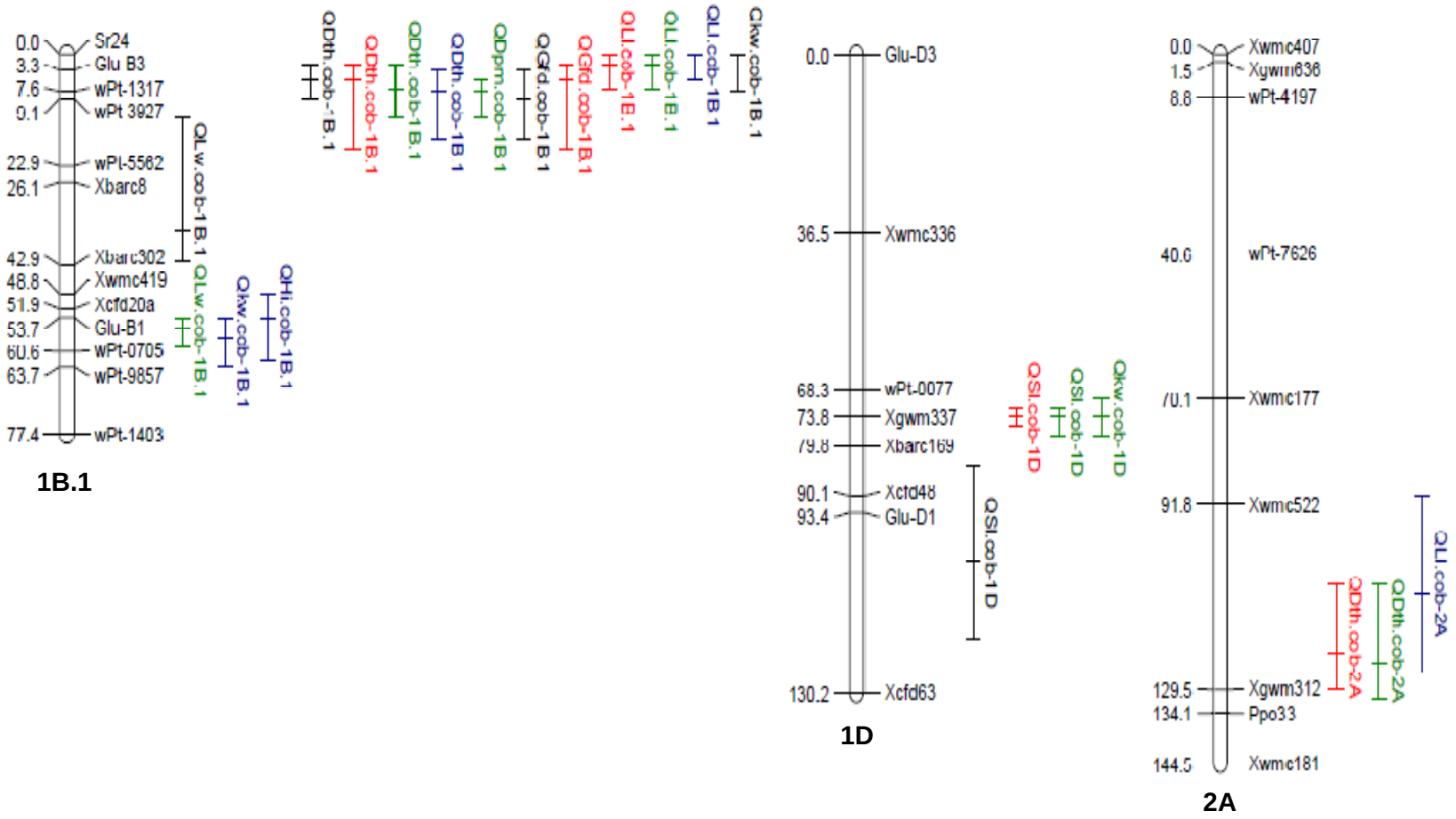
Fig. 3.1 Molecular marker linkage map showing QTL intervals associated with various agronomic traits in the CO940610/Platte population. Genetic distances (cM) are to the left of the linkage group and locus names are listed to the right. Different colors of QTL names indicate the environments in which they were detected†. The 1-LOD support intervals for QTL locations were calculated by finding the points on either side of the estimated QTL position central bar within an interval that corresponded to a decrease in LOD score of 1 unit.



Dth, days to heading; Dpm, days to physiological maturity; Gfd, grain filling duration; Gfr, grain filling rate; Ht, plant height; Ll, leaf length; Lw, leaf width; Sl, spike length; Agb, above ground biomass, 1mg, one meter grain weight; Hi, harvest index; Gy, grain yield; Kw, kernel weight; Fls, flag leaf senescence; Ndvi, Normalized difference vegetation index; Phs, pre-harvest sprouting; Dsi, drought susceptibility index

† Fort Collins full irrigation
Fort Collins limited irrigation
Greeley full irrigation
Greeley limited irrigation

Fig. 3.1 Continued.



Dth, days to heading; Dpm, days to physiological maturity; Gfd, grain filling duration; Gfr, grain filling rate; Ht, plant height; Ll, leaf length; Lw, leaf width; Sl, spike length; Agb, above ground biomass, 1mg, one meter grain weight; Hi, harvest index; Gy, grain yield; Kw, kernel weight; Fls, flag leaf senescence; Ndvi, Normalized difference vegetation index; Phs, pre-harvest sprouting; Dsi, drought susceptibility index

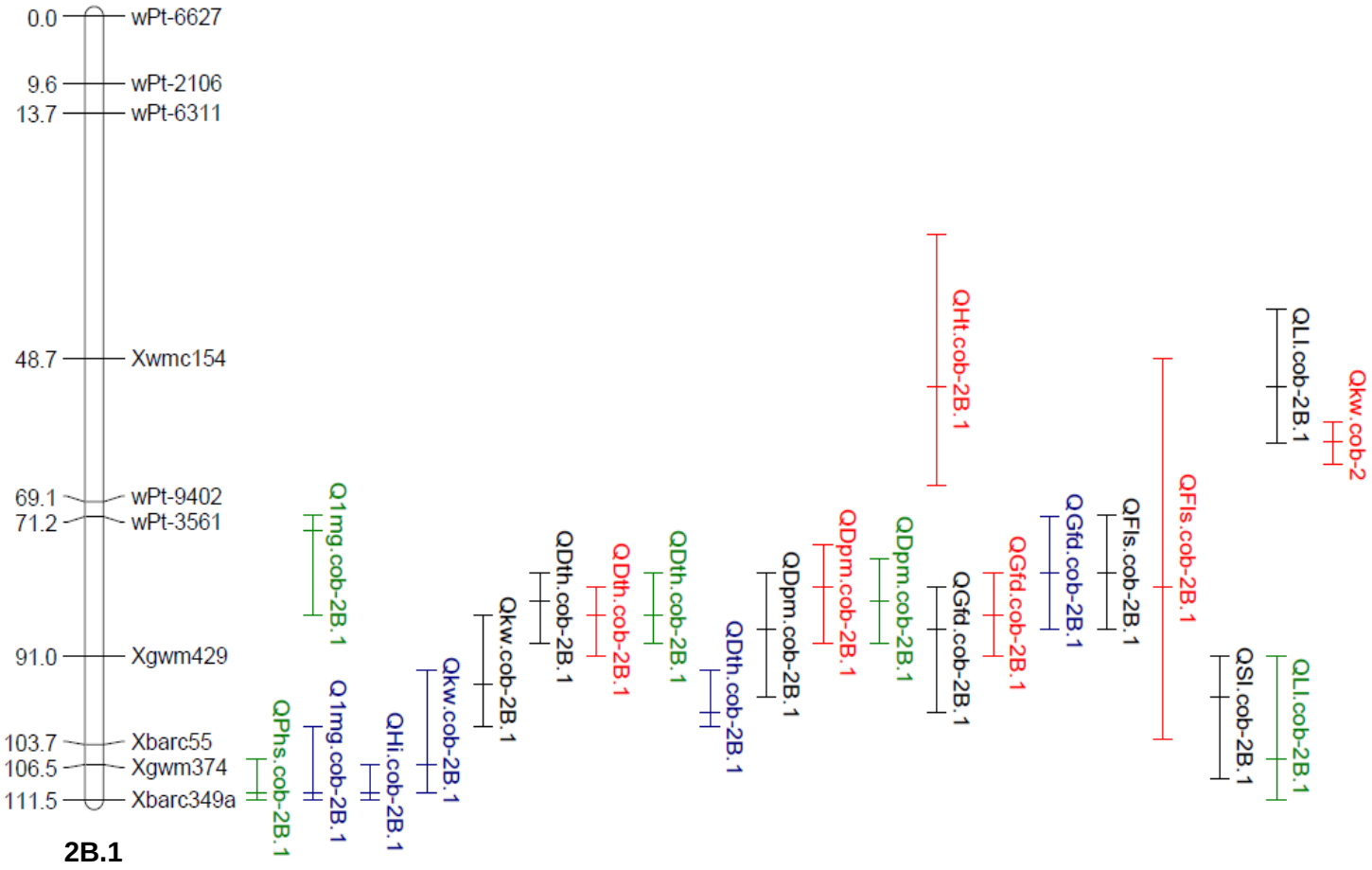
† Fort Collins full irrigation

Fort Collins limited irrigation

Greeley full irrigation

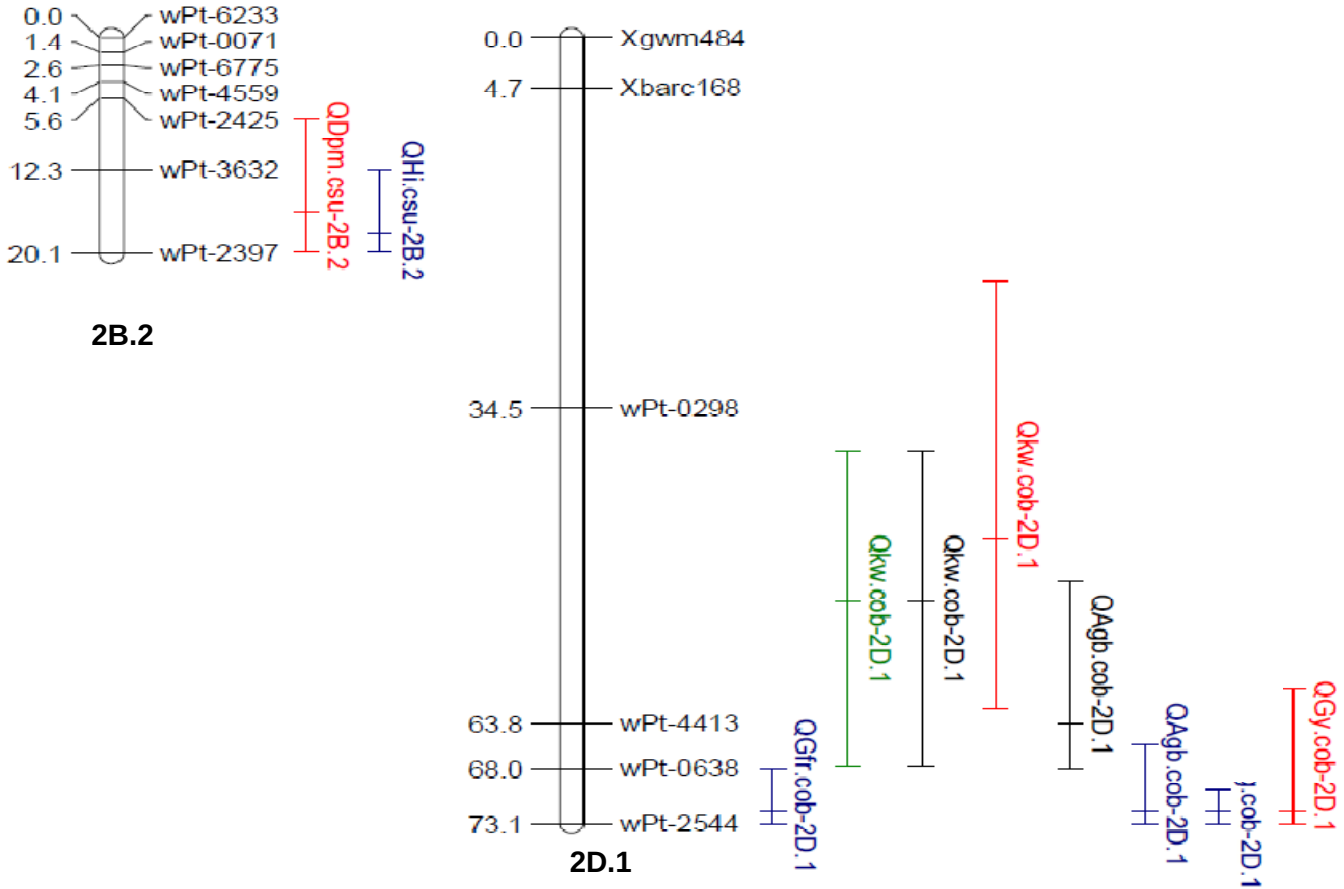
Greeley limited irrigation

Fig. 3.1 Continued.



Dth, days to heading; Dpm, days to physiological maturity; Gfd, grain filling duration; Gfr, grain filling rate; Ht, plant height; Ll, leaf length; Lw, leaf width; Sl, spike length; Agb, above ground biomass, 1mg, one meter grain weight; Hi, harvest index; Gy, grain yield; Kw, kernel weight; Fls, flag leaf senescence; Ndvi, Normalized difference vegetation index; Phs, pre-harvest sprouting; Dsi, drought susceptibility index

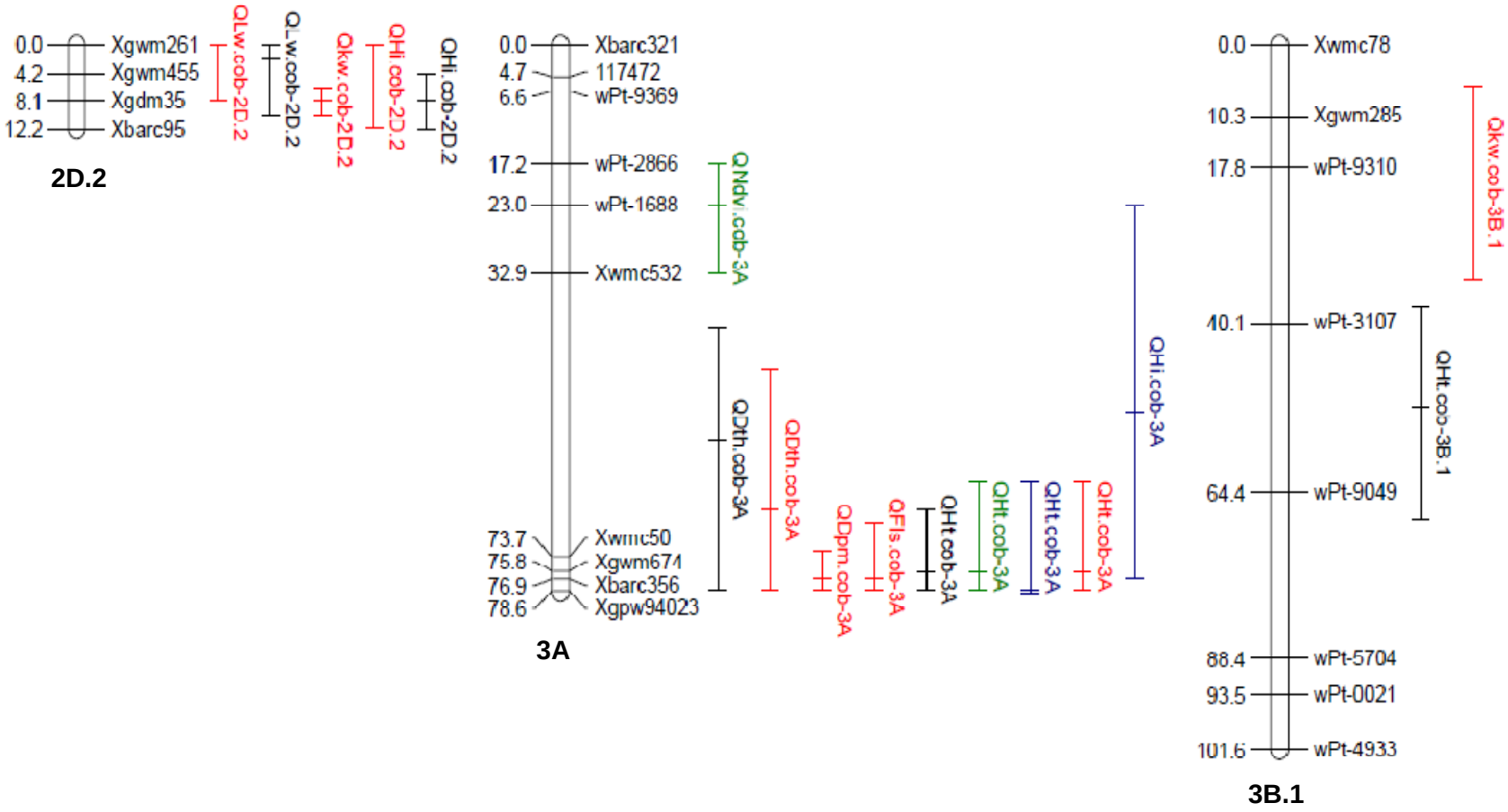
Fig. 3.1 Continued.



Dth, days to heading; Dpm, days to physiological maturity; Gfd, grain filling duration; Gfr, grain filling rate; Ht, plant height; Ll, leaf length; Lw, leaf width; Sl, spike length; Agb, above ground biomass, 1mg, one meter grain weight; Hi, harvest index; Gy, grain yield; Kw, kernel weight; Fls, flag leaf senescence; Ndvi, Normalized difference vegetation index; Phs, pre-harvest sprouting; Dsi, drought susceptibility index

† Fort Collins full irrigation
Fort Collins limited irrigation
Greeley full irrigation
Greeley limited irrigation

Fig. 3.1 Continued.



Dth, days to heading; Dpm, days to physiological maturity; Gfd, grain filling duration; Gfr, grain filling rate; Ht, plant height; Ll, leaf length; Lw, leaf width; Sl, spike length; Agb, above ground biomass, 1mg, one meter grain weight; Hi, harvest index; Gy, grain yield; Kw, kernel weight; Fls, flag leaf senescence; Ndvi, Normalized difference vegetation index; Phs, pre-harvest sprouting; Dsi, drought susceptibility index

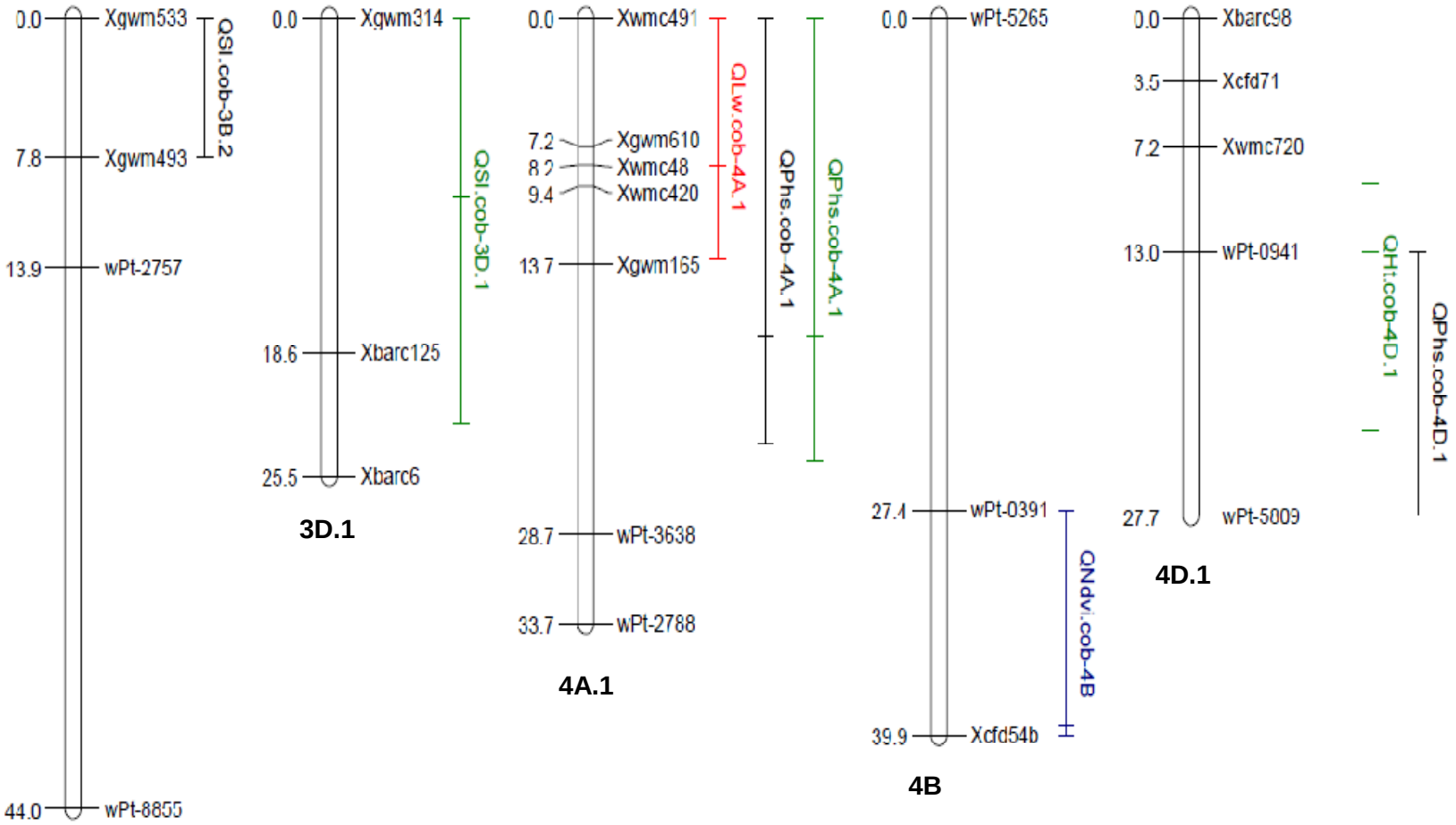
† Fort Collins full irrigation

Fort Collins limited irrigation

Greeley full irrigation

Greeley limited irrigation

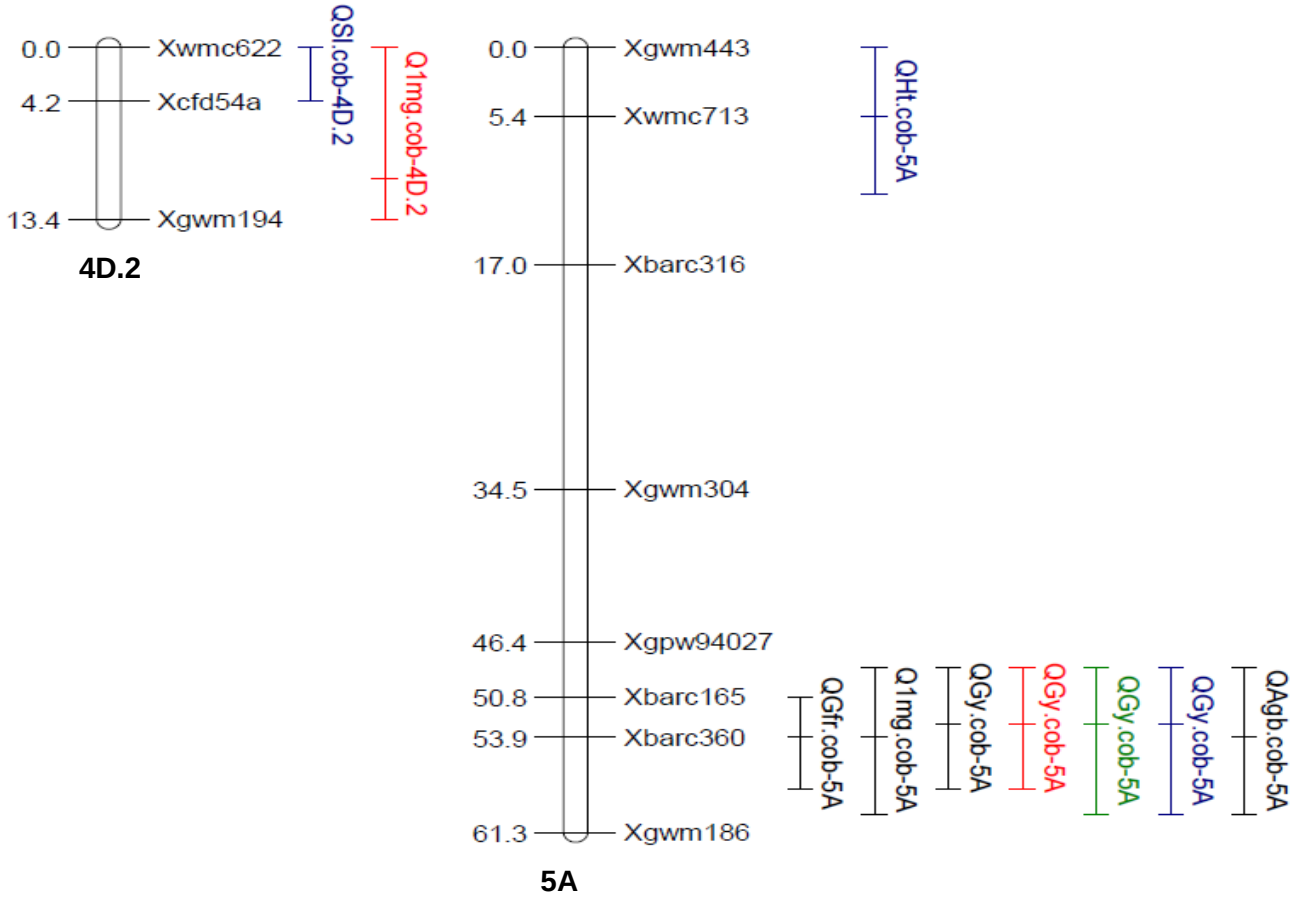
Fig. 3.1 Continued.



Dth, days to heading; Dpm, days to physiological maturity; Gfd, grain filling duration; Gfr, grain filling rate; Ht, plant height; Ll, leaf length; Lw, leaf width; Sl, spike length; Agb, above ground biomass, 1mg, one meter grain weight; Hi, harvest index; Gy, grain yield; Kw, kernel weight; Fls, flag leaf senescence; Ndvi, Normalized difference vegetation index; Phs, pre-harvest sprouting; Dsi, drought susceptibility index

† Fort Collins full irrigation
Fort Collins limited irrigation
Greeley full irrigation
Greeley limited irrigation

Fig. 3.1 Continued.



Dth, days to heading; Dpm, days to physiological maturity; Gfd, grain filling duration; Gfr, grain filling rate; Ht, plant height; Ll, leaf length; Lw, leaf width; Sl, spike length; Agb, above ground biomass, 1mg, one meter grain weight; Hi, harvest index; Gy, grain yield; Kw, kernel weight; Fls, flag leaf senescence; Ndvi, Normalized difference vegetation index; Phs, pre-harvest sprouting; Dsi, drought susceptibility index

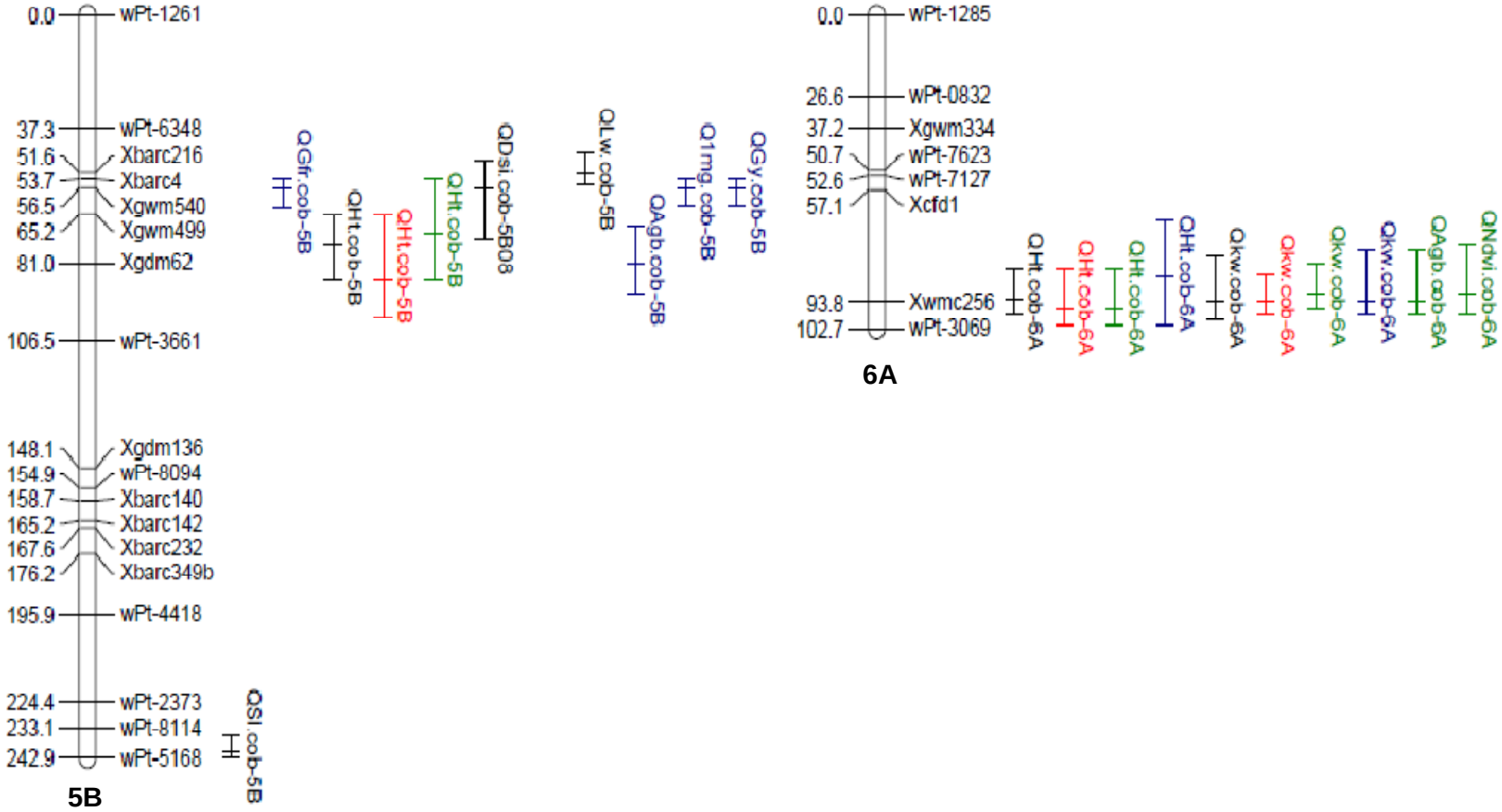
† Fort Collins full irrigation

Fort Collins limited irrigation

Greeley full irrigation

Greeley limited irrigation

Fig. 3.1 Continued.



Dth, days to heading; Dpm, days to physiological maturity; Gfd, grain filling duration; Gfr, grain filling rate; Ht, plant height; Ll, leaf length; Lw, leaf width; Sl, spike length; Agb, above ground biomass, 1mg, one meter grain weight; Hi, harvest index; Gy, grain yield; Kw, kernel weight; Fls, flag leaf senescence; Ndvi, Normalized difference vegetation index; Phs, pre-harvest sprouting; Dsi, drought susceptibility index

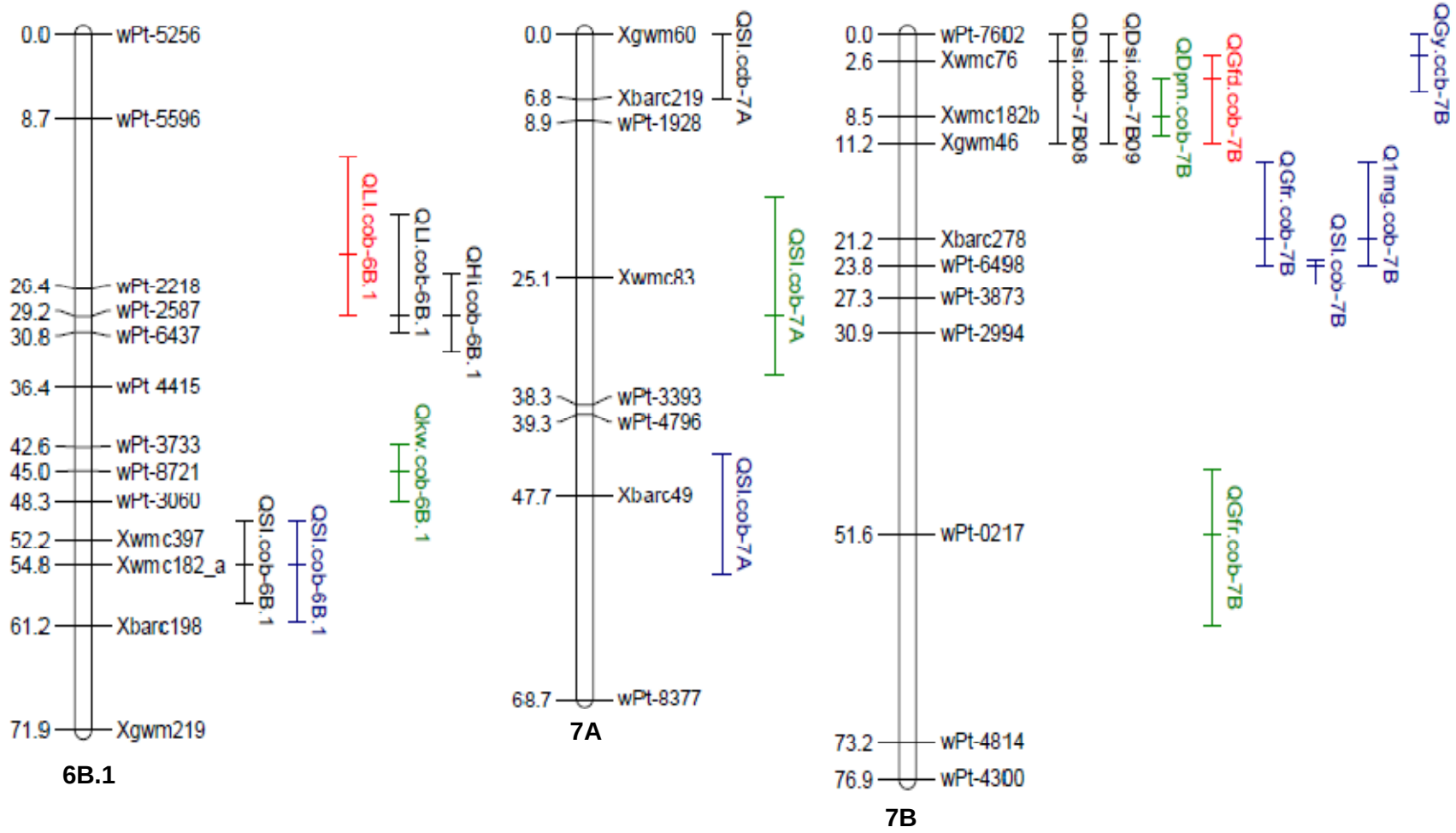
† Fort Collins full irrigation

Fort Collins limited irrigation

Greeley full irrigation

Greeley limited irrigation

Fig. 3.1 Continued.



Dth, days to heading; Dpm, days to physiological maturity; Gfd, grain filling duration; Gfr, grain filling rate; Ht, plant height; Ll, leaf length; Lw, leaf width; Sl, spike length; Agb, above ground biomass, 1mg, one meter grain weight; Hi, harvest index; Gy, grain yield; Kw, kernel weight; Fls, flag leaf senescence; Ndvi, Normalized difference vegetation index; Phs, pre-harvest sprouting; Dsi, drought susceptibility index

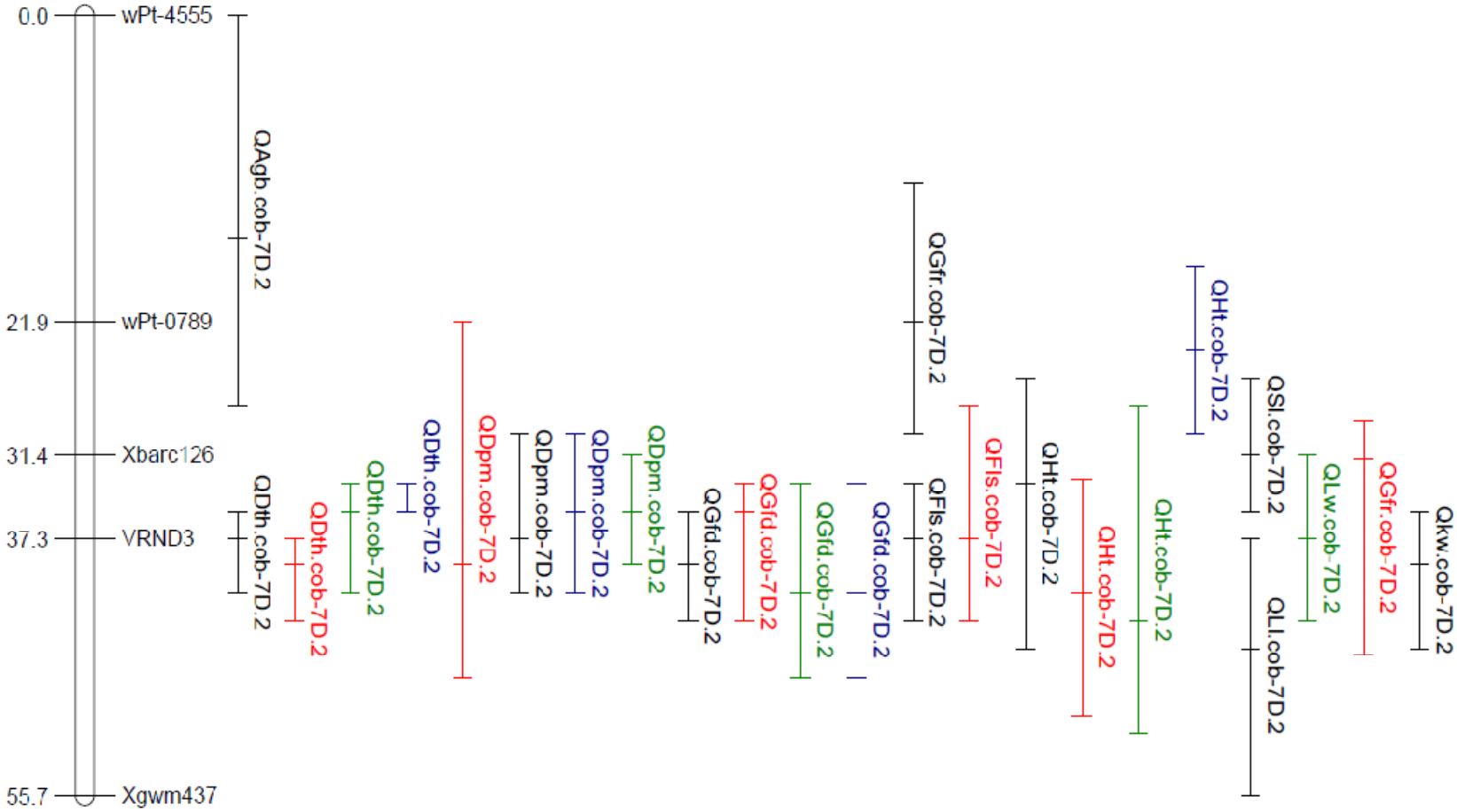
† Fort Collins full irrigation

Fort Collins limited irrigation

Greeley full irrigation

Greeley limited irrigation

Fig. 3.1 Continued.



7D.2

Dth, days to heading; Dpm, days to physiological maturity; Gfd, grain filling duration; Gfr, grain filling rate; Ht, plant height; Ll, leaf length; Lw, leaf width; Sl, spike length; Agb, above ground biomass, 1mg, one meter grain weight; Hi, harvest index; Gy, grain yield; Tkw, kernel weight; Fls, flag leaf senescence; Ndvi, Normalized difference vegetation index; Phs, pre-harvest sprouting; Dsi, drought susceptibility index

† Fort Collins full irrigation

Fort Collins limited irrigation

Greeley full irrigation

Greeley limited irrigation

the full and limited irrigation treatments. The QTL distribution in homoeologous chromosomes for Group 1 through Group 7 was 23 (17.9%), 38 (29.7%), 12 (9.4%), 7 (5.5%), 15 (11.7%), 10 (7.8%), and 23 (17.9%), respectively. QTL were distributed among 24 of the 31 linkage groups. Only groups 1B.2, 3D.2, 4A.2, 5D, 6B.2, 6D, and 7D.1 did not have LOD scores that reached the significance permutation-based threshold.

3.2.4.1. Phenological parameters

Five phenological parameters were measured in this population: days to heading (Dth), days to physiological maturity (Dpm), grain filling duration (Gfd), grain filling rate (Gfr), and flag leaf senescence (Fls). Thirty-four QTL were detected for the phenological parameters with major and minor effects (Table 3.9, Fig. 3.1). Clusters of phenological parameter QTL were found in linkage groups 1B.1, 2B.1, and 7D.2. Marker intervals *wPt-3561–Xgwm429* (2B.1) and *Xbarc126–VRND3* (7D.2) were significantly associated with many phenological parameters (Figs. 3.2 and 3.3). Another cluster of significant QTL, identified on chromosome 1B.1 within the interval *Glu-B3–wPt-1317*, influenced some phenological parameters but was inconsistent among environments.

3.2.4.1.1. Days to heading (Dth)

Seven QTL were detected with minor and major effects under different moisture levels, individually explaining 3.7 to 39.3% of the phenotypic variation (Table 3.7, Fig. 3.1). A major QTL, designated *QDth.cob-7D.2,* was detected on chromosome 7D.2 and was consistent over all environments. This QTL was located within the interval *Xbarc126-Vrn-D3* and accounted for 32.1 to 42.6% of the phenotypic variation. Platte contributed the allele at *QDth.cob-7D.2,* which had positive average additive effects of 1.03 to 1.51 days. Another major QTL, designated *QDth.cob-2B.1*, was detected on chromosome 2B.1 in all environments. This QTL was located within the intervals *wPt-3561-Xgwm429* or Xgwm429-Xbarc55, and accounted for 21.5 to 24.7% of phenotypic

variation. CO94610 contributed the allele at *QDth.cob-2B.1,* which increased heading by 0.85 to 1.14 days. A minor QTL, designated *QDth.cob-1B.1*, was detected on chromosome 1B.1 in all environments and explained 2.7 to 6.7% of the phenotypic variation. Less consistent or environment-specific chromosome regions associated with Dth were identified on linkage groups 2A and 3A.

3.2.4.1.2. Days to physiological maturity (Dpm)

Eight QTL were detected under different moisture levels that individually explained 6.5 to 21.7% of the phenotypic variation (Table 3.9, Fig. 3.1). As expected, the QTL location and effects were very similar to results for Dth. A major QTL, designated *QDpm.cob-7D.2*, was identified on chromosome 7D.2 and was consistent over all environments, with Platte contributing the positive allele in all cases. An intermediate effect QTL on chromosome 2B.1 was detected in three environments (08FW, 09GW, and 08FD) within interval *wPt-3561-Xgwm429*. The percentage of phenotypic variation explained by this individual QTL ranged from 15.2 to 18.0%. Other QTL were detected on linkage groups 1B.1, 3A, and 7B, but were inconsistent among environments.

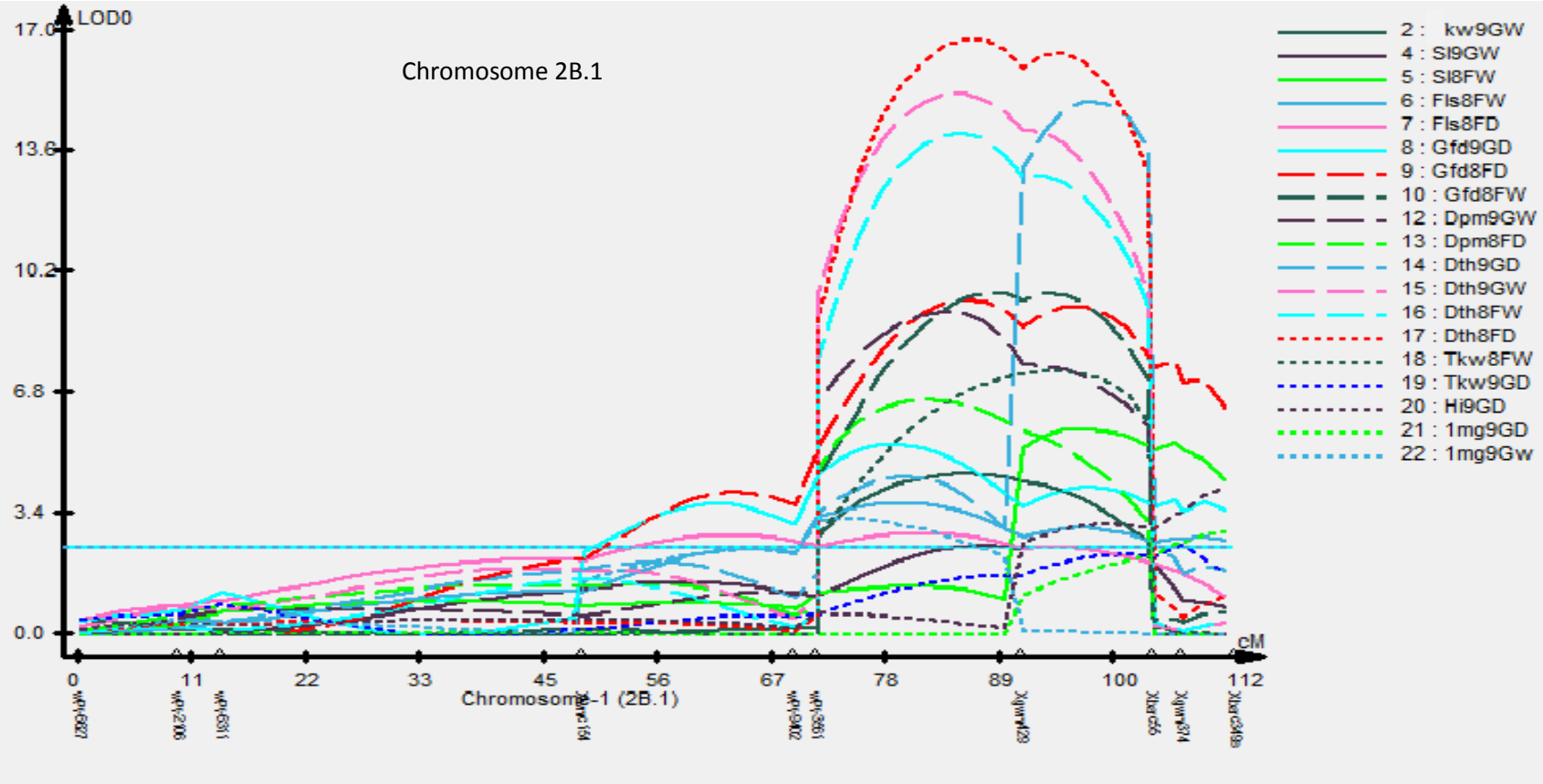
3.2.4.1.3. Grain filling duration (Gfd)

Seven QTL with major and minor effects were detected under different moisture levels and individually explained 3.7 to 37.3% of the phenotypic variation (Table 3.9, Fig. 3.1). A major QTL, designated *QGfd.cob-7D.2*, was identified on chromosome 7D.2 within interval *Xbarc126-Vrn-D3* and was consistent over all environments. CO940610 contributed the alleles that had the positive effect on Gfd in all environments, and the QTL accounted for 15.5 to 37.3% of phenotypic variation. Another moderate-effect QTL, designated *QGfd.cob-2B.1*, was identified on chromosome 2B.1, in three environments.

3.2.4.1.4. Grain filling rate (Gfr)

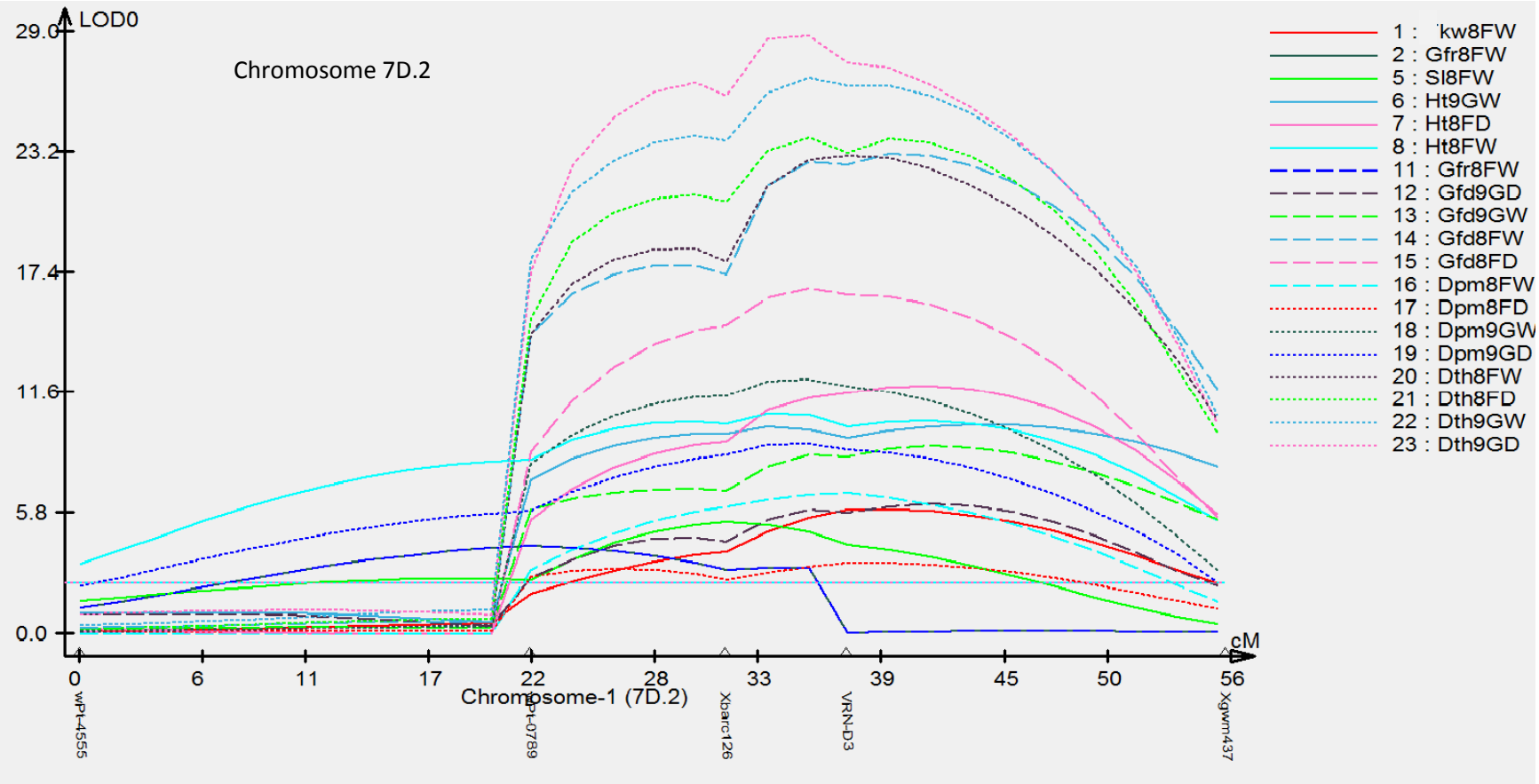
Seven QTL with intermediate effects were detected in different environments and individually explained 6.0 to 9.6% of the phenotypic variation (Table 3.9, Fig. 3.1).

Fig. 3.2 QTL Cartographer LOD curves on chromosome 2B.1 for agronomic traits of CO940610/Platte population under two irrigation levels in the 2007-08 and 2008-09 growing seasons†.



† The first two or three letters of each LOD curve label indicate trait name: Kw, kernel weight; Sl, spike length; Fls, flag leaf senescence; Gfd, grain filling duration; Dpm, days to physiological maturity; Dth, days to heading; Hi, harvest index; 1mg, one-meter grain weight. The last portion of the label indicates environment: 8FD, Fort Collins Dry, 2008; 8FW, Fort Collins Wet, 2008; 9GD, Greeley Dry, 2009; 9GW, Greeley Wet 2009.

Fig 3.3 QTL Cartographer LOD curves on chromosome 7D.2 for agronomic traits of CO940610/Platte population under two irrigation levels in the 2007-08 and 2008-09 growing seasons



† The first two or three letters of each LOD curve label indicate trait name: Kw, kernel weight; Gfr, grain filling rate; Sl, spike length; Ht, plant height; Gfd, grain filling duration; Dpm, days to physiological maturity; Dth, days to heading. The last portion of the label indicates environment: 8FD, Fort Collins Dry, 2008; 8FW, Fort Collins Wet, 2008; 9GD, Greeley Dry, 2009; 9GW, Greeley Wet 2009.

All QTL were inconsistent among environments, except on chromosome 7B, where QTL were detected in two environments (09GW and 09GD). However, the QTL had different flanking markers and relatively low LOD scores of 2.63 and 3.32.

3.2.4.1.5. Flag leaf senescence (Fls)

Fls was only measured in 2008, and the results revealed a total of three minor QTL. Two QTL, designated *QFls.cob-2B.1* and *QFls.cob-7D.2*, were detected in both moisture treatments and individually explained 6.5 to 9.5% of the phenotypic variation (Table 3.9, Fig. 3.1). The 7D.2 QTL was located within the interval flanked by *Xbarc126* and *Vrn-D3.* Another QTL was detected on chromosome 3A in 08FD with a LOD score of 5.6.

3.2.4.2. Morphological traits

Four morphological traits were measured in this population: plant height (Ht), spike length (Sl), leaf length (Ll), and leaf width (Lw). Forty-four QTL with major and minor effects were detected for morphological traits in the four environments (Table 3.9, Fig. 3.1). QTL clusters of morphological traits were found on linkage groups 5B and 7D.2. Marker interval *Xbarc126-Vrn-D3* on chromosome 7D.2 was significantly associated with some morphological traits, but was inconsistent among environments.

3.2.4.2.1. Plant height (Ht)

Ten QTL with major and minor effects were detected under different moisture levels and individually explained 3.7 to 26.1 % of the phenotypic variation (Table 3.9, Fig. 3.1). Three QTL, designated *QHt.cob-5B, QHt.cob-6A,* and *QHt.cob-7D.2*, were detected on chromosomes 5B, 6A, and 7D.2, and individually explained 4.1 to 26.1% of the phenotypic variation. The QTL on chromosome 6A was located within the interval *Xwmc256-wPt-3069* and was consistent over the four environments. In addition, other significant QTL were detected on linkage groups 2B.1, 3A, 3B.1, 4D.1, and 5B, in different environments.

3.2.4.2.2. Spike length (Sl)

Sl had the highest number of significant QTL among plant morphological parameters. Seventeen QTL were detected with intermediate to minor effects under different moisture levels and individually explained 4.4 to 15.5% of the phenotypic variation (Table 3.9, Fig. 3.1). Two QTL, designated *QSl.cob-1A.1* and *QSl.cob-1D*, were detected in all environments. Individually they explained 5.1 to 15.5% of the phenotypic variation. Platte contributed the alleles that had the positive effect on Sl in all environments for the above mentioned QTL. Another QTL effect, on chromosome 2B.1, was detected in three environments (08FW, 09GW, and 08FD) within interval *Xgwm429-Xbarc55*. The percentage of phenotypic variation explained by this individual QTL ranged from 5.9 to 12.0%, with LOD scores from 2.51 to 5.82. Other QTL were detected on linkage groups 1A.1, 3B2, 3D.1, 4D.2, 5B, 7A, 7B, and 7D.2, but were inconsistent among environments.

3.2.4.2.3. Leaf length (Ll)

Nine QTL with intermediate effects were detected under different moisture levels that individually explained 5.2 to 11.0% of the phenotypic variation (Table 3.9, Fig. 3.1). Three QTL, designated *QLl.cob-1B.1*, *QLl.cob-2B.1*, and *QLl.cob-6B.1,* were detected in two environments and accounted for 5.2 to 11.0% of the phenotypic variation. Less consistent or environment-specific chromosome regions associated with Ll were identified on linkage groups 2A and 7D.2.

3.2.4.2.4. Leaf width (Lw)

Eight QTL were detected in three environments (08FW, 09GW, and 08FD) with R^2 values ranging from 5.1 to 9.5% of the phenotypic variation (Table 3.9, Fig. 3.1). QTL detected on chromosome 2D.2 in two environments (08FW and 08FD) shared the same marker interval (*Xgwm261-Xgwm455*), while another QTL on chromosome 1B.1 was also detected in two environments (09GW and 08FD), but with different marker intervals.

Other QTL were detected on chromosomes 1A.1, 4A.1, and 7D.2, and were inconsistent over environments.

3.2.4.3. Yield and yield components

Five yield-related traits were measured in this population: kernel weight (Kw), above ground biomass (Agb), harvest index (Hi), one-meter grain weight (1mg), and grain yield (Gy). Forty-two QTL were detected for yield parameters, with major and minor effects in the four environments (Table 3.9, Fig. 3.1). Clusters of yield parameters were found on linkage groups 1B.1, 2B.1, 2D.1, 5A and 6A. Marker interval *Xbarc165-Xbarc360* on chromosome 5A was significantly associated with GY and Agb. Another cluster of significant QTL, identified on chromosome 6A within the interval flanked by the markers *Xwmc256-wPt-3069*, influenced some yield parameters, but was inconsistent among environments.

3.2.4.3.1. Kernel weight (Kw)

Kw had the highest number of significant QTL among yield-related parameters. Fifteen QTL were detected under different moisture levels and individually explained 3.9 to 16.0% of the phenotypic variation (Table 3.8, Fig. 3.1). Two QTL, designated *QKw.cob-2B.1* and *QKw.cob-6A*, were detected in all environments, but with somewhat different flanking markers. Individually they explained 3.9 to 16.0% of the phenotypic variation. The Platte allele increased kernel weight at the 2B QTL, while CO940610 contributed the positive allele at the 6A QTL. Another QTL, designated *QKw.cob-1A.1* was detected in two environments (09GW and 09GD); R^2 values were 8.0 and 9.6%, respectively, and the Platte allele increased the trait value. Less consistent or environment-specific chromosome regions associated with Kw were identified on linkage groups 2D.1, 2D.2, 3B.1, and 7D.2.

3.2.4.3.2. Above ground biomass (Agb)

Eight QTL with intermediate effects were detected under different moisture levels, and individually explaining 5.6 to 8.2% of the phenotypic variation (Table 3.9, Fig. 3.1). One QTL, designated *QAgb.cob-2D.1*, was detected in three environments (08FW, 08FD, and 09GD) and individually explained 5.6 to 8.2%, of the phenotypic variation. Other QTL were detected on chromosomes 2D.1, 4D.2, 5A, and 5B but were inconsistent over environments.

3.2.4.3.3 Harvest index (Hi)

Eight QTL with intermediate effects were detected under different moisture levels and individually explained 5.1 to 8.7% of the phenotypic variation (Table 3.9, Fig. 3.1). Only one QTL, designated *QHi.cob-2D.2,* was detected in two environments (08FW and 08FD), where it accounted for 6.3 and 6.5%, respectively, of the phenotypic variation. CO940610 contributed the favorable allele. Less consistent or environment-specific chromosomes regions associated with Hi were identified in linkage groups 1A.1, 1B.1, 2B.1, 2B2, 3A, and 6B.1 with LOD score ranging from 5.1 to 8.7.

3.2.4.3.4. One meter grain weight (1mg)

Seven QTL with intermediate effects were detected under different moisture levels and individually explained 5.5 to 9.1% of the phenotypic variation (Table 3.9, Fig. 3.1). One QTL, designated *QOmg.cob-2B.1*, was detected in two environments (09GW and 09GD), with R^2 values of 7.8 and 5.5%, respectively. Other QTL, detected on chromosomes 2D.1, 4D.2, 5A, 5B, and 7B, were inconsistent over environments.

3.2.4.3.5. Grain yield (Gy)

Four QTL with intermediate effects were detected under different moisture levels, explaining 8.0 to 12.1% of the phenotypic variation (Table 3.9, Fig. 3.1). One QTL, designated *QGy.cob-5A*, was consistently detected in all four environments within the marker interval *Xbarc165-Xbarc360*, accounting for 7.7 to 11.0%, of the phenotypic

variation. Platte contributed the favorable allele at the 5A QTL, which increased yield by 94 to 166 kg ha^{-1}. Less consistent or environment-specific chromosome regions associated with Gy were identified on linkage groups 2D.1, 5B, and 7B and individually explained 8.8 to 12.1% of the phenotypic variation.

3.2.4.4. Pre-harvest sprouting (Phs)

Phs was only evaluated under the full irrigation treatment. A total of three QTL were detected in 08FW and 09GW and explained 5.8 to 13.3% of the phenotypic variation (Table 3.9, Fig. 3.1). One QTL, designated *QPHS.cob-4A.1*, was detected in Fort Collins within marker interval *Xwmc420-Xgwm165*, and accounted for 13.3%, of the phenotypic variation. CO940610 contributed the favorable allele, reducing the Phs index by 0.03. Other QTL were detected on linkage groups 2B.1 and 4D.1, and individually explained 6.5 and 12.2%, respectively, of the phenotypic variation.

3.2.4.5. Normalized difference vegetation index (Ndvi)

Ndvi was only measured in the 2009 growing season in both treatments. Three QTL were detected that explained 5.4 to 7.3% of the phenotypic variation (Table 3.9, Fig. 3.1). QTL were detected on chromosomes 3A, 4B, and 6A and were inconsistent over environments.

3.2.4.6. Yield drought susceptibility index (Dsi)

Two QTL for Dsi were detected in Greeley and explained 9.8 to 11.0% of the phenotypic variation (Table 3.9, Fig. 3.1). The QTL were designated *QDsi.cob-5B* and *QDsi.cob-7B*, and had LOD scores ranging from 4.38 to 5.95. CO940610 contributed the favorable allele at both QTL, i.e., the allele that decreased the value of Dsi.

3.2.5. Stability of QTL across environments

In general, most of the intermediate and major QTL were consistent across environments and had approximately the same magnitude with some exceptions; we selected three agronomic traits as examples to graphically compare the presence and

size of QTL across environments (Fig. 3.4). Two major QTL for days to heading with the same magnitude designated *QDth.cob-2B.1* and *QDth.cob-7D.2* were consistent under two irrigation treatments (Fig. 3.4a). Two QTL designated *QDth.cob-1B.1* and *QDth.cob-3A* were consistent in 08FW and 08FD. For plant height, four QTL were consistent across environments with the same R^2 except the 6A QTL position which had higher R^2=26 at Greeley location under the full irrigation treatment (Fig. 3.4b). A QTL was detected for grain yield in all environments designated *QGy.cob-5A* with the same magnitude except at the Greeley location under full irrigation treatment which had a higher R^2 value (Fig. 3.4c). Under limited irrigation at Greeley environment we identified two QTL designated *QGy.cob-5B* and *QGy.cob-7B*.

Fig 3.4. Comparison of presence and size of QTL for three agronomic traits across environments

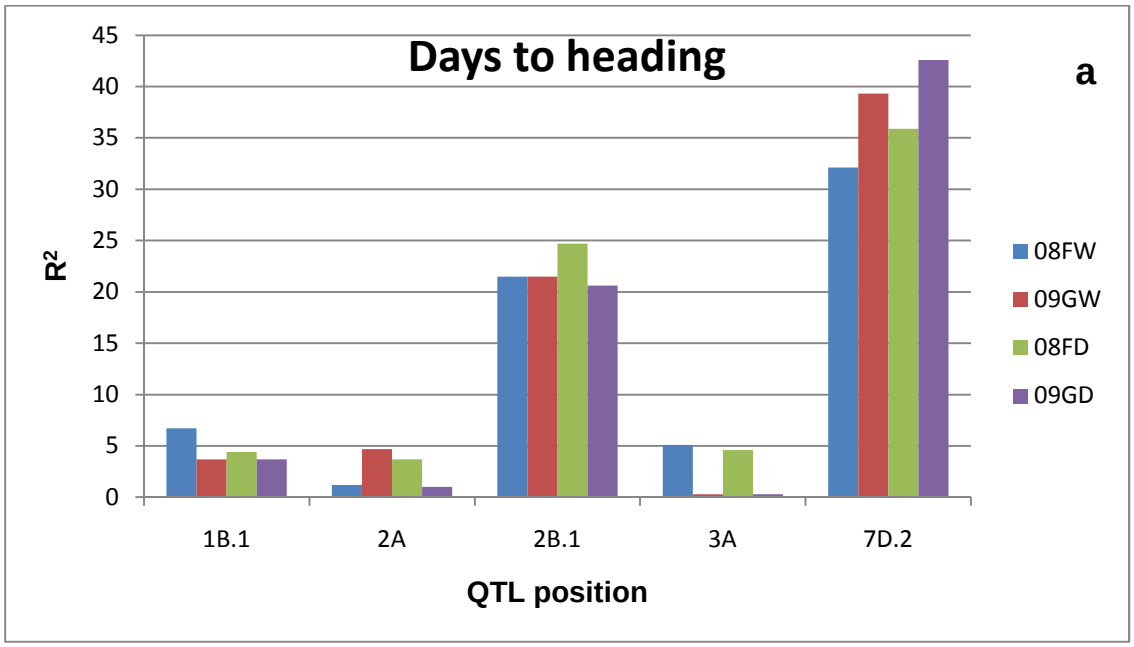
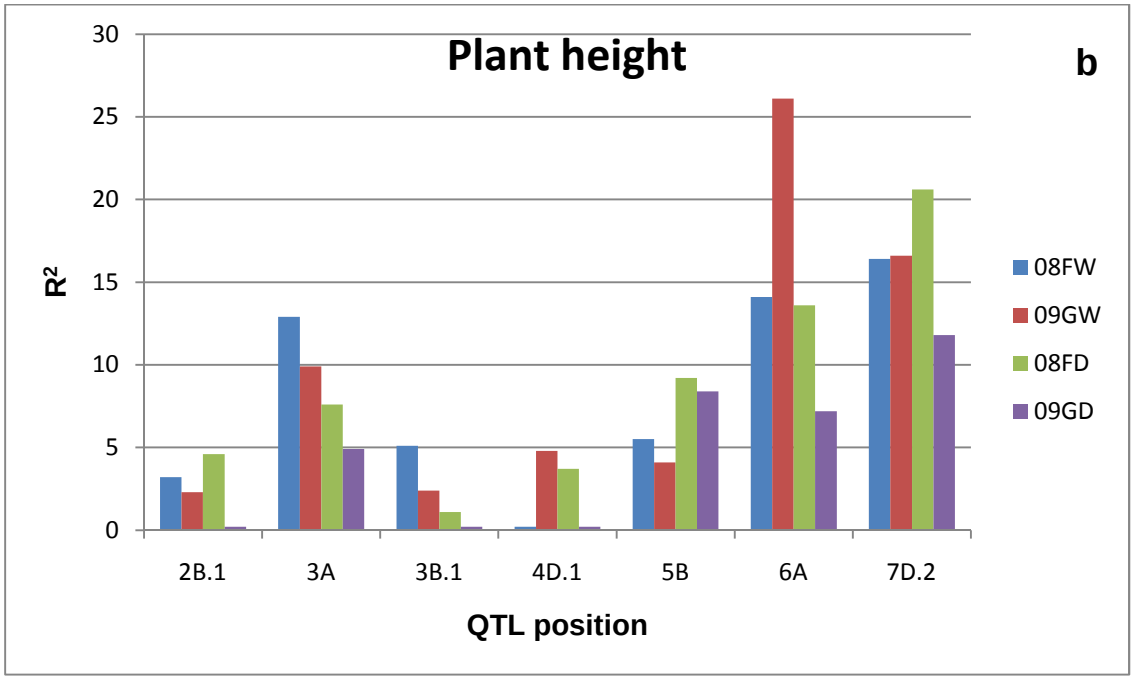
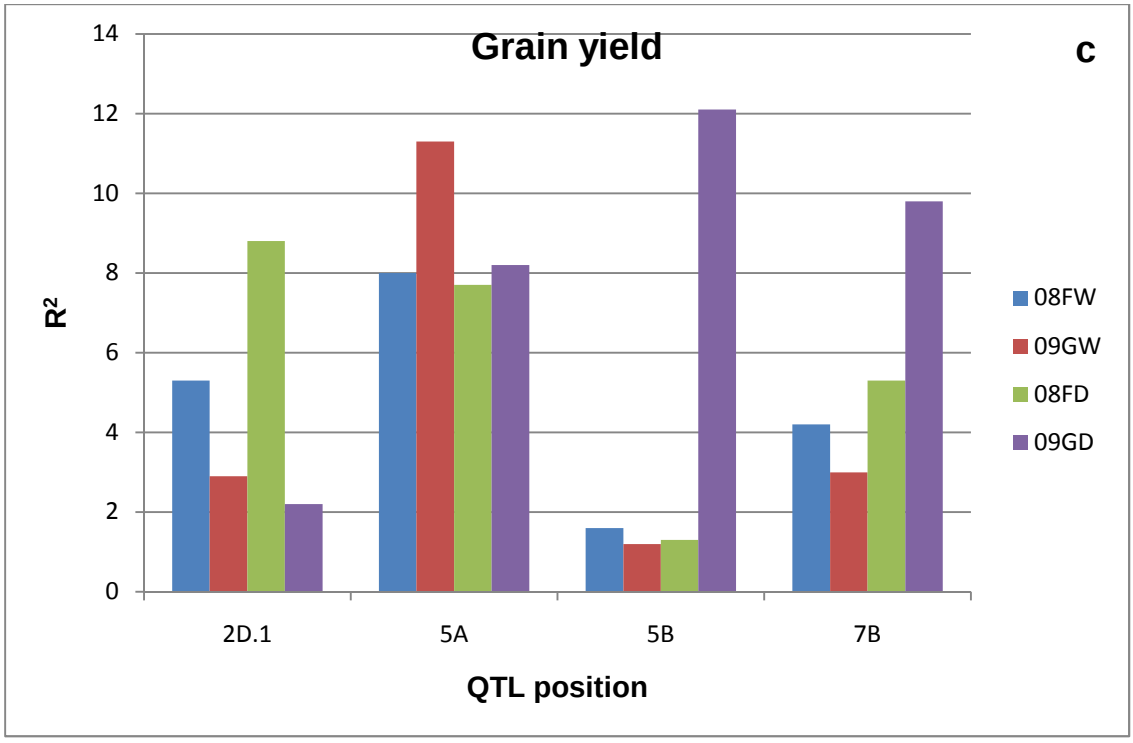


Fig 3.3. Continued





3.3 Discussion

3.3.1. Trait means, correlation, and heritability estimates

The major effect of drought in the present study was examined by two side-by-side trials at two locations: Fort Collins in 2007-08 and Greeley in 2008-09. One trial was grown under moderate moisture stress ("dry") and one under fully irrigated ("wet") conditions, for a total of four environments. The DH lines grown at Greeley in 2008-09 had higher mean values under both moisture treatments compared to Fort Collins, possibly due to less precipitation in 2008 compared to 2009 (Table A1). Therefore, the soil moisture conditions due to both irrigation and precipitation were likely a major environmental difference between the two locations. Overall, grain yield under drought was reduced by 795.8 kg ha^{-1} (21.4%) at Fort Collins and by 704.7 kg ha^{-1} (18.7%) at Greeley (Tables 3.1 and 3.2). Giunta et al. (1993) reported that moisture stress around anthesis had a negative effect on wheat yield. Furthermore, moisture stress from anthesis to maturity reduces grain yield (Guttieri et al., 2001; Weightman et al., 2008) through reduction in grain filling rate. CO940610 had higher grain yields compared to Platte under both moisture levels at both locations (Table 3.5). Grain yield of CO940610 was reduced by 891.9 kg ha^{-1} (21.2%) and 572.6 kg ha^{-1} (13.6%) in Fort Collins and Greeley, respectively, whereas Platte's grain yield was reduced by 889.9 kg ha^{-1} (23.9%) and 736.6 kg ha^{-1} (19.9%) in Fort Collins and Greeley, respectively. This confirms our assumption that CO940610 is more drought tolerant than Platte. Plant height of the DH population was reduced by 11.5 cm (14.5%) at Fort Collins, and by 16.6 cm (18.2%) at Greeley under drought conditions. Platte produced shorter plants than CO940610 under different moisture treatments at both locations. All agronomic traits in our study showed evidence of transgressive segregation, indicating that alleles from both parents influenced the traits (Fig. A1).

In general, most of phenological parameters were negatively correlated with grain yield under both moisture treatments, in agreement with results by Kumar et al. (2006). Later flowering plants entered the grain filling period during a drier, warmer time of the season, and consequently their yield was reduced. Heritability estimates varied considerably from trait to trait. In general, most traits had low to moderate heritability, except days to heading, days to physiological maturity, plant height, and kernel weight. Above ground biomass had the lowest heritability estimate, most likely due to the high variability in sample collection, while days to heading had the highest values among agronomic traits (Table 3.8). Dth has high heritability because it can be evaluated relatively precisely, and it depends largely on a small number of major genes controlling sensitivity to photoperiod and vernalization requirements (Griffiths et al., 2009). Low heritability estimates for some of the agronomic traits in our study indicate that a large part of the expression of these traits is environmentally controlled, making them difficult to manipulate at the genetic level in a breeding program. Yield usually has a low heritability, especially under moisture stress, and is significantly influenced by the environment (Cuthbert et al., 2008; Hai et al., 2008; Huang et al., 2006; Quarrie et al., 2006; Wiersma et al., 2001). However, in our study heritability estimates for grain yield had moderately high values (0.568 to 0.676) in each environment. High estimates of heritability provided evidence for predictable G x E interaction and relatively little effect of the environment (Kumar et al., 2006). McIntyre et al. (2010) showed similar results for a wheat QTL study under different moisture levels; heritability in that study was high (>0.70) for Dth, Ht, and Tw, and moderately high (0.40–0.70) for Gy and Hi.

3.3.2. QTL mapping

In general, distribution of QTL was balanced between the full and limited irrigation treatments: 64 (50.0%) were detected under full irrigation and 62 (48.4%)

under the limited irrigation treatment. For some traits (Dth, Dpm, Ht, Sl, and Gy), most of the detected QTL were consistent between both irrigation treatments.

3.3.2.1. Phenological parameters

Heading date is an important trait in wheat breeding programs, especially where occurrence of drought is a concern. Optimum Dth allows the plant to escape drought, late frost, and other abiotic and biotic stresses and attain the desired yield level (Spielmeyer et al., 2007). Three categories of genes influence heading date through their control of vernalization response (*Vrn*) (Wang et al., 2009), photoperiod response (*Ppd*) (Scarth and Law 1983), and earliness per se genes (*Eps*) (Lin et al., 2008).

Thirty-four QTL were detected for phenological parameters with major and minor effects (Table 3.9, Fig. 3.1, and Fig. 3.2). QTL for Dth have been reported in several wheat populations (Sourdille et al., 2000, 2003; Borner et al., 2002; Hanocq et al., 2004; Marza et al., 2006; Mclntyre et al., 2010). Two major QTL detected for Dth in our study were consistent across environments. They were designated *QDth.cob-2B.1* and *QDth.cob-7D.2*, and explained from 20.6 to 42.6% of the phenotypic variation. The major QTL on 2B.1 was observed within the *wPt-3561–Xgwm429* interval (Fig. 3.1). This QTL seems likely to be coincidental with the well characterized photoperiod response gene *Ppd-B1*. This locus has already been reported by several researchers (Sourdille et al., 2003; Hanocq et al., 2004; Lin et al., 2008; Maccaferri et al., 2008; Baga et al., 2009; Zhang et al., 2009d). In all environments, the QTL *QDth.cob-7D.2* was detected on chromosome arm 7DS (Fig. 3.2). This location is consistent with the vernalization response gene *Vrn-D3* described by Wang et al. (2009). A minor QTL, designated *QDth.cob-2A,* was detected in three environments and suggests *Ppd-A1* as a feasible candidate for this QTL. However, its position on chromosome 2AS has not yet been clearly defined (Hanocq et al., 2007). The map position of *QDth.cob-2A* coincides with the position of *Ppd-A1* on the basis of published studies and the homoeologous

relationships with *Ppd-B1* and *Ppd-D1* (Sourdille et al., 2003; Hanocq et al., 2004; Kuchel et al., 2006).

Earliness per se genes are known to map to groups 2 and 4, and to chromosomes 3A, 6B, and 7B (Shah et al., 1999). QTL identified for Dth in the current study map to the same chromosomes and were coincident with QTL for other phenological parameters. Several QTL for phenological parameters in this study were detected on chromosome 7BS (Dpm, Gfd, and Gfr) (Fig. 3.2). Lin et al. (2008) reported a major early flowering QTL on chromosome 7BS. In the same region Kuchel et al. (2006) mapped a photoperiod QTL associated with heading date under short day winter conditions. Sourdille et al. (2000) detected two minor QTL in the same region which might relate to earliness per se and photoperiod response.

3.3.2.2. Morphological traits

Forty-four QTL were detected for morphological traits with major and minor effects in the four environments (Table 3.9, Fig. 3.1). Previous studies have reported QTL for Ht on most wheat chromosomes (Borner et al., 2002). Apparently, all QTL for Ht identified in our population were reported previously (Table 1.3). Dwarfing genes reduce plant height, increase the lodging resistance, and often increase yield in wheat (Butler et al., 2005; Ellis et al., 2004). Several *Rht* genes have been identified, of which two gibberellic acid-insensitive semi-dwarfing genes *Rht-B1b* (*Rht1*) and *Rht-D1b* (*Rht2*), have been used in wheat breeding programs and are located on chromosomes 4B and 4D, respectively. CO940610 and Platte carry the same alleles at those loci (*Rht-B1b* and *Rht-D1a*) according to an allelic variation study conducted by Dr. Jorge Dubcovsky, University of California-Davis (personal communication). Two major QTL, designated *QHt.cob-6A* and *QHt.cob-7D.2,* explained 7.2 to 26.1% of the phenotypic variation, were consistent in all environments, and appear to be coincident with QTL reported in previous studies by Hai et al. (2008), Marza et al. (2006), and Spielmeyer et al. (2007).

Furthermore, *QHt.cob-7D.2,* seems likely to be colocalized with vernalization locus *Vrn-D3* (Wang et al., 2009).

A spike length (Sl) QTL, designated *QSl.cob-1A.1*, was detected in all environments, explained 5.6 to 15.5% of the phenotypic variation, and mapped near the HMW-GS locus *Glu-A1*. This region has been associated with spike length in several populations (Börner et al., 2002; Chu et al., 2008; Ma et al., 2007; Sourdille et al., 2000; Marza et al., 2006). Another QTL, designated *QSl.cob-5B,* had a moderate effect R^2 (5.3%), and was identified only in 08FW. A QTL for Sl on chromosome 5B was reported by Ma et al. (2007) and Marza et al. (2006), but we could not determine its correspondence with *QSl.cob-5B*.

3.3.2.3. Yield and yield components

Forty-two QTL were detected for yield and yield components with major and minor effects in the four environments (Table 3.9, Fig. 3.1). In previous reports, QTL for yield and yield components have been detected in different population types and multiple environments, and were distributed across most of the wheat genome (Kato et al., 2000; Gross et al., 2003; Huang et al., 2003; McCartney et al., 2005; Quarrie et al., 2005; Kumar et al., 2007; Marza et al., 2006; McIntyre et al., 2010). QTL affecting several traits are common and may be due to pleiotropy or close linkage. Such QTL clusters for yield parameters were observed in our study on linkage groups 1B.1, 2B.1, 2D.1, 5A and 6A. On chromosome 2D.1, QTL for grain yield, one meter grain weight, above ground biomass, and kernel weight clustered in the interval *wPt-0298*–*wPt-4413*. Among these, the QTL for kernel weight and above ground biomass were consistent in more than one environment.

The most significant QTL identified for grain yield in this study was located on chromosome 5AL (*QGy.cob-5A*) in the *Xbarc165*–*Xbarc360* marker interval. It was consistent across environments, was coincident with QTL for at least one yield

component, and was detected in the vicinity of the vernalization gene *Vrn-A1* on 5AL (Shindo et al., 2003). Chromosome 5A is known to carry a number of major QTL affecting yield and yield components and some of these occur in positions similar to ours (Cuthbert et al., 2008; Quarrie et al., 2005; Wang et al., 2009). The presence of a single Platte allele at *QGy.cob-5A* increased Gy 93.73 to 166.23 kg ha^{-1}. However, for all the other Gy QTL (on chromosomes 2D, 5B, and 7B), the CO940610 allele was associated with higher yield.

3.3.2.4. Pre-harvest sprouting (Phs)

In our study we identified a QTL, designated *QPHS.cob-4A.1*, which was detected in one environment in which the trait was evaluated within marker interval *Xwmc420-Xgwm165*; it explained 13.3%, of the phenotypic variation. CO940610 contributed the favorable alleles for reducing Phs. Previous QTL analysis identified a common, highly significant QTL for Phs located on chromosome 4A (Anderson et al., 1993; Mares and Mrva, 2001; Kato et al., 2001; Flintham et al., 2002; Mares et al., 2005; Ogbonnaya et al., 2008; Tan et al., 2006). Our 4A QTL were detected near *Xwmc40,* as was reported by Ogbonnaya et al. (2008) and Tan et al. (2006). Noda et al. (2002) have suggested that sensitivity of wheat embryos to germination inhibition by abscisic acid (ABA) is controlled primarily by a gene(s) located on the long arm of chromosome 4A. The QTL detected in one environment on linkage group 4D.1 (R^2= 12.2%) in this study has not been reported previously.

3.3.2.5. Normalized difference vegetation index

To the best of our knowledge, this study is the first to report QTL analysis for normalized difference vegetation index (Ndvi). Based on 2009 QTL analysis we identified three QTL, on chromosomes 3A, 4B, and 6A, each in just one environment. However, these QTL are only marginally significant and have minor effects, consistent with the trait's low heritability. Although the Ndvi method may have potential for indirect

assessment of canopy biomass, leaf area index, light-absorption, and potential photosynthesis capacity (Araus et al., 2001), it will need to be evaluated with greater precision to be useful in breeding and genetics studies.

3.3.2.6. Drought susceptibility index

Only a limited number of studies have investigated Dsi via QTL analysis, especially in wheat. Kirigwi et al. (2007) identified QTL for Dsi on chromosome 4A in a RIL wheat population (n=127) with a range of 13 to 48% of phenotypic variation. In our study we identified QTL, designated *QDsi.cob-5B* and *QDsi.cob-7B*, in 2009-09 with LOD scores ranging from 4.38 to 5.95 and R^2 values from 9.8 to 11.0%. CO940610 contributed the alleles that had the favorable effects on Dsi, i.e., that reduced the yield difference between the wet and dry treatments.

A QTL for grain yield per se in the Greeley dry treatment was co-localized with the Dsi QTL on 5B (Fig. 3.1). The CO940610 alleles increased yield per se under limited irrigation and decreased susceptibility to drought, indicating that those alleles confer a relative yield advantage in drier but not wetter conditions. Another observation in that same chromosome 5B region is that a QTL for plant height was detected in three of four environments (Fig. 3.1). The CO940610 allele at that QTL increased plant height (Table 3.9), suggesting that taller plants in this population had a relative yield advantage in drier conditions. However, none of the other plant height QTL colocalized with yield QTL, thus reducing the plausibility of this explanation.

The Dsi QTL on chromosome 7B also coincided with a grain yield per se QTL detected in the Greeley dry treatment, and again CO940610 provided the favorable alleles for both traits. QTL for days to physiological maturity and grain filling duration are located in the same chromosome region, but were only detected in the Greeley wet treatment, so are unlikely to account for the improved performance in drier conditions. A cluster of QTL for quality traits (Chapter 2) was also detected in the same region. These

traits included grain protein concentration, mixograph peak time, mixograph right slope, mixograph right width, flour color b, and grain ash concentration.

3.3.3. Stability of QTL across environments

Distribution of QTL was balanced between the full and limited irrigation treatments: 64 (50.0%) were detected under full irrigation and 62 (48.4%) under the limited irrigation treatment. In general, most of the QTL especially the intermediate and the major QTL had approximately R^2 across all environments.

In summary, a population of 185 DH hard winter lines was evaluated in field trials under moderate soil moisture stress conditions to identify QTL for phenological parameters, yield and yield components, normalized difference vegetation index, and drought susceptibility index. All agronomic traits showed a wide range of trait mean values under both irrigation treatments with higher mean values under full irrigation. A total of 128 QTL was detected in four environments with approximately equal numbers of QTL detected in the full and the limited irrigation treatment. Many QTL for correlated traits were mapped in the same genomic regions, forming QTL clusters.

Considering (1) the detection of QTL for Dsi in Greeley; (2) their collocation with grain yield QTL in one of the dry environments; and (3) the consistent direction of CO940610 allele effects at these loci, these two regions on chromosomes 5B and 7B are our best candidates for location of drought tolerance genes. Validation of these QTL is proceeding along two paths. First an independent recombinant inbred line population developed for the same parents is being evaluated in irrigated and rainfed environments in 2009-10; analysis of phenotypic and relevant marker data will allow confirmation of QTL location and effects. Second, development of near isogenic lines for the 7B region is currently underway; when complete, comparison of near isogenic pairs of lines will provide a powerful evaluation of the effect of the candidate region.

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APPENDIX

Table A.1. Segregation distortion among SSR and DArT markers for the C0940610/Platte population.

Locus	Number of DH lines with indicated marker Score			χ^2‡
	A	B	-†	
wPt-8855	41	132	41	47.9****
Xbarc196	150	60	4	38.6****
wPt-8377	132	50	32	36.9****
wPt-1261	124	52	38	29.5****
wPt-0298	56	121	37	23.9****
wPt-1285	117	55	42	22.4****
wPt-5809	112	56	46	18.7****
wPt-1973	61	116	37	17.1****
wPt-0217	65	118	31	15.5****
wPt-7636	104	56	54	14.4***
wPt-7215	113	64	37	13.6***
wPt-5265	67	116	31	13.1***
wPt-3638	61	101	52	9.9***
Xwmc491	72	112	30	8.7***
wPt-4933	99	64	51	7.5**
Xgwm165	71	106	37	6.9**
Xgwm540	87	124	3	6.5**
Xwmc420	74	108	32	6.4**
wPt-3789	66	98	50	6.2**
Xgdm62	88	123	3	5.8**
wPt-6654	96	66	52	5.7**
Xwmc48	89	123	2	5.5**
Xwmc336	74	104	36	5.1**
wPt-8721	73	103	38	5.1**
Xgwm610	90	121	3	4.6**
Xbarc216	90	119	5	4.0**

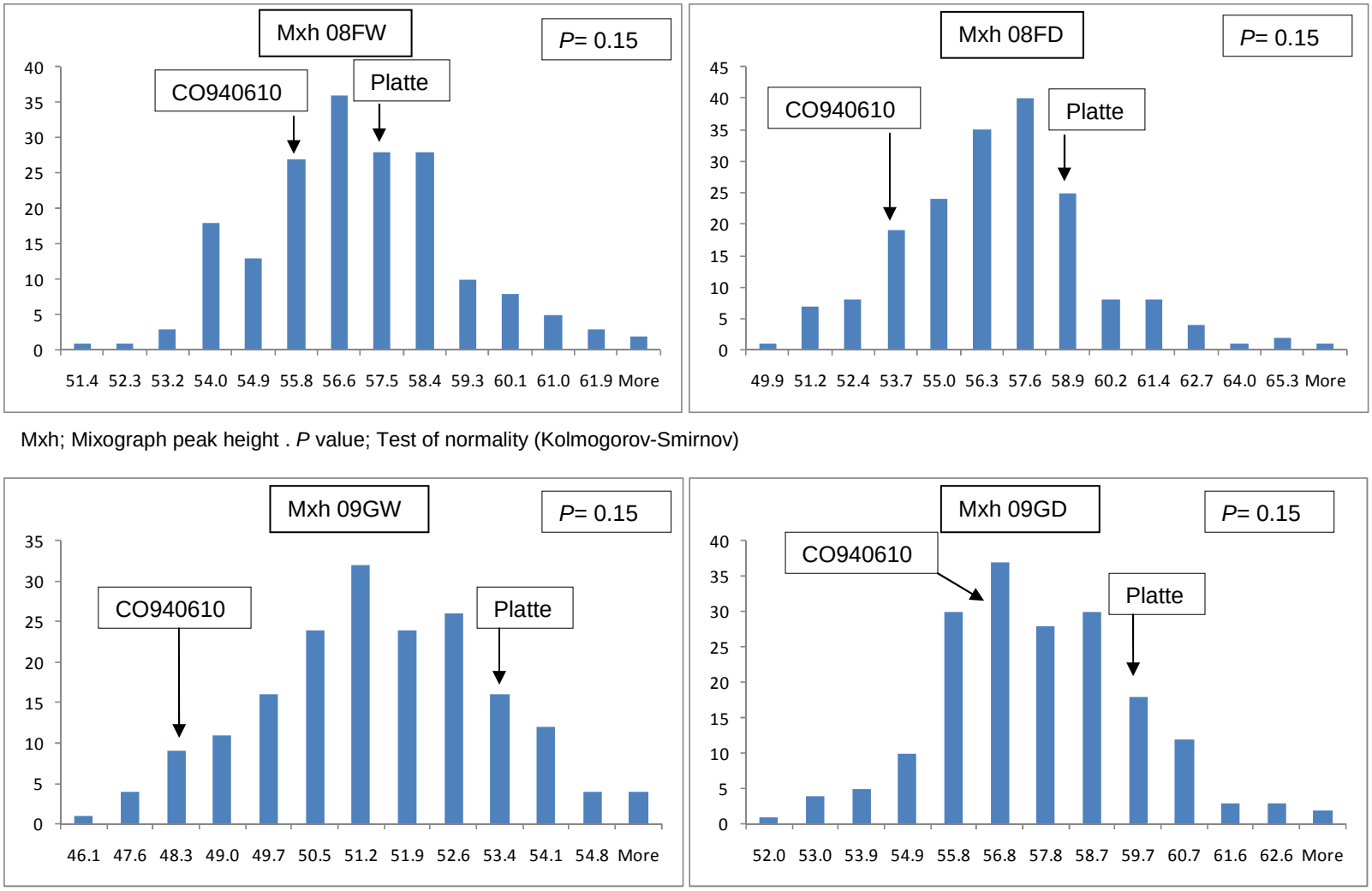
† Missing data.

‡ Chi square value and significance.

,*,**** significant at 0.01, 0.001, and 0.0001 significance level.

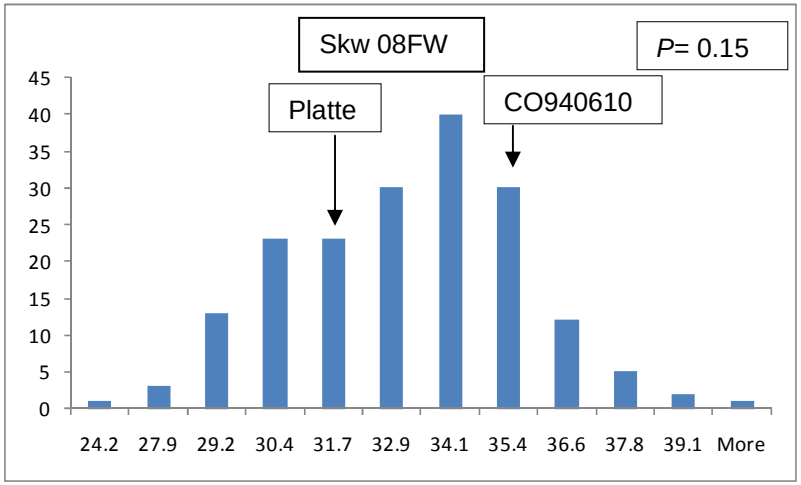
Table A2. Weather information for Fort Collins and Greeley in January to July of 2008 and 2009, respectively. (Obtained from http://ccc.atmos.colostate.edu/ ~coagmet/)

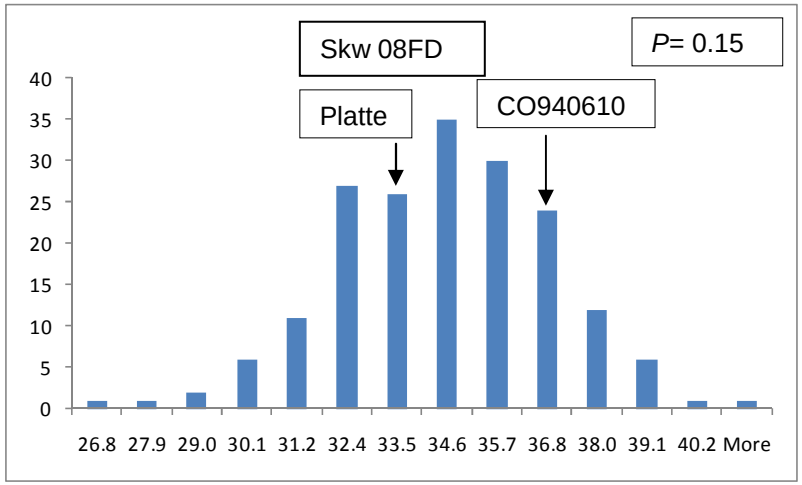
Month	Location	Maximum temperature (C)	Minimum temperature (C)	Precipitation cm
January	Fort Collins	13.8	-19.3	0.0
	Greeley	19.7	-24.5	0.0
February	Fort Collins	17.2	-15.5	0.0
	Greeley	20.6	-14.7	0.05
March	Fort Collins	23.1	-12.8	0.78
	Greeley	25.4	-13.8	0.88
April	Fort Collins	26.2	-8.3	4.01
	Greeley	28.4	-9.8	4.72
May	Fort Collins	30.3	-7.3	3.08
	Greeley	33.2	3.4	2.79
June	Fort Collins	32.2	7.2	0.30
	Greeley	33.4	6.8	7.72
July	Fort Collins	35.6	9.0	1.21
	Greeley	36.2	10	4.36



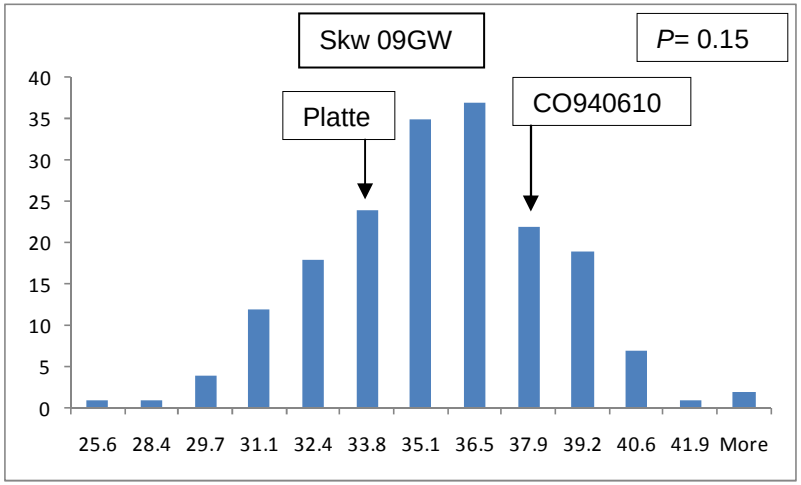
Mxh; Mixograph peak height . *P* value; Test of normality (Kolmogorov-Smirnov)

Fig. A1. Frequency distributions for quality traits for the CO940610/Platte DH population in the 2007-08 and 2008-09 growing seasons.





Skw; single kernel weight . *P* value; Test of normality (Kolmogorov-Smirnov)



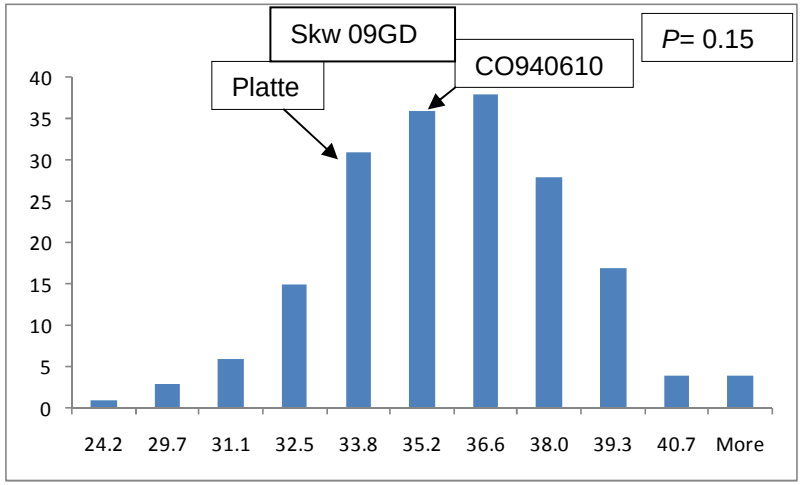
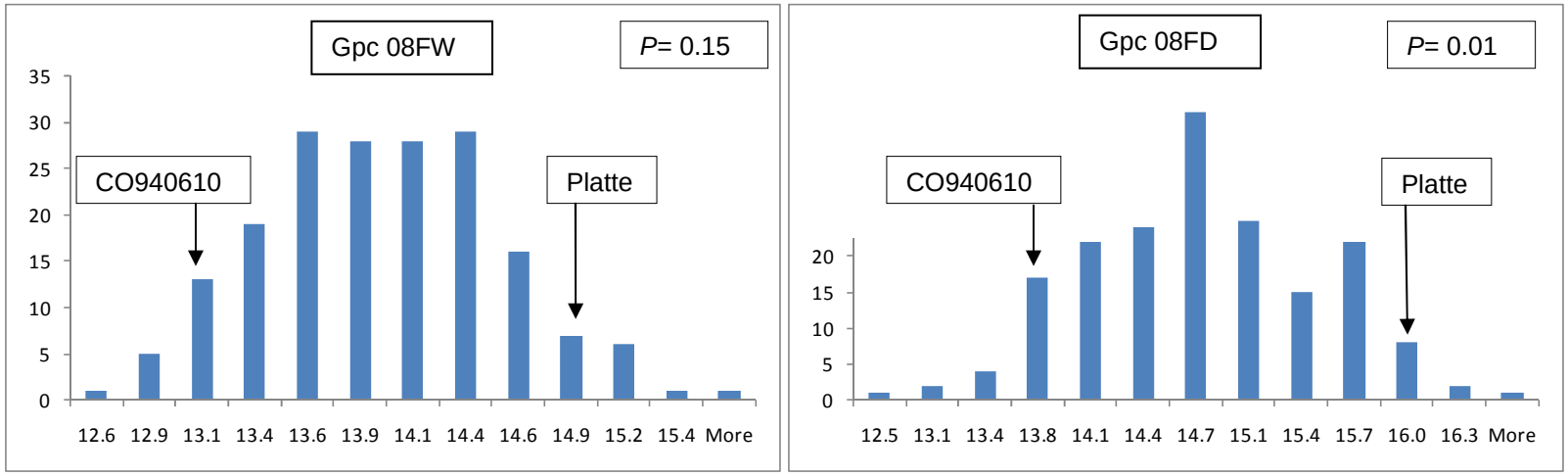


Fig. A.1. Continued



Gpc; Grain protein concentration. *P* value; Test of normality (Kolmogorov-Smirnov)

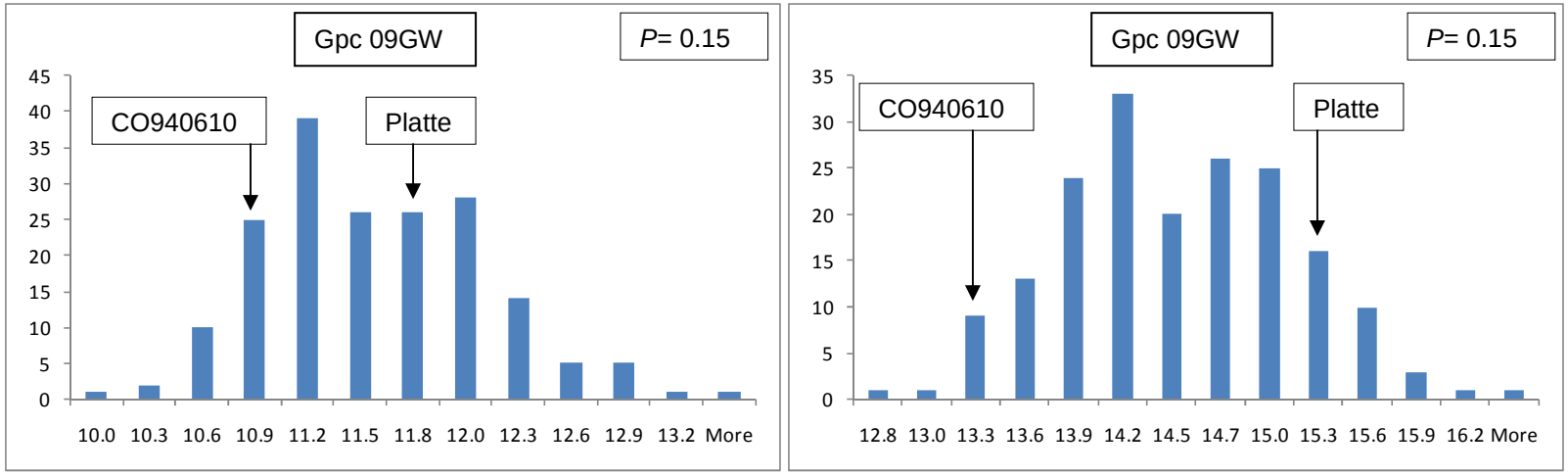
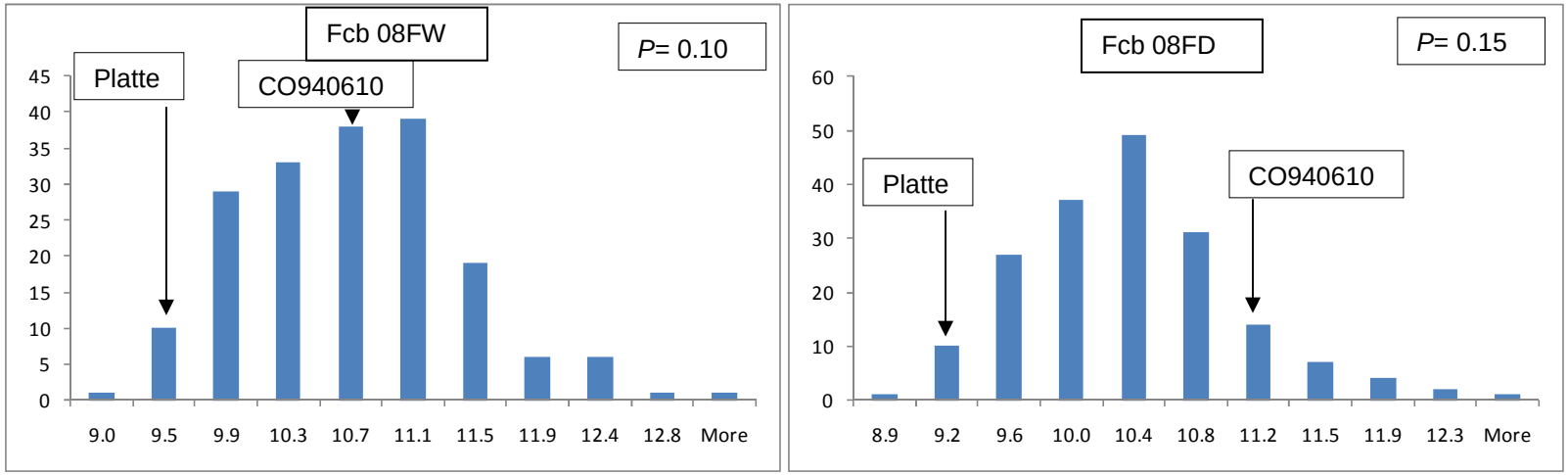


Fig. A.1. Continued



Fcb; Flour color b . *P* value; Test of normality (Kolmogorov-Smirnov)

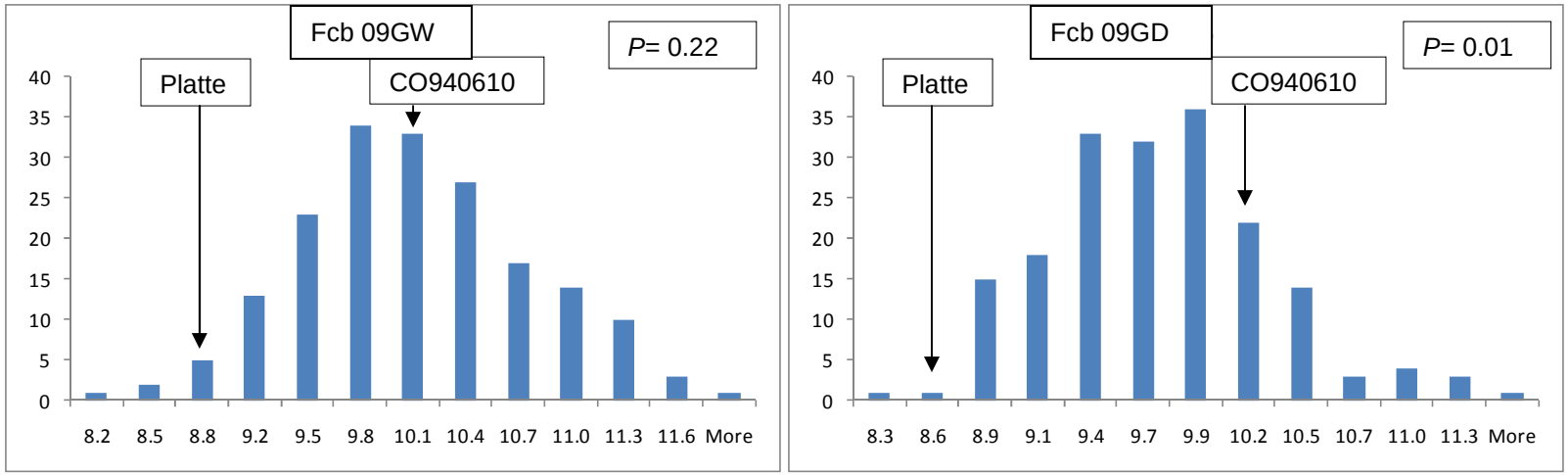
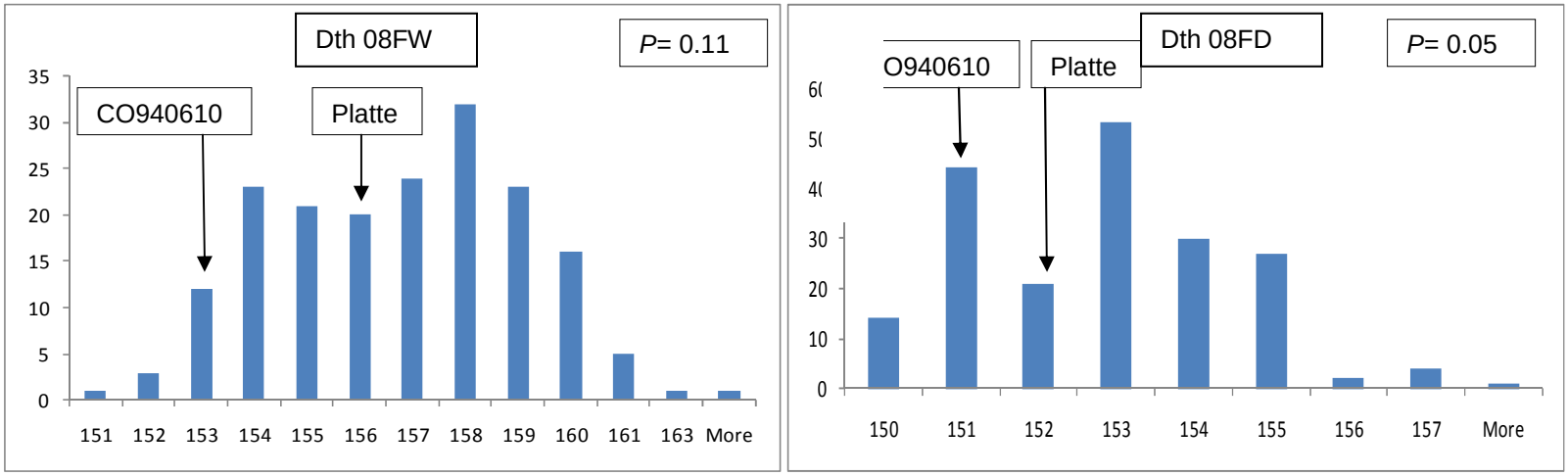


Fig. A.1. Continued



Dth; Days to heading. *P* value; Test of normality (Kolmogorov-Smirnov)

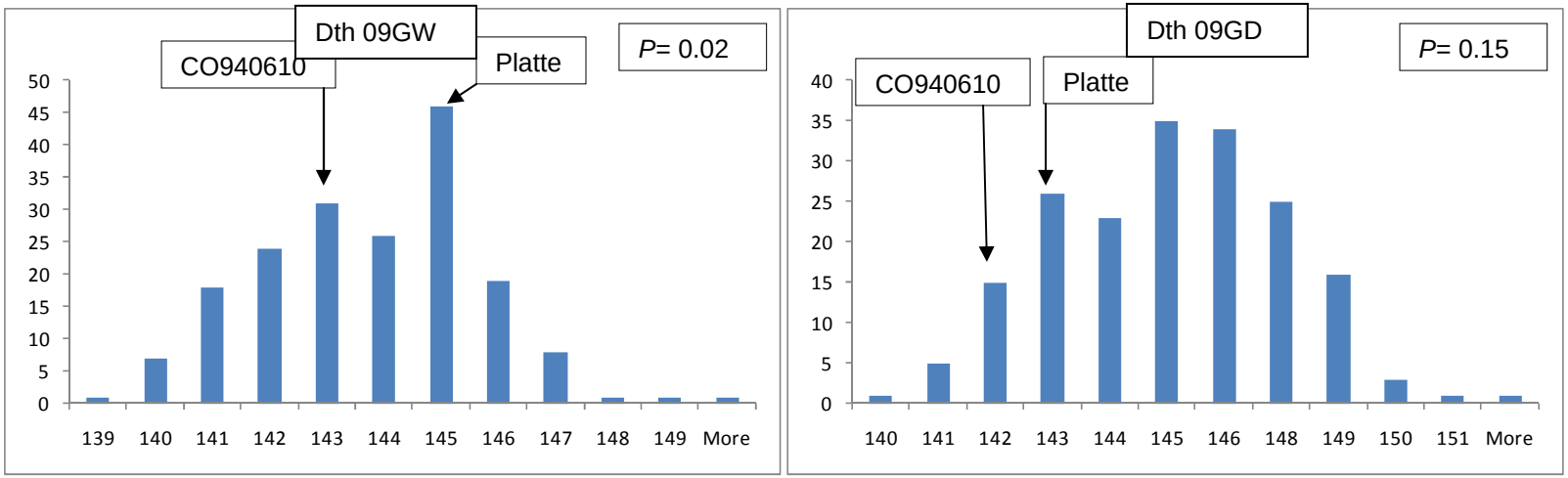
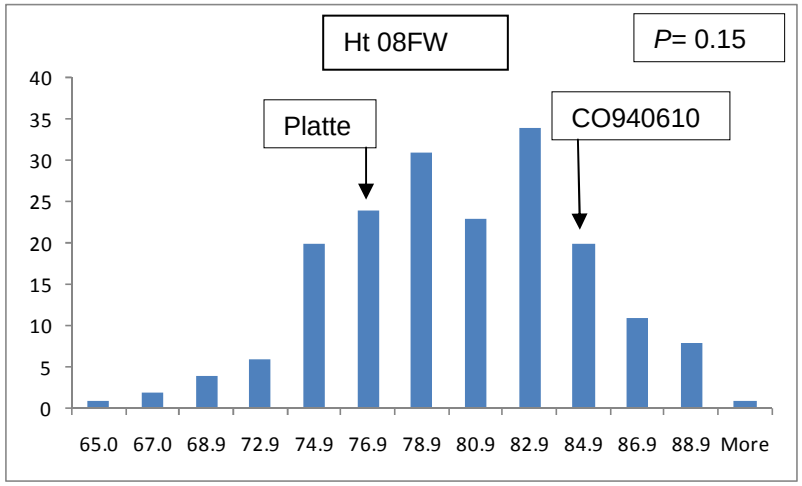
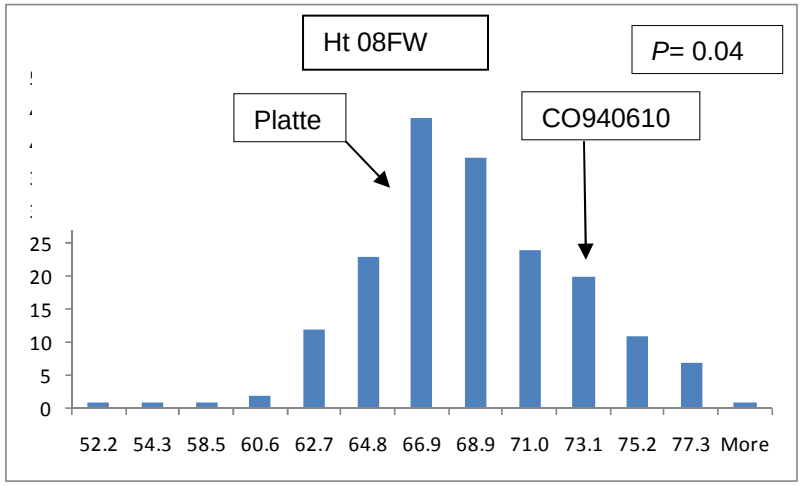
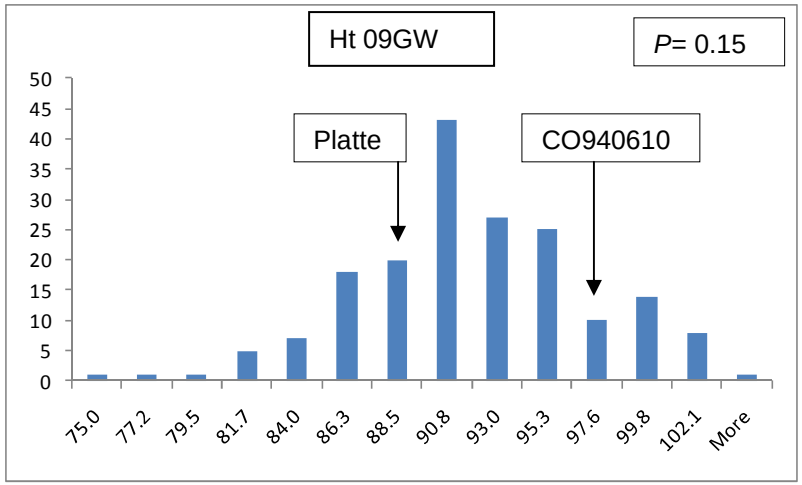


Fig. A.2. Frequency distribution for agronomic traits for CO940610/Platte DH population in the 2007-08 and 2008-09 growing seasons.





Ht; Plant height . *P* value; Test of normality (Kolmogorov-Smirnov)



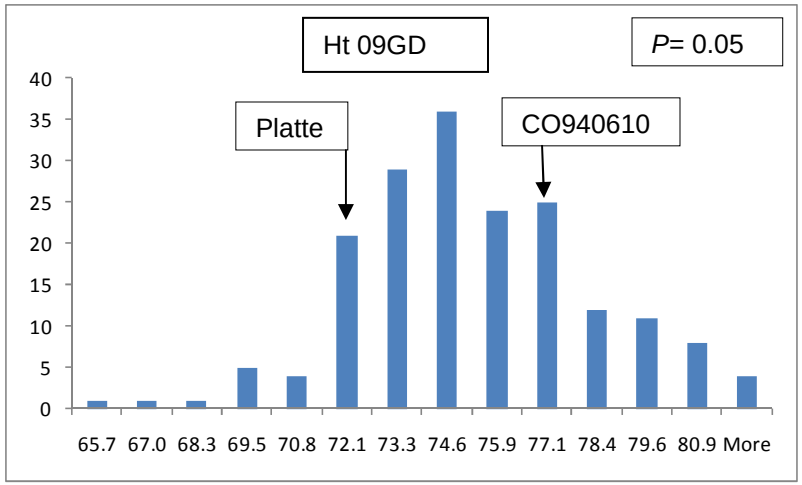
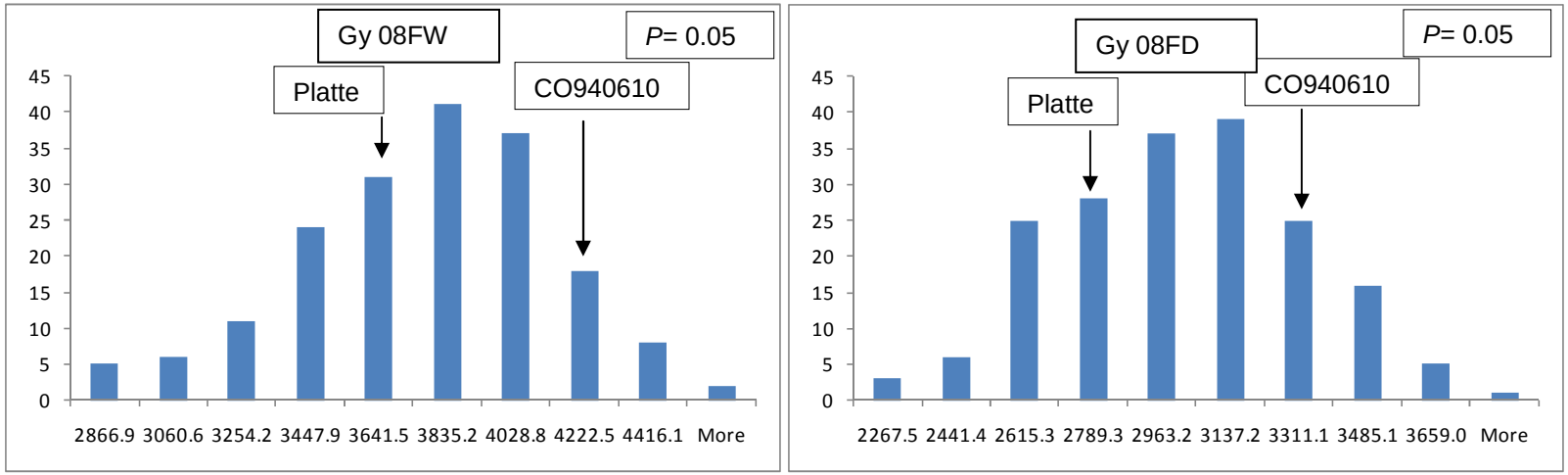


Fig. A.2. Continued



Gy; Grain yield . *P* value; Test of normality (Kolmogorov-Smirnov)

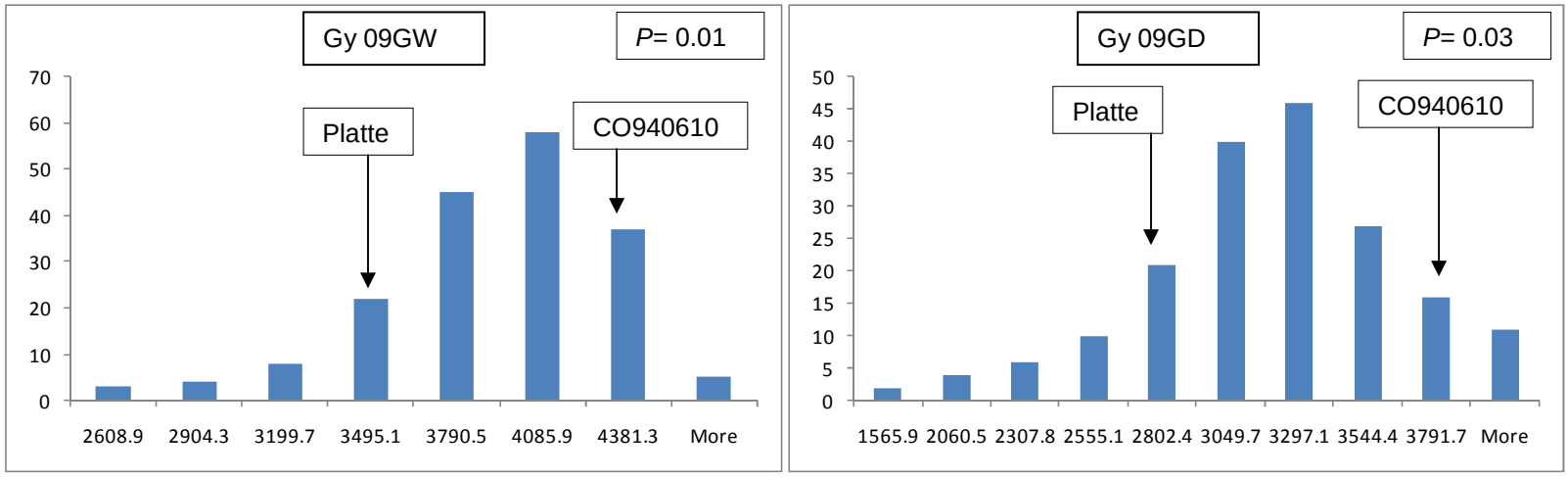
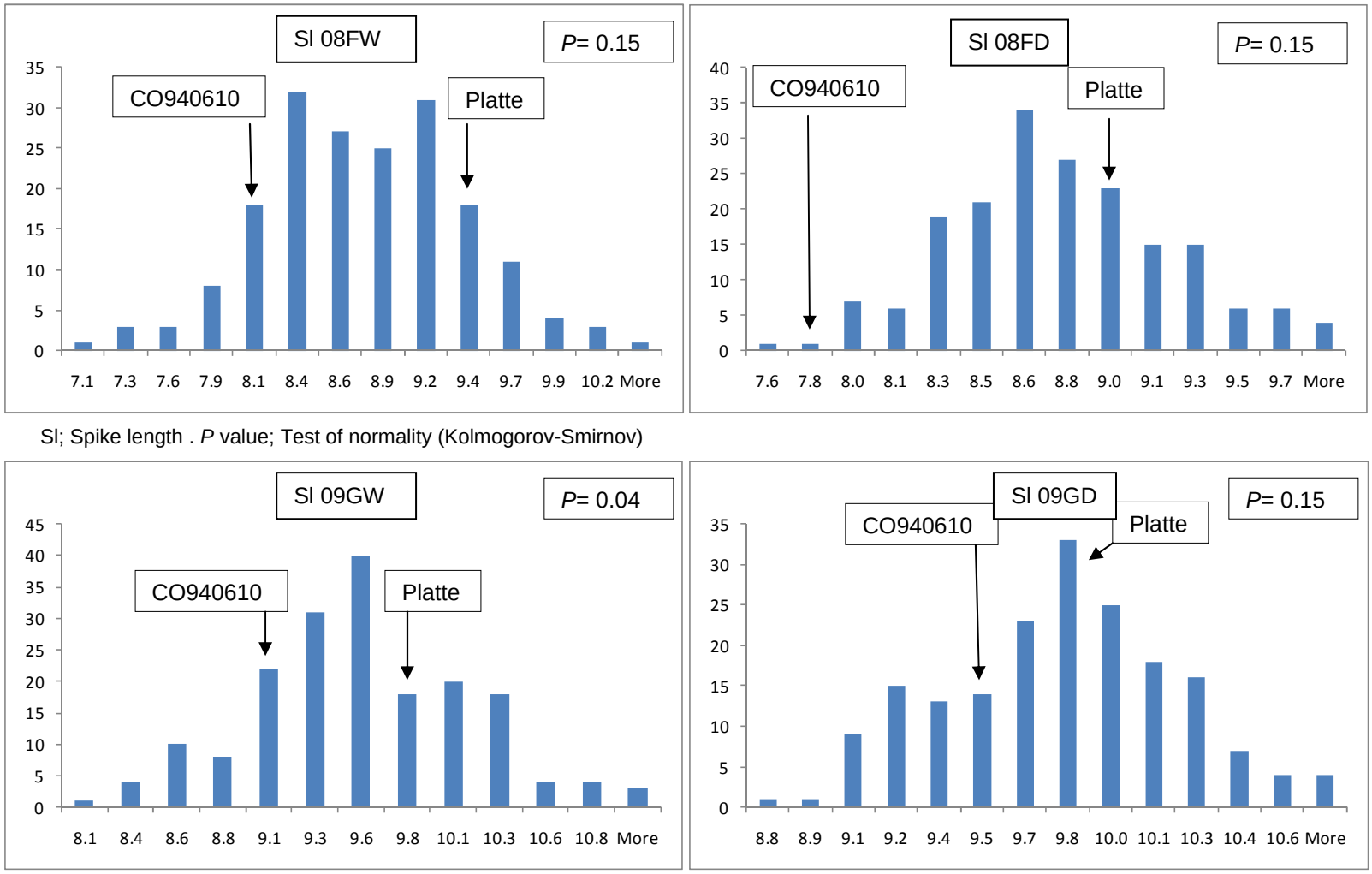


Fig. A.2. Continued



Sl; Spike length . *P* value; Test of normality (Kolmogorov-Smirnov)

Fig. A.2. Continued