Mapping QTL for Agronomic Traits on Wheat Chromosome 3A and a Comparison of Recombinant Inbred Chromosome Line Populations

M. Liakat Ali, P. Stephen Baenziger,* Zakaria Al Ajlouni, B. Todd Campbell, K. S. Gill, K. M. Eskridge, A. Mujeeb-Kazi, and Ismail Dweikat

ABSTRACT

Variation for wheat (*Triticum aestivum* L.) grain yield and agronomic traits was used to map quantitative trait loci (QTL) in a 'Cheyenne' (CNN) × [CNN ('Wichita' 3A)] recombinant inbred chromosome line (RICL) population consisting of 223 CNN(RICLs3A) and 7 check cultivars that were evaluated in six environments in Nebraska during 2005–2007. A chromosome 3A linkage map spanning 106 cM was constructed using 32 microsatellite markers. Composite interval mapping detected 19 QTL for seven agronomic traits that individually accounted for 4.6 to 16.8% of the phenotypic variation. Three small genomic segments, spanning 3.4, 5.3, and 5.3 cM, contained most of the QTL. Two yield QTL were detected in two environments and in data pooled over environments. For grain volume weight, a QTL was detected in five of the six environments while a plant height QTL was detected in all environments. Wichita (WI) alleles contributed to the increased trait values for yield, spikes per square meter, and grain volume weight, while CNN contributed alleles to the increased 1000-kernel weight, plant height, and anthesis date. Both CNN and WI contained alleles for increased number of kernels per spike. The 223 CNN(RICLs3A) set had greater power to detect QTL than the two smaller subsets—128 CNN(RICLs3A) developed using doubled haploids and 95 CNN(RICLs3A) developed using recombinant monosomic lines. Neither of the subsets performed consistently better than the other in detecting QTL.

M.L. Ali, Univ. of Arkansas, Rice Res. and Ext. Cent., 2900 Highway 130E, Stuttgart, AR 72160; P.S. Baenziger and Ismail Dweikat, Dep. of Agron. and Hortic., K.M. Eskridge, Dep. of Statistics, Univ. of Nebraska, Lincoln, NE 68583-0915; Z. Al-Ajlouni, Dep. of Plant Prod., Jordan Univ. of Sci. and Technol., Irbid-Jordan, Postal Code 22110, Jordan; B.T. Campbell, USDA-ARS, Costal Plains Res. Cent., 2611 W. Lucas St., Florence, SC 29501; K.S. Gill, Dep. of Crop and Soil Sci., Washington State Univ., Pullman, WA 99164; A. Mujeeb-Kazi, Natl. Inst. of Biotechnol. & Genet. Eng. (NIBGE), Faisalabad, Pakistan. Received 20 June 2010. *Corresponding author (pbaenziger1@unl.edu).

Abbreviations: AD, anthesis date; CNN, Cheyenne; DH, doubled haploid; GEI, genotype × environment interaction; GVWT, grain volume weight; GYLD, grain yield; KPS, kernels per spike; PHT, plant height; QTL, quantitative trait loci; RFLPs, restriction fragment length polymorphisms; RICLs, recombinant inbred chromosome lines; RMLs, recombinant monosomic lines; SPSM, spikes per square meter; SSRs, simple sequence repeats; STM, sequence-tagged microsatellite; TKWT, 1000-kernel weight; WI, Wichita.

Identification of genetic factors influencing grain yield (GYLD) in wheat is of great interest to many breeding programs, especially for improving yield across environments. Grain yield improvement is difficult using traditional breeding methods because grain yield is a complex quantitative trait controlled by many genes that are affected by the environment. The advent of molecular markers has greatly facilitated mapping and genetic dissection of complex quantitative traits and improvement of crop varieties. The mapping of quantitative traits in wheat is complicated due to polyploidy and large genome size, estimated to be around 16,000 Mbp/1C (Arumuganathan and Earle, 1991), about 85 to 96% of which represents

Published in Crop Sci. 51:553–566 (2011).
doi: 10.2135/cropsci2010.06.0359
Published online 10 Jan. 2010.

repeated sequences mainly comprised of known retrotransposon-like sequences (Sidhu and Gill, 2004).

The availability of chromosome substitution lines and recombinant inbred chromosome lines (RICLs) has been used to overcome the challenges of genetic analysis of complex traits in wheat. While chromosome substitution lines are suitable to study the genetic and phenotypic effect of whole chromosomes individually, RICLs allow genetic analysis of specific chromosome regions. Recombinant inbred chromosome lines can be used to identify and map gene(s) controlling agronomic traits by genetic approaches (Law, 1966; Law et al., 1976; Yen and Baenziger, 1992; Berke et al., 1992b; Shah et al. (1999a,b); Paterson et al., 1990; Joppa et al., 1997; Kato et al., 2000; Campbell et al., 2003). Recombinant inbred chromosome lines are more desirable than recombinant inbred lines (RILs) for studying the effect of a specific chromosomal region, because RICLs have a more uniform genetic background and thus reduce potential epistatic variation. Further, targeting a chromosome, RICLs simplify construction of genetic linkage maps. In a simulation study, Kaeppler (1997) demonstrated that a RICL population provided greater power than a RIL population of similar size to detect QTL.

Capitalizing on the reciprocal chromosome substitution lines (Morris, 1964–1984) involving two historically important Great Plains cultivars, 'Cheyenne' (CNN) and 'Wichita' (WI), a series of studies was initiated in Nebraska in the 1980s to study the genetic architecture of GYLD and agronomic traits. Initially, Berke et al. (1992a,b) evaluated a set of reciprocal chromosomal substitution lines for grain yield and other agronomic traits and reported that WI chromosome 3A increased GYLD by 19% when placed in a CNN background. Quantitative trait loci were identified for plant height (PHT), kernels per spike (KPS), 1000-kernel weight (TKWT), and spike number per square meter (SPSM) but not for GYLD and grain volume weight (GVWT) in a RICL population of 50 lines derived from the cross CNN × CNN (WI 3A) [hereafter referred to as CNN(RICLs3A)] (Shah et al., 1999a,b). Subsequently, in an attempt to increase QTL detection precision, a larger population of 95 CNN(RICLs3A) was evaluated for GYLD and other agronomic traits in multiple environments (Campbell et al., 2003). A number of QTL for GYLD and other agronomic traits were detected using a linkage map comprised of 20 markers (15 restriction fragment length polymorphisms [RFLPs] and 5 simple sequence repeats [SSRs]) (Campbell et al., 2003). Although the larger population size of 95 did improve the ability to detect and localize QTL, there were several large gaps in the map and some QTL were positioned distantly from the flanking markers. A larger mapping population reduces bias in estimation of QTL effects by reducing the chance of sampling bias (Melchinger et al., 1998) and provides a more accurate and higher resolution of marker-trait association (Keurentjes et al., 2007; Bernardo, 2004; Robin et al., 2003; Darvasi et al., 1993), thus allowing detection of QTL with smaller effects (Haley and Andersson, 1997; Vales et al., 2005). Mapping resolution can also be improved somewhat by increasing marker density (Darvasi et al., 1993).

In the present research, we used a larger population of CNN(RICLs3A) with the addition of doubled haploid-derived lines and more markers with a goal of making a more precise evaluation of the traits to uncover additional QTL, improve resolution of the QTL, and make a more accurate estimate of QTL effects. Recombinant inbred chromosome lines can be created using recombinant monosomic lines (RMLs) methods as described by Shah et al. (1999a,b) and Yen and Baenziger (1992), or by using wheat by maize (*Zea mays* L.) doubled haploid (DH) line methods (Lizarazu et al., 1992). The development of RICLs through doubled haploids is a simpler approach than through RMLs, which is lengthy and involves tedious cytogenetic techniques. A study in barley (*Hordeum vulgare* L.) reported QTL detection differences between RICL and DH populations derived from the same cross combination (Hori et al., 2005). Similarly, some QTL detection differed between two population types, RILs and DH lines derived from the same cross in rice (*Oryza sativa* L., He et al., 2001). However, there is no report available in wheat on the comparative behavior of these two RICL population types (i.e., RMLs vs. DH lines) in the mapping of QTL, and thus, a knowledge of the comparative performance of these population types will be helpful for future QTL mapping efforts.

To better understand the genetic architecture of agronomic performance attributed to chromosome 3A, the primary objective of this study was to map and evaluate more precisely the effects of QTL for GYLD, SPSM, KPS, TKWT, GVWT, PHT, and anthesis date (AD) with a population of 223 CNN(RICLs3A). The second objective was to compare the performance of 95 RML-derived CNN(RICLs3A), 128 DH-derived CNN(RICLs3A), and the combined 223 CNN(RICLs3A) on the detection of QTL.

MATERIALS AND METHODS

Plant Materials and Trait Evaluation

A population of 223 3A recombinant inbred chromosome lines [CNN(RICLs3A)] developed from a cross between CNN and CNN (WI 3A), check cultivars ('Goodstreak', 'Pronghorn', 'Arapahoe', 'Jagger', and 'Wichita') and the two parents [CNN and CNN(WI3A)] were evaluated in six environments. The CNN(RICLs3A) lines were developed in three phases: the first 50 RML-derived RICLs [hereafter referred to as CNN(RICLs3A)-RML] were previously described by Shah et al. (1999a,b), the second 45 RML-derived RICLs [CNN(RICLs3A)-RML] were described by Yen and Baenziger (1992), and the third 128 DH-derived RICLs [hereafter referred to as CNN(RICLs3A)-DH] were developed using the methods of Lizarazu et al. (1992) at the DH facility at CIMMYT, Mexico.

The CNN(RICLs3A) population was evaluated in three locations in Nebraska (Lincoln, Mead, and Sidney) during the growing season of 2005, in two locations (Lincoln and Mead) during 2006, and only in Mead during 2007 for GYLD (t ha^{-1}), SPSM, KPS, GVWT (kg hL^{-1}), TKWT(g), PHT (cm), and AD (d after Jan. 1), as described by Campbell et al. (2003). Briefly, each entry was grown in a four-row plot 2.4 m long with 30-cm row spacing in a randomized complete block design (RCB) with four replications. Traits were measured following the procedures outlined by Shah et al. (1999a) and Campbell et al. (2003). For the 2005 Lincoln trial, data were not recorded for GYLD, SPSM, KPS, and TKWT because some of the plots were partially affected by soilborne wheat mosaic virus. However, the other two traits, the AD and PHT, were recorded on the healthy plants grown in the unaffected portion of these plots. The plots were sprayed at heading with Headline fungicide (pyraclostrobin, ceramic acid, [2-[[[1-(4-chlorophenyl)-1*H*-pyrazol-3-yl]methyl]phenyl] methoxy, methyl ester; BASF, Research Triangle Park, NC) at the recommended rate to control fungal diseases in all experiments. Though diseases were present in nearby untreated plots, minimal to no fungal diseases developed in these experimental plots.

DNA Marker Analysis and Map Construction

A sap extraction method was used to isolate genomic DNA from fresh leaf tissues of each RICL and the parental lines (Kuleung et al., 2004). About one gram of fresh leaves from 3–4 wk-old seedlings were placed in between the two rollers of a sap extraction apparatus (Ravenel Specialties, Seneca, SC) and 5 mL of the extraction buffer (50 m*M* Tris-HCL, 25 m*M* EDTA, 1 *M* NaCl, 1% CTAB, 1 m*M* of 1, 10-phenanthroline, 0.15% 2-mercaptoethanol) was slowly added to the rollers. The solution mixed with extracted sap was collected in a 15-mL Falcon tube, incubated at 65°C for 2 h, then equal volume of chloroform/isoamyl alcohol (24:1) was added and mixed for 20 min on a rotary shaker followed by spinning at 3400 rpm for 15 min. The supernatant was transferred to a new tube and precipitated with cold isopropanol and the DNA pellets were washed with 70% ethyl alcohol. The extracted DNA was then resuspended in 500 μL of TE buffer and the DNA concentration quantified by spectrophotometry (TKO100 Fluorometer, Hoefer Scientific Instruments, San Francisco, CA). Primer sequence information of SSR markers with prefixes 'barc', 'wmc', 'gwm', 'cfa', and 'psp' were obtained from the GrainGenes website (http://wheat.pw.usda.gov/GG2/index.shtml [verified 2 Dec. 2010]) while those with an 'hbg' prefix were from Torada et al. (2006). Sequence information of STM (Sequence-tagged microsatellite) primers was obtained from Hayden et al. (2006). All primers were synthesized by Operon Technologies (Huntsville, AL). The polymerase chain reaction (PCR) mix preparation, PCR conditions, gel electrophoresis, and gel staining were performed as described by Kuleung et al. (2004). Annealing temperature varied from 50 to 60°C, which was determined after an initial amplification and polymorphism test with all the primers on the two parents. The gel was photographed using Bio-Rad Gel Doc 2000 gel documentation system (Bio-Rad, Hercules, CA) and the allelic composition was scored manually.

The linkage map was constructed using MAPMAKER/EXP version 3.0b (Lander et al., 1987) with the Kosambi mapping function (Kosambi, 1944). Initial linkage groups were identified using the "Group" command with a logarithm of odds (LOD) score of 5.0 and recombination of 0.4. The order of the markers of the linkage group was determined using the commands "Compare," "Order," and "Ripple." The "Try" command was used to add ungrouped or new markers to the initial linkage group. The chromosome was oriented as per the International Triticeae Mapping Initiative (ITMI) map (Song et al., 2005a) and Wheat Microsatellite Consortium (WMC) map (Somers et al., 2004) with the short arm at the top.

Phenotypic Data Analysis

Analysis of variance (ANOVA) was conducted for each environment using the Proc Mixed method of the SAS program (SAS Institute Inc, Cary, NC) to test the significance of variation among the CNN(RICLs3A), and between the parents, CNN and CNN (WI3A). Variance components were estimated by considering the genotypes and replications as random effects. To assess the genotype (G) × environment (E) interaction (GEI), analyses of variance were performed for all genotypes, CNN(RICLs3A) × E, Parent × E, and check cultivars × E using the GLM procedure of SAS (SAS Institute, 1999). Correlation analyses among the evaluated traits were conducted using data pooled over environments with PROC CORR method of SAS (SAS Institute).

QTL Analysis

Composite interval mapping (CIM) was conducted using QTL Cartographer version 2.5 (Wang et al., 2006) to identify QTL affecting each trait. For CIM, forward and backward stepwise regressions were performed to select five markers as cofactors, and the analysis was conducted using model 6 (standard model) with a moving window size of 10 cM. At each interval, the significance of the QTL-trait association was tested by the likelihood ratio statistics (LRS; Haley and Knott, 1992). For all traits, QTL analyses were performed using the LSMEANS data for individual environments, as well as the pooled data averaged over all environments. A significant threshold was estimated by 1000 permutations at $P < 0.01$ (Churchill and Doerge, 1994) by QTL Cartographer for each trait in each environment and for data combined over all environments for the combined 223 CNN(RICLs3A) set, 128 CNN(RICLs3A)-DH set and 95 CNN(RICLs3A)-RML set. The estimated significant threshold LOD values were used as thresholds to declare the presence of putative QTL. Phenotypic variance explained by a QTL (R^2) was calculated at the peak LOD value of the plot. Confidence intervals (CI) were estimated by marking positions ± 1 LOD from the peak (Hackett, 2002; Lander & Botstein, 1989).

RESULTS

Linkage Maps, Marker Segregation, and Recombination

Out of 90 SSR markers mapped to chromosome 3A, 31 (34%) were found to be polymorphic between the parents, CNN and CNN (WI3A). Only one STM primer pair produced clear polymorphic bands. These 32 polymorphic markers were used to construct linkage maps for the entire set of 223 CNN(RICLs3A) as well as for the subpopulation sets, 95 CNN(RICLs3A)-RML and 128 CNN(RICLs3A)-DH.

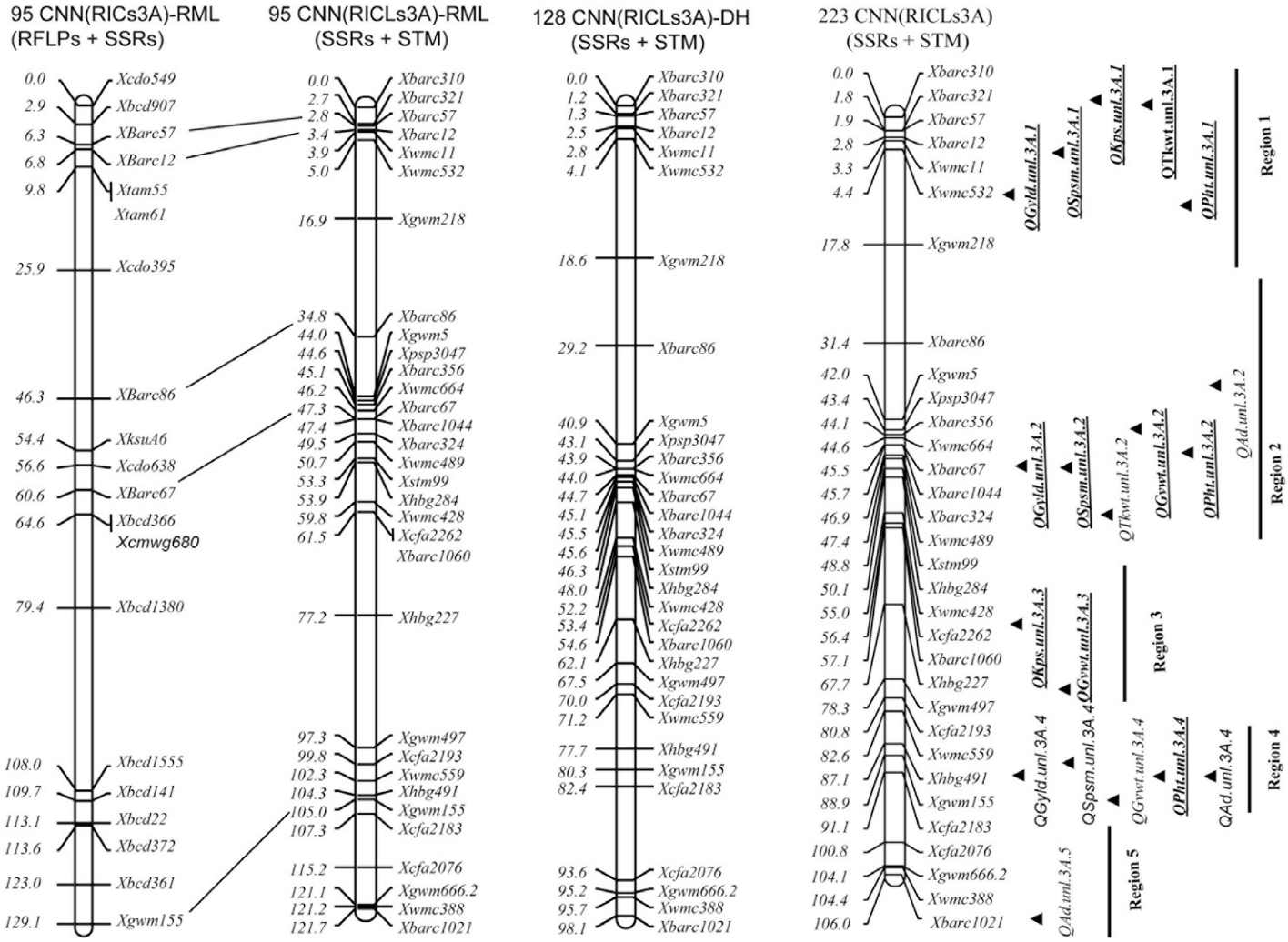

Figure 1. Genetic linkage maps of wheat chromosome 3A of 95 CNN(RICLs3A)-RML (1999–2001 evaluation set, RFLPs + SSRs), 95 CNN(RICLs3A)-RML (2005–2007 evaluation set, SSRs + STM), 128 CNN(RICLs3A)-DH set (SSRs + STM), and combined 223 CNN(RICLs3A) set (SSRs + STM). Marker names are on the right side of the chromosome while the marker positions (cM) from the first marker (from the top) are on the left side. Five SSR markers of 95 CNN(RICLs3A)-RML (RFLPs + SSRs) are common with 95 CNN(RICLs3A)-RML (SSRs + STM), 128 CNN(RICLs3A)-DH, and the combined 223 CNN(RICLs3A) maps. The positions of the common SSR markers between the two 95 CNN(RICLs3A)-RML maps (RFLPs + SSRs and SSRs + STM) are connected by solid lines. The locations of QTL for GYLD, SPSM, KPS, TKWT, GVWT, PHT, and AD detected by composite interval mapping are shown on the 223 CNN(RICLs3A) map only. The position of the LOD peak of each QTL on the linkage map is indicated by an arrowhead. Out of 19 QTL shown on the figure, 12 (bold and underlined) were detected in the analyses with data combined across environments while 7 other QTL were detected in individual environments only (Table 3).

The linkage map constructed for the combined 223 CNN(RICLs3A) population spanned 106 cM with an average spacing of 3.31 cM between the markers (Fig. 1). All 32 markers followed an expected Mendelian 1:1 segregation ratio at a probability of 0.01. In general, the order of the SSR markers was in good agreement with that on the maps developed by Song et al. (2005a) and Somers et al. (2004), as was the map length of 106 cM. The markers were uniformly distributed along the chromosome except for three gaps that were larger than 10 cM. Despite screening all the available SSR markers for these gaps, we failed to identify polymorphic markers for these regions, a possible indication that these regions were conserved in CNN and WI.

The linkage map constructed for the 95 CNN(RICLs3A)-RML spanned a length of 121.7 cM (Fig. 1). Six markers on the distal short arm of chromosome 3A showed distorted segregation and skewed in favor of the CNN(WI3A) parent. The 128 CNN(RICLs3A)-DH set produced a linkage map with a length of 98.1 cM (Fig. 1). For this subpopulation, 10 markers located at the middle region of the chromosome deviated from the 1:1 segregation and also were skewed toward the CNN(WI3A) parent. Comparing the maps of the 95 CNN(RICLs3A)-RML set and the 128 CNN(RICLs3A)-DH set, a recombination difference was observed between the two populations primarily in one region of the chromosome between the markers *Xbarc1060* and *Xgwm497*. In the

Table 1. Analysis of variance of grain yield (GYLD), spike number m^{-2} (SPSM), kernels per spike (KPS), and 1000-kernel weight (TKWT) over five environments and grain volume weight (GVWT), plant height (PHT), and anthesis date (AD) over six environments from 2005 to 2007 for CNN, CNN (WI3A), and 223 CNN(RICLs3A).

Source	df	GYLD MS	SPSM MS	KPS MS	TKWT MS	df	GVWT MS	PHT MS	AD (d after Jan. 1) MS
		t ha^{-1}			g		kg hL^{-1}	cm	
Environment (E)	4	394682**	6401595.0**	19125.2**	1333.3**	5	7054.3**	77700.8**	26677.4**
Rep (E)	15	15261.3**	178123.5**	219.8**	186.6**	18	31.9**	798.6**	57.7**
Genotypes (G)	229	673.4**	20459.2**	23.0**	23.8**	229	5.9**	129.7**	42.4**
CNN(RICLs3A)	222	505.1**	18696.5**	20.1**	22.9**	222	4.7**	114.9**	35.7**
Checks	4	3432.8**	56773.9**	88.9**	61.7**	4	24.0**	997.1**	59.7**
Parents	1	4555.5**	170050.6**	28.0	1.8	1	19.1**	121.0*	105.8**
G × E	916	345.4**	14957.7**	15.6**	7.3**	1145	2.9**	42.7**	2.2**
CNN(RICLs3A) × E	888	317.2**	14729.2**	15.2**	7.2**	1110	2.5**	42.0**	2.2**
Checks × E	16	1215.3**	24658.2**	30.6**	10.4**	20	5.1**	78.8**	3.9**
Parents × E	4	732.5	27067.5*	12.1	2.6	5	2.6**	73.8**	5.4**
Pooled error	3359	205.1	11066.5	12.8	5.8	4115	1.5	26.2	0.9
Mean CNN(RICLs3A)		3.67	465.2	25.9	31.50		75.4	102.6	146.8
Mean CNN (WI3A)		3.89	519.7	28.3	31.10		76.4	102.0	145.2
Mean CNN		3.42	380.3	29.5	30.15		75.1	105.9	147.7
Mean parents		3.58	452.0	28.9	30.61		75.7	103.9	146.4
CV (%)		12.30	22.6	13.8	7.65		1.6	5.0	0.7

*Significantly different from zero at the 0.05 level of probability.

**Significantly different from zero at the 0.01 level of probability.

RML-derived map, this interval spanned 35.8 cM (34 recombinants) while in the DH-derived map, the same interval spanned 12.9 cM (22 recombinants). On the combined 223 CNN(RICLs3A) set map, the distance was 21.2 cM (56 recombinants) for the same interval.

Phenotypic Trait Evaluation

The two parents, CNN and CNN (WI3A), were significantly different for GYLD, SPSM, GVWT, PHT, and AD (Table 1), but not significantly different for KPS and TKWT. The mean CNN(RICLs3A) population scores were close to the midparent values for all the traits except for KPS where the population value was lower than the midparent value. Significant differences were observed among all the genotypes, CNN(RICLs3A), and the check cultivars for all of the seven traits. The CNN(RICLs3A) × E, check cultivars × E, and parents × E interactions were significant for all the traits except for GYLD, KPS, and TKWT for parents × E interactions (Table 1).

Correlations among the pooled trait data were evaluated to predict associations among the traits (Table 2). Grain yield was found to be positively correlated with GVWT, SPSM, and TKWT while negatively correlated with PHT and AD. The negative correlation of GYLD with PHT and AD indicated that early maturing, shorter plants produced higher GYLD. Kernels per spike was not correlated with GYLD based on the pooled data. As expected, the two traits, AD and PHT, that showed negative correlation with grain yield, were found to be positively correlated. Spikes per square meter had a negative correlation with KPS and TKWT. Both SPSM and TKWT were positively correlated with GYLD. Based on the standardized path coefficients, Dhungana et al. (2007) observed a highly significant direct positive effect of GEI of SPSM on grain yield GEI, which ultimately increased grain yield.

QTL Identification in the 223 CNN(RICLs3A) Population

A total of 19 QTL corresponding to the seven traits including GYLD were identified using composite interval mapping (Fig. 1). The results of the QTL analysis for individual environments and combined environments are summarized in Table 3. To facilitate description of the QTL and their comparison among the population sets, chromosome 3A was arbitrarily divided into 5 regions containing the detected QTL (Fig. 1). Region 1 spanned the segment within *Xbarc310–Xgwm218*, Region 2 within *Xbarc86–Xstm99*, Region 3 within *Xhbg284–Xgwm497*, Region 4 within *Xcfa2193–Xgwm155*, and Region 5 within

Table 2. Phenotypic correlations of 223 CNN(RICLs3A) for grain yield (GYLD), spikes per square meter (SPSM), kernels per spike (KPS), 1000-kernel weight (TKWT), grain volume weight (GVWT), plant height (PHT), and anthesis date (AD) based on data pooled across Nebraska environments (n = 223).

	SPSM	KPS	TKWT	GVWT	PHT	AD
GYLD	0.64**	−0.06	0.18**	0.29**	−0.39**	−0.45**
SPSM		−0.47**	−0.18**	0.31**	−0.38**	−0.213**
KPS			−0.30**	−24**	0.20**	0.32**
TKWT				0.13*	−0.15*	−0.63**
GVWT					−0.35**	−0.35**
PHT						0.50**

*Significantly different from zero at 0.05 level of probability.

**Significantly different from zero at 0.01 level of probability.

Table 3. Quantitative trait loci (QTL) for grain yield, spikes per square meter, kernels per spike, and 1000-kernel weight in individual environments and combined across five environments, and for grain volume weight, plant height, and anthesis date in individual environments and combined across six environments detected by composite interval mapping in 223 CNN(RICLs3A).

Trait	Environment†	QTL	Marker interval‡	Position (cM)§	Distance from the nearest marker (cM)¶	Var (%)#	Add. effect††	LOD‡‡
Grain yield	Mead 2005	*QGyld.unl.3A.1*	*Xwmc532-Xgwm218*	4.5	0.1	12.6	+163 Kg ha^{-1}	6.8
	Mead 2006	*QGyld.unl.3A.1*	*Xwmc532-Xgwm218*	8.0	3.6	10.6	+63	4.6
		QGyld.unl.3A.4	*Xhbg491-Xgwm155*	87.1	0.0	5.3	+45	2.9
	Lincoln 2006	*QGyld.unl.3A.2*	*Xhbg284-Xwmc428*	52.1	2.0	7.5	+135	3.3
	Mead 2007	*QGyld.unl.3A.2*	*Xpsp3047-Xbarc356*	44.5	1.1	11.4	+101	6.7
	Combined	*QGyld.unl.3A.1*	*Xwmc532-Xgwm218*	4.4	0.0	12.1	+61	7.2
		QGyld.unl.3A.2	*Xwmc664-Xbarc67*	45.4	0.1	5.2	+47	3.2
Spikes per square meter	Mead 2005	*QSpsm.unl.3A.1*	*Xbarc12-Xwmc11*	2.8	0.0	15.4	+31.2 spikes	8.5
	Lincoln 2006	*QSpsm.unl.3A.2*	*Xpsp3047-Xbarc356*	43.6	0.5	11.4	+19.3	6.1
	Mead 2006	*QSpsm.unl.3A.4*	*Xwmc559-Xhbg491*	85.5	1.6	5.6	+9.5	2.6
	Combined	*QSpsm.unl.3A.1*	*Xbarc12-Xwmc11*	2.8	0.0	8.6	+8.2	5.4
		QSpsm.unl.3A.2	*Xwmc664-Xbarc67*	45.4	0.1	10.6	+10.9	6.5
Kernels per spike	Lincoln 2006	*QKps.unl.3A.1*	*Xbarc310-Xbarc321*	1.8	0.0	4.7	+42 kernels	2.5
		QKps.unl.3A.3	*Xhbg284-Xwmc428*	53.1	1.9	8.5	−0.71	3.8
	Mead 2005	*QKps.unl.3A.3*	*Xcfa2262- Xbarc1060*	56.4	0.0	6.3	−0.42	3.2
	Mead 2006	*QKps.unl.3A.3*	*Xbarc1060-Xhbg227*	64.0	3.7	7.7	−0.66	3.3
	Combined	*QKps.unl.3A.1*	*Xbarc310-Xbarc321*	1.0	0.8	9.7	+0.38	5.1
		QKps.unl.3A.3	*Xwmc428-Xcfa2262*	56.1	0.3	7.0	−0.31	3.9
1000-kernel weight	Mead 2005	*QTkwt.unl.3A.2*	*Xbarc1044-Xbarc324*	46.8	0.1	6.9	−0.70 g	3.6
	Mead 2006	*QTkwt.unl.3A.1*	*Xbarc57-Xbarc12*	2.8	0.0	6.4	−0.33	3.3
	Lincoln 2006	*QTkwt.unl.3A.1*	*Xbarc57-Xbarc12*	2.8	0.0	10.7	−0.41	5.6
	Combined	*QTkwt.unl.3A.1*	*Xbarc321-Xbarc57*	1.8	0.0	8.0	−0.31	4.3
Grain volume weight	Lincoln 2005	*QGvwt.unl.3A.2*	*Xbarc356-Xwmc664*	44.5	0.1	8.5	+0.40 Kg hL^{-1}	5.1
	Lincon 2006	*QGvwt.unl.3A.2*	*Xpsp3047-Xbarc356*	44.2	0.1	10.8	+0.17	6.3
	Mead 2005	*QGvwt.unl.3A.2*	*Xbarc356-Xwmc664*	44.1	0.0	5.8	+0.31	3.4
		QGvwt.unl.3A.4	*Xgwm155-Xcfa2183*	90.8	0.3	4.6	+0.35	2.6
	Sidney 2005	*QGvwt.unl.3A.2*	*Xbarc67-Xbarc1044*	45.7	0.0	5.0	+0.42	3.0
	Mead 2007	*QGvwt.unl.3A.2*	*Xbarc1044-Xbarc324*	45.7	0.0	10.1	+0.25	5.3
	Mead 2006	*QGvwt.unl.3A.3*	*Xgwm497-Xcfa2193*	80.8	0.0	6.4	+0.18	3.8
	Combined	*QGvwt.unl.3A.2*	*Xpsp3047-Xbarc356*	44.1	0.0	8.3	+0.20	6.7
		QGvwt.unl.3A.3	*Xhbg227-Xgwm497*	73.7	4.6	10.0	+0.20	5.2
Plant height	Lincoln 2005	*QPht.unl.3A.1*	*Xwmc532-Xgwm218*	8.0	3.6	7.3	–1.50 cm	3.1
	Lincoln 2006	*QPht.unl.3A.1*	*Xwmc11-Xwmc532*	4.4	0.0	6.2	−0.97	3.2
	Mead 2006	*QPht.unl.3A.1*	*Xbarc310-Xbarc321*	1.8	0.0	5.8	−0.57	3.0
	Mead 2007	*QPht.unl.3A.1*	*Xbarc57-Xbarc12*	2.8	0.0	5.1	−0.74	2.5
	Mead 2005	*QPht.unl.3A.1*	*Xwmc532-Xgwm218*	10.0	5.6	12.2	–1.13	6.0
		QPht.unl.3A.2	*Xbarc324-Xwmc489*	47.3	0.1	9.3	–1.0	6.2
	Sidney 2005	*QPht.unl.3A.1*	*Xwmc532-Xgwm218*	7.5	3.1	12.6	–1.53	7.7
		QPht.unl.3A.2	*Xbarc86-Xgwm5*	42.0	0.0	14.6	–1.86	9.4
	Combined	*QPht.unl.3A.1*	*Xwmc11-Xwmc532*	4.3	0.1	16.8	−0.92	10.9
		QPht.unl.3A.2	*Xbarc67- Xbarc1044*	45.5	0.0	5.4	−0.60	3.8
		QPht.unl.3A.4	*Xwmc559-Xhbg491*	87.1	0.0	3.9	−0.56	2.8
Anthesis date	Sidney 2005	*QAd.unl.3A.2*	*Xgwm5-Xpsp3047*	42.0	0.0	13.5	−0.32 d	7.2
	Mead 2007	*QAd.unl.3A.4*	*Xhbg491-Xgwm155*	87.1	0.0	5.2	−0.43	2.8
		QAd.unl.3A.5	*Xwmc388-Xbarc1021*	105.3	0.7	5.8	+0.46	3.0

† Environment specifying the location and year under which field evaluation of CNN(RICLs3A) was conducted.

‡ Markers flanking a QTL located at the highest LOD peak.

§ Position of a QTL from the first marker on the linkage map.

¶ Distance of a QTL location from the nearest flanking marker.

Phenotypic variance (R^2) accounted for by a QTL, estimated based on the additive effect only.

†† Additive genetic effect, a positive sign means that Wichita allele increased the trait value while a negative sign means it decreased the trait value.

‡‡ Logarithm of odds score was recorded at the highest peak of a QTL LOD plot. The underlined LOD scores are below the estimated threshold value but ≥ 2.5 (the average value of the entire data set) and shown only if the same QTL was detected significantly in any other environment or combined across environments.

Xcfa2183–Xbarc1021. Region 1 contained five, Region 2 six, Region 3 two, Region 4 five, and Region 5 one QTL affecting different traits. The number of QTL identified for an individual trait ranged from one to three. The identified QTL individually accounted for 3.9 to 16.8% of the total variation for the seven agronomic traits (Table 3).

Grain Yield

Three QTL were found to be associated with GYLD of which *QGyld.unl.3A.1* was localized in Region 1, *QGyld.unl.3A.2* was in Region 2, and *QGyld,unl.3A.4* was in Region 4 (Fig. 1, Table 3). *QGyld.unl.3A.1* was detected in two individual environments as well as in the analysis with the data combined over environments explaining 10.6 to 12.6% of the total phenotypic variation. Similarly, *QGyld.unl.3A.2* was detected in two environments and in the analysis with data combined across environments, and explained 5.2 to 11.4% of the phenotypic variation. The QTL *QGyld.unl.3A.4* was detected only in one environment, Mead 2006. All these QTL were located at a distance of 0.0 cM to 3.6 cM from the nearest flanking markers. For all the QTL, the WI alleles provided favorable additive effects ranging from 45.0 to 163 kg ha^{-1}.

Spikes per Square Meter

Three QTL for SPSM were detected in three individual environments; two also were detected in the combined data across the environments and explained 5.6 to 15.4% of the total phenotypic variation (Table 3). The first QTL *QSpsm.unl.3A.1* located in Region 1 (Fig. 1) was detected in the Mead 2005 trial and in the data combined across environments with high LOD scores of 8.5 and 5.4, respectively. The second QTL *QSpsm.unl.3A.2* located in Region 2 (Fig. 1) was detected in the Lincoln 2006 environment and in the combined analysis with high LOD values of 6.1 and 6.5, respectively. The third QTL designated *QSpsm.unl.3A.4* was detected only in the Mead 2006 environment and was localized in Region 4 with a LOD score of 2.9. Each of the detected QTL was located very close to the nearest flanking markers at a distance of 0.0 to 1.6 cM. For all three QTL, favorable alleles were donated from WI and demonstrated additive effects resulting in an increase of 8.2 to 31.2 SPSM.

Kernels per Spike

For KPS, only two QTL were identified in three out of the five environments and in the data combined across environments, and accounted for phenotypic variation of 6.3 to 9.7% (Table 3). The QTL *QKps.unl.3A.1* located in Region 1 was detected only for the data combined over environments. The QTL *QKps.unl.3A.3* located in Region 3 was detected in three environments (Mead 2005, Lincoln 2006, and Mead 2006) as well as in the combined data across environments. Both of the KPS QTL were localized within 0.8 cM of the nearest flanking markers in the combined analyses (Table 3). The allele for increased KPS for QTL *QKps.unl.3A.1* was contributed by WI whereas for QTL *QKps.unl.3A.3* it was contributed by CNN. The favorable alleles of these QTL resulted in an increase of 0.31 to 0.71 KPS.

1000-Kernel Weight

Of the two QTL associated with TKWT, only one (*QTkwt.unl.3A.1*) was detected consistently in two environments (Mead 2006 and Lincoln 2006) and in data combined across environments. These QTL explained 6.4 to 10.7% of the total phenotypic variation (Table 3, Fig. 1). The other QTL *QTkwt.unl.3A.2* (Region 2) was detected only in one environment and accounted for 6.9% of the phenotypic variation and was not detected in the combined analysis. For both QTL, CNN contributed to the increase of seed weight, meaning that the substitution of WI alleles for CNN alleles resulted in a decrease of 0.31 to 0.70 g in TKWT. The detected QTL were localized 0.0 to 0.1 cM from the nearest flanking markers.

Grain Volume Weight

A total of three QTL affecting GVWT were detected in three genomic regions of chromosome 3A accounting for 4.6 to 10.8% of the phenotypic variation (Table 3). Out of the three, QTL *QGvwt.unl.3A.2* located in Region 2 in the interval that spanned 44.1 to 45.7 cM from the first marker was detected in five individual environments as well as in the combined analysis (Fig. 1). Another QTL, *QGvwt.unl.3A.3,* was located in Region 3 within the interval 73.7 to 80.8 cM and was detected only in one environment (Mead 2006) and in the combined environments data. The third QTL (*QGvwt.unl.3A.4*) was located at the 90.8 cM position in Region 4 and was detected only in a single environment (Mead 2005). All of the GVWT QTL were localized within 0.3 cM from the nearest flanking markers in all analyses except one (*QGvwt.unl.3A.3* in combined analysis). For all these QTL, WI alleles contributed to the increase of grain volume weight, providing additive effects from 0.15 to 0.42 kg hL^{-1}.

Plant Height

Out of three QTL associated with PHT, QTL *QPht.unl.3A.1* (Region 1) was detected with significant LOD scores (ranging from 3.0 to 10.9) in five out of the six environments and in the data combined across environments. We also detected this QTL in the sixth environment (Mead 2007) with a LOD score of 2.5 that fell just below the significant threshold of 2.6. This QTL explained 5.8 to 16.8% of the total phenotypic variation (Table 3). The second QTL (*QPht.unl.3A.2*) was localized in Region 2 and was detected in two environments (Mead 2005 and Sidney 2005) and in the data combined across environments accounting for 9.3 to 14.6% of the total phenotypic variation. The third QTL (*QPht.unl.3A.4*) was detected in the combined analysis

only and accounted for 3.9% of the phenotypic variation. All the PHT QTL were localized within 5.6 cM from the nearest flanking markers, but in most analyses within 0.1 cM (Table 3). At all QTL, WI alleles contributed to the decrease of plant height and provided additive effects from 0.57- to 1.86-cm reduction in plant height.

Anthesis Date

A total of three QTL influencing AD were detected in two environments and accounted for 5.2 to 13.5% of the phenotypic variation (Table 3). None of these QTL was detected in the combined analysis. The QTL *QAd.unl.3A.2* (Region 2) was detected only in Sidney 2005 with a LOD score of 7.2 while QTL *QAd.unl.3A.4* (Region 4) and *QAD.unl.3A.5* (Region 5) were detected only in Mead 2007 with LOD scores of 2.8 and 3.0, respectively. All of these QTL were localized at 0.0 to 0.7 cM from the nearest flanking markers (Table 3). The alleles of the QTL *QAd.unl.3A.2* and *QAd.unl.3A.4* that decreased AD were derived from WI with additive effects of 0.32 to 0.43 d, respectively. On the contrary, the WI allele at *QAd.unl.3A.5* locus contributed to the increase of AD with an additive effect of 0.46 d.

Comparison among the CNN(RICLs3A) Populations

Quantitative trait loci detection efficiency was compared among the combined 223 CNN(RICLs-3A), the 128 CNN(RICLs3A)-DH and the 95 CNN(RICLs3A)-RML populations. QTL analyses for the 95 CNN(RICLs3A)-RML were conducted using phenotypic data collected from the 2005–2007 evaluation as part of the combined 223 CNN(RICLs3A) population. Data collected by Campbell et al. (2003) from their 1999–2001 evaluation also was used. The QTL analysis for 95 CNN(RICLs3A)-RML 1999–2001 evaluation was repeated using the original marker data (15 RFLPs and 5 SSRs) and following the current QTL analysis conditions of 1000 permutations and a 0.01 significance level. In the previous report by Campbell et al. (2003), less stringent threshold LOD values were used as they were generated using 300 permutations at a significance level of 0.05. Only 5 SSR markers (*Xbarc57, Xbarc12, Xbarc86, Xbarc67,* and *Xgwm155*) of the map of 95 CNN(RICLs3A)-RML 1999–2001 evaluation set were common with the current linkage maps, and based on these five anchor markers we tried to make a reasonable comparison. The CNN(RICLs3A) linkage map for 2005–2007 covered a greater genomic region of chromosome 3A compared with the 95 CNN(RICLs3A)-RML 1999–2001 set map because the last common marker *Xgwm155* was located at the distal end of the long arm on the map of the 95 CNN(RICLs3A)-RML 1999–2001 set while it was 17 cM proximal to the long arm end on the 223 CNN(RICLs3A) map (Fig. 1) and also at similar positions in other two subpopulation maps.

For GYLD, three QTL were detected in the combined 223 CNN(RICLs3A) set (Regions 1, 2, and 4), two GYLD QTL in the 128 CNN(RICLs3A)-DH set (Regions 1 and 2), and one QTL was evident in both the 95 CNN(RICLs3A)-RML (2005–2007 and 1999–2001 evaluation) sets (Region 2; Table 4). For SPSM, three QTL were detected in the 223 CNN(RICLs3A) set (Regions 1, 2, and 4), two QTL were evident in the 128 CNN(RICLs3A)-DH set (Regions 1 and 2) and in the 95 CNN(RICLs3A)-RML (2005–2007 and 1999–2001 evaluation) sets (Regions 2 and 3; Table 4). For KPS, two QTL were identified in the combined 223 CNN(RICLs3A) set and in the 128 CNN(RICLs3A)-DH set (Regions 1 and 3), while only one QTL was evident in the 95 CNN(RICLs3A)-RML sets (Region 3 for the set evaluated in 2005–2007 and Region 1 for the set evaluated in 1999–2001; Table 4). For TKWT, two QTL were detected in the combined 223 CNN(RICLs3A) set (Regions 1 and 2), while only one QTL was detected in the 128 CNN(RICLs3A)-DH set and in both sets of 95 CNN(RICLs3A)-RML (Region 1; Table 4). For GVWT, three QTL (Regions 2, 3, and 4) were detected in the combined 223 CNN(RICLs3A) set of which the Region 2 QTL was detected in five individual environments. Three GVWT QTL were also detected in the 128 CNN(RICLs3A)-DH set (Regions 2, 3, and 4), while only two QTL were detected in each of the 95 CNN(RICLs3A)-RML sets (Regions 2 and 3 for the 2005–2007 set and Regions 3 and 4 for the 1999–2001 set; Table 4). For PHT, three QTL in the combined 223 CNN(RICLs3A) set and in the 128 CNN(RICLs3A)-DH set were detected (Regions 1, 2, and 4), while 4 QTL were evident in the 95 CNN(RICLs3A)-RML 2005–2007 set (Regions 1, 2, 3, and 4) and two QTL were evident in the 95 CNN(RICLs3A)-RML 1999–2001 set (Table 4). For AD, three QTL were detected in the combined 223 CNN(RICLs3A) set (Regions 2, 4, and 5), while two AD QTL were evident in the 128 CNN(RICLs3A)-DH set (Regions 2 and 3), and no QTL were evident in either of the 95 CNN(RICLs3A)-RML sets (Table 4). For every trait except PHT, the combined 223 CNN(RICLs3A) set detected the most QTL.

DISCUSSION

QTL-Rich Regions and Pleiotropic Effects

Three small genomic segments of Region 1, Region 2, and Region 4 clearly harbor most of the agronomic trait QTL identified in this study (Fig. 1) based on the combined 223 CNN(RICLs3A) set. Region 1 contains QTL, *QGyld.unl.3A.1, QSpsm.unl.3A.1, QKps.unl.3A.1, QTkwt.unl.3A.1,* and *QPht.unl.3A.1* influencing GYLD, SPSM, KPS, TKWT, and PHT, respectively. Based on the analyses of the combined data across environments, these QTL were localized on a segment spanning 3.4 cM (position 1.0–4.4 cM) (Table 3, Fig. 1). Region 2 contains QTL, *QGyld.unl.3A.2,*

Table 4. Comparative quantitative trait loci (QTL) detection for grain yield and other agronomic traits in the combined 223 CNN(RICLs3A) set, 128 CNN(RICLs3A)-DH set and 95 CNN(RICLs3A)-RML set evaluated in 2005–2007 and 95 CNN(RICLs3A)-RML set evaluated in 1999–2001 in individual environments and data combined across environments.

	2005–2007 Evaluation					1999–2001 Evaluation		
			223 CNN(RICLs3A) (Combined set)	128 CNN(RICLs3A)-DH	95 CNN(RICLs3A)-RML	95CNN(RICLs3A)-RML		
Trait	Environment†	QTL‡	LOD§	LOD§	LOD§	Environment†	QTL‡	LOD§
Grain yield								
	Mead 2005	*QGyld.unl.3A.1*	6.8	4.1	–	Lincoln 2000	*QGyld.unl.3A.2*	3.1
	Mead 2006	*QGyld.unl.3A.1*	4.6	3.1	–	Lincoln 2001	*QGyld.unl.3A.2*	3.5
		QGyld.unl.3A.2	–	–	2.7	Mead 2001	*QGyld.unl.3A.2*	6.9
		QGyld.unl.3A.4	2.9	–	–	Combined	*QGyld.unl.3A.2*	4.2
	Lincoln 2006	*QGyld.unl.3A.2*	3.3	–	3.6			
	Mead 2007	*QGyld.unl.3A.2*	6.7	3.4	3.6			
	Combined	*QGyld.unl.3A.1*	7.2	3.0	–			
		QGyld.unl.3A.2	3.2	–	4.5			
Spikes per square meter								
	Mead 2005	*QSpsm.unl.3A.1*	8.5	5.5	–	Lincoln 2001	*QSpsm.unl.3A.2*	3.0
	Lincoln 2006	*QSpsm.unl.3A.2*	6.1	2.9	5.6	Mead 2001	*QSpsm.unl.3A.2*	2.7
		QSpsm.unl.3A.3	–	–	3.9	Combined	*QSpsm.unl.3A.3*	4.0
	Mead 2006	*QSpsm.unl.3A.4*	2.6	–	–			
	Mead 2007	*QSpsm.unl.3A.3*	–	–	3.3			
	Combined	*QSpsm.unl.3A.1*	5.4	2.9	–			
		QSpsm.unl.3A.2	6.5	4.8	3.5			
Kernels per spike								
	Lincoln 2006	*QKps.unl.3A.1*	2.5	–	–			
		QKps.unl.3A.3	3.8	–	3.1	Sidney 2001	*QKps.unl.3A.1*	3.3
	Mead 2005	*QKps.unl.3A.3*	3.2	–	3.2	Combined	*QKps.unl.3A.1*	2.8
	Mead 2006	*QKps.unl.3A.3*	3.3	–	–			
	Combined	*QKps.unl.3A.1*	5.1	3.4	–			
		QKps.unl.3A.3	3.9	2.7	–			
1000-kernel weight								
	Mead 2005	*QTkwt.unl.3A.2*	3.6	–	–			
	Mead 2006	*QTkwt.unl.3A.1*	3.3	–	–	Lincoln 2001	*QTkwt.unl.3A.1*	3.11
	Lincoln 2006	*QTkwt.unl.3A.1*	5.6	3.1	4.4			
	Combined	*QTkwt.unl.3A.1*	4.3	3.6	–			
Grain volume weight								
	Lincoln 2005	*QGvwt.unl.3A.2*	5.1	3.21	4.2	Lincoln 1999	*QGvwt.unl.3A.3*	3.1
	Lincon 2006	*QGvwt.unl.3A.2*	6.3	–	–	Lincoln 2001	*QGvwt.unl.3A.3*	4.2
	Mead 2005	*QGvwt.unl.3A.2*	3.4	–	3.5		*QGvwt.unl.3A.4*	3.9
		QGvwt.unl.3A.3	–	3.0	–	Combined	*QGvwt.unl.3A.3*	5.8
		QGvwt.unl.3A.4	2.7	–	–			
	Sidney 2005	*QGvwt.unl.3A.2*	3.0	–	–			
		QGvwt.unl.3A.4	–	3.2	–			
	Mead 2007	*QGvwt.unl.3A.2*	5.3	–	–			
		QGvwt.unl.3A.3	–	5.9	–			
	Mead 2006	*QGvwt.unl.3A.3*	3.8	4.6	4.1			
	Combined	*QGvwt.unl.3A.2*	6.7	–	5.9			
		QGvwt.unl.3A.3	5.2	12.8	4.8			
Plant height								
	Lincoln 2005	*QPht.unl.3A.1*	3.1	–	–	Sidney 2000	*QPht.unl.3A.2*	4.3
	Lincoln 2006	*QPht.unl.3A.1*	3.2	–	4.6		*QPht.unl.3A.3*	4.3
		QPht.unl.3A.3	–	–	4.8			
	Mead 2006	*QPht.unl.3A.1*	3.0	–	–			
	Mead 2007	*QPht.unl.3A.1*	2.5	–	–			
	Mead 2005	*QPht.unl.3A.1*	6.0	6.4	–			

(cont'd)

Table 4. Continued.

			2005–2007 Evaluation			1999–2001 Evaluation		
			223 CNN(RICLs3A) (Combined set)	128 CNN(RICLs3A)-DH	95 CNN(RICLs3A)-RML	95CNN(RICLs3A)-RML		
Trait	Environment†	QTL‡	LOD§	LOD§	LOD§	Environment†	QTL‡	LOD§
		QPht.unl.3A.2	6.2	3.2	3.3			
		QPht.unl.3A.4	–	–	3.6			
	Sidney 2005	*QPht.unl.3A.1*	7.7	–	3.7			
		QPht.unl.3A.2	9.4	8.5	6.1			
	Combined	*QPht.unl.3A.1*	10.9	5.1	5.9			
		QPht.unl.3A.2	3.8	4.6	3.8			
		QPht.unl.3A.4	2.8	3.2	4.2			
Anthesis date								
	Sidney 2005	*QAd.unl.3A.2*	7.2	5.6	–	No QTL was detected		
	Mead 2007	*QAd.unl.3A.4*	2.8	–	–			
		QAd.unl.3A.5	3.0	–	–			
	Lincoln 2005	*QAdl.unl.3A.3*	–	2.9	–			

† Environment specifying the location and year under which field evaluation of CNN(RICLs3A) was conducted.

‡ A QTL was designated based on the name of the trait and location (region) on the chromosome 3A.

§ Logarithm of odds score was recorded at the highest peak of a QTL LOD plot. The underlined LOD score is below the estimated threshold value but equal or more than the average value of the entire data set, and shown only if the same QTL was detected significantly in any other environment or data combined across environments.

QSpsm.unl.3A.2, QTkwt.unl.3A.2, *QGvwt.unl.3A.2*, *QPht.unl.3A.2,* and *QAd.unl.3A.2* affecting GYLD, SPSM, TKWT, GVWT, PHT, and AD, respectively, on a segment spanning 5.3 cM (position 42.0–47.3 cM) in all analyses (Table 3, Fig. 1). Region 4 contains QTL, *QGyld.unl.3A.4*, *QSpsm.unl.3A.4*, *QGvwt.unl.3A.4*, *QPht.unl.3A.4,* and *QAd.unl.3A.4* affecting GYLD, SPSM, GVWT, PHT, and AD, respectively, on a segment spanning 5.3 cM (position 85.5–90.8 cM). In many cases, co-localization of the QTL was consistent over environments.

As would be expected with the co-localized QTL (Kumar et al., 2007), GYLD showed positive correlations with GVWT, SPSM, and TKWT and a negative correlation with PHT (Table 2). A negative correlation between GYLD and PHT indicates higher grain yield is associated with shorter plants. Berke et al. (1992a) also observed an association of grain yield and plant height, and they concluded the increase in grain yield of the substitution lines, CNN (WI 3A) and CNN (WI 6A), might be due to earliness and reduced plant height of these lines. In fact, both CNN and WI are tall or conventional height cultivars, so this height reduction is not associated with the well-known *Rht* semidwarfing loci located on group 4 chromosomes (Borner et al., 1997; Ellis et al., 2002). Classical quantitative genetics assumes that trait correlation is a causal effect of pleiotropic or closely linked genes. Therefore, it is expected that the QTL for the correlated traits would be mapped in the same genomic position. The observed phenotypic correlation of higher GYLD with increased SPSM and GVWT and decreased PHT could be attributable to the co-localized QTL (as observed in Region 1 and 2) associated with these traits, the favorable alleles of which originated from the same parent, WI. These coincident QTL on chromosome 3A were detected in data combined across environments. Other studies also revealed the detection of coincidence of yield QTL with the QTL for yield components or other developmental traits (Wang et al., 2009; Cuthbert et al., 2008; Kumar et al., 2007; Kato et al., 2000).

Consistency of QTL Detection across Environments

We evaluated the 223 CNN(RICLs3A) population for GYLD, SPSM, KPS, and TKWT in five environments and GVWT, PHT, and AD in six environments (three locations over 1–3 yr). A total of 19 QTL were found to be associated with these traits, but only one QTL (*QPht.unl.3A.1*) for PHT was detected virtually in all environments evaluated. For GVWT, one (*QGvwt.unl.3A.2*) out of three associated QTL was detected in five environments. For GYLD, two (Region 1 and 2) out of three associated QTL were detected commonly in two environments only. Similarly, for KPS, one (*QKps.unl.3A.3*) of the two associated QTL was detected in three out of five environments. All other QTL affecting GYLD, GVWT, SPSM, KPS, TKWT, PHT, and AD were detected in only one or two environments, and some were also detected in the analyses with data combined across environments. Estimated additive effects of the individual QTL across the environments also varied. The inability of the current trials to consistently identify all or most of the QTL and uniform QTL effects across the environments suggests the sensitivity of the QTL to the environments. Detection of QTL in one environment but not in another was considered to be an indication of GEI and QTL × E interaction (Zhuang et al., 2002). Even those QTL that were readily detected in different environments still might have significant GEI effects (Xing et al., 2002;

Yue et al., 2006). In studies with 95 CNN(RICLs3A)-RML evaluated in 1999–2001 (Campbell et al., 2003) and with 50 CNN(RICLs3A)-RML (Shah et al., 1999b), QTL for GYLD and other related traits were not identified consistently across all the environments as was observed in the current combined 223 CNN(RICLs3A) population. The observed significant CNN(RICLs3A) × E interaction for all the traits (Table 1) supports the sensitivity of the QTL to the environment that resulted in the failure of their consistent detection and uniform effects. The check cultivars included in the test showed significant GEI for all the traits while the parents showed significant GEI for SPSM, GVWT, PHT, and AD (Table 1). This further indicates the presence of environmental interaction effects that impacted the QTL detection in the CNN(RICLs3A) population. The parents, CNN and CNN(WI3A), were not consistently different for all the traits in every environment (data not shown), indicating that the favorable QTL alleles may not have been expressed at detectable levels in some of the environments.

In addition to the studies involving CNN(RICLs3A), environmental sensitivity of QTL influencing grain yield and other agronomic traits has also been reported in wheat (Quarrie et al., 2005; Kuchel et al., 2007a; Kumar et al., 2007; Wang et al., 2009), rice (Hittalmani et al., 2003; Xing et al., 2002), maize (Lima et al., 2006; Vargas et al., 2006), and barley (Zhu et al., 1999; Bezant et al., 1997). Each of these studies failed to detect all or most of the QTL or uniform QTL effects consistently across all of their test environments, suggesting the presence of QTL × E interactions. The six environments (2005–2007) under which the current population sets were evaluated and the environments (1999–2001) under which the 95 CNN(RICLs3A)-RML set were evaluated were different with regard to the average annual temperature, precipitation, solar irradiation, humidity, and other weather elements and soils (Peterson, 1992). Methods to study the effects of temperature, precipitation, and solar irradiation during vegetative and reproductive stages on QTL × environment interactions were proposed by Campbell et al. (2004) and Dhungana et al. (2007), who found temperature and precipitation were the main factors to explain QTL × environment interactions.

Recombination Difference between CNN(RICLs3A)-RML and CNN(RICLs3A)-DH

Among the three maps developed using the common 32 microsatellite markers, the 128 CNN(RICLs3A)-DH set produced the smallest linkage map as shown in Fig. 1. Similar to the 95 CNN(RICLs3A)-RML (1999–2001) map composed of 15 RFLP and 5 microsatellite markers, the current three linkage maps illustrate two significant gaps in regions flanked by *Xwmc532* to *Xbarc86* and *Xbarc1060* to *Xgwm497*. However, the gap present in the RML-derived map of the 95 CNN(RICLs3A) 2005–2007 set from *Xbarc1060* to *Xgwm497* is much larger than that in the DH-derived map of the 128 CNN(RICLs3A) set. This indicates that recombination within this region differs between the RML- and DH-derived CNN(RICLs3A). The distance from *Xbarc1060* to *Xgwm497* is 35.8 cM in the RML-derived map, while the distance is 12.9 cM in the DH-derived map. The 22.-cM difference between the RML and DH maps for this interval accounts for most of the difference in the total lengths of the two linkage maps. The difference in recombination in this region between the RML- and DH-derived maps could be a result of differential population size (128 vs. 95), chance, or some unknown biological difference between the RML and DH methods used to develop RICLs in this study. Interestingly, the other major gap present within chromosome 3A (*Xwmc532 to Xbarc86*) is consistently large in both the RML- and DH-derived linkage maps. This finding indicates that this region is inherently low in recombination or has been conserved through breeding. Similar significant differences in total map length between the population types derived from the same cross combinations were also reported, such as, RIL vs. DH in rice (He et al., 2001) and BC_1 vs. DH in cotton (*Gossypium* spp., Song et al., 2005b).

Comparative Power on the Detection of QTL Displayed by the CNN(RICLs3A) Sets

In the present study we observed that the highest number of QTL was identified in the combined 223 CNN(RICLs3A) set with more frequent detections across individual environments than that in the other smaller subpopulation sets. For seven agronomic traits, 19 QTL in the 223 CNN(RICLs3A) set were detected compared with 15 QTL in the 128 CNN(RICLs3A)-DH set, 12 QTL in the 95 CNN(RICLs3A)-RML 2005–2007 set, and 9 QTL in 95 CNN(RICLs3A)-RML 1999–2001 set. Considering data across environments, 12 QTL in the 223 CNN(RICLs3A) set were detected compared with 10 QTL in the 128 CNN(RICLs3A)-DH set, 7 QTL in the 95 CNN(RICLs3A)-RML 2005–2007 set, and 4 QTL in the 95 CNN(RICLs3A)-RML 1999–2001 set. As expected, QTL were detected in the greatest number of individual environments for most of the traits in the 223 CNN(RICLs3A) set. For example, Region 1 PHT QTL (*QPht.unl.3A.1*) was detected in six individual environments in the 223 CNN(RICLs3A) set while it was detected only in one environment in the 128 CNN(RICLs3A)-DH set, two environments in the 95 CNN(RICLs3A) 2005–2007 set, and was not detected in the 95 CNN(RICLs3A) 1999–2001 set. Similar results were also observed with Region 2 GVWT QTL (*QGvwt.unl.3A.2*) and Region 3 KPS QTL (*QKps.unl.3A.3*).

Darvasi et al. (1993) suggested that the number of lines is more important than the number of markers in the detection of increased number of QTL once a reasonable number of markers has been mapped. The maps of the 223 CNN(RICLs3A),

128 CNN(RICLs3A)-DH, and the 95 CNN(RICLs3A)-RML (2005–2007 trial) sets were composed of the same 32 markers. Thus, we could conclude that the detection of greater number of QTL in the 223 CNN(RICLs3A) set is attributable to the larger population size, as expected. By using the increased number of CNN(RICLs3A), in the current study we increased the power to detect QTL, improved the estimation of QTL effects (in agreement with Vales et al., 2005; Haley and Andersson, 1997; Kaeppler, 1997; Hackett, 2002), and localized the QTL to smaller segments similar to the findings by Robin et al. (2003). The increased number of RICLs in the 223 CNN(RICLs3A) also increased the reliability of QTL detection (Bernardo, 2004) and enhanced the resolution supporting the research by Keurentjes et al. (2007) that an increase in the number of recombinant lines increases the number of observations of each genotype at a given genomic position and also increases the recombination events which can improve resolution.

Common QTL with Other Populations

Generally, it is difficult to make a comparison of QTL across genetic backgrounds because of the absence of common markers between studies. However, we were able to identify a few QTL located in similar genomic locations directly based on the common markers or indirectly based on the positions of the relevant markers on the reference maps. Wang et al. (2009) detected a QTL for grain number per ear (syn. KPS) at the interval between SSR markers *Xwmc505* and *Xwmc264* on chromosome 3A in a Chinese winter wheat population, which maps near our QTL *QKps.unl.3A.3* close to the marker *Xwmc428*. Marker *Xwmc428* is positioned between *Xwmc505* and *Xwmc264* on the microsatellite consensus map (Somers et al., 2004). Kumar et al. (2007) reported a QTL affecting tiller number per plant (similar to SPSM) close to SSR marker *Xgwm720* (genomic position 44.5 cM from the first marker) on Chromosome 3A in an Indian bread wheat population. At a similar genomic position (45.4 cM) close to the SSR markers *Xwmc664/Xbarc67,* we identified a QTL, *QSpsm.unl.3A.2*. Cuthbert et al. (2008) reported detection of a QTL affecting days to heading (a trait related to AD) on chromosome 3A located close to the SSR marker *Xwmc664* in a spring wheat population. QTL *QAd.unl.3A.2* affecting AD in our study was also located close to the SSR marker *Xwmc664* (Fig. 1). Conservation of QTL across genetic backgrounds was also previously reported (Lin et al., 2009; Kumar et al., 2007; Guzman et al., 2007; Brummer et al., 1997).

CONCLUSIONS

Although our comparison of DH- and RML-derived CNN(RICLs3A) did show differences in the recombination events sampled within each population type, it appears the two methods of RICLs development did not affect the power to detect QTL significantly. Thus, we think that the RICLs derived from DHs should be preferred as their development is simpler than the RICLs derived from RMLs. Due to the increased number of lines, improved resolution, and closely spaced markers, new QTL were identified in the combined 223 CNN(RICLs3A) population, and the QTL for GYLD and other related agronomic traits were localized in smaller genomic regions. Quantitative trait loci explaining a larger portion of phenotypic variation influencing most of the agronomic traits are located in two genomic regions (Region 1 and 2). The favorable alleles for GYLD, SPSM, GVWT, KPS, and PHT originated from Wichita and most of them were co-localized on chromosome 3A, indicating their tight linkage or pleiotropic effects (of genes). The co-localization of the favorable alleles originated from Wichita provides an excellent opportunity for marker-assisted selection for these traits using a small set of tightly linked markers and for finer mapping (currently underway).

Acknowledgments

The research was supported by USDA–CSREES-NRI Grant 2004-14700. We thank very much Mitchell Montgmery and Gregory Dorn, Research Technologists, Dep. of Agron. and Hortic., Univ. of Nebraska-Lincoln, for their help with the greenhouse and field experiments, and the graduate students of the wheat breeding group, Neway Mengistu, Lekgari A. Lekgari, and Javed Sidqi, for their help with the field experiments.

References

Arumuganathan, K., and E.D. Earle. 1991. Nuclear DNA content of some important plant species. Plant Mol. Biol. Rep. 9:208–219.

Berke, T.G., P.S. Baenziger, and R. Morris. 1992a. Chromosomal location of wheat quantitative trait loci affecting agronomic performance of seven traits, using reciprocal chromosome substitutions. Crop Sci. 32:621–627.

Berke, T.G., P.S. Baenziger, and R. Morris. 1992b. Chromosomal location of wheat quantitative trait loci affecting stability of six traits, using reciprocal chromosome substitutions. Crop Sci. 32:628–633.

Bernardo, R. 2004. What proportion of declared QTL in plants are false? Theor. Appl. Genet. 109:419–424.

Bezant, J., D. Laurie, N. Pratchett, J. Chojecki, and M. Kearsey. 1997. Mapping QTL controlling yield and yield components in a spring barley (*Hordeum vulagare* L.) cross using marker regression. Mol. Breed. 3:29–38.

Borner, A., M. Roder, and V. Korzan. 1997. Comparative molecular mapping of GA insensitive Rht loci on chromosomes 4B and 4D of common wheat (*Triticum aestivum* L.). Theor. Appl. Genet. 95:1133–1137.

Brummer, E.C., G.L. Graef, J. Orf, J.R. Wilcox, and R.C. Shoemaker. 1997. Mapping QTL for seed protein and oil content in eight soybean populations. Crop Sci. 37:370–378.

Campbell, B.T., P.S. Baenziger, K.M. Eskridge, H. Budak, N.A. Streck, A. Weiss, K.S. Gill, and M. Erayman. 2004. Using environmental covariates to explain genotype × environment and QTL × environment interactions for agronomic traits on chromosome 3A of wheat. Crop Sci. 44:620–627.

Campbell, B.T., P.S. Baenziger, K.S. Gill, K.M. Eskridge, H. Budak, M. Erayman, I. Dweikat, and Y. Yen. 2003. Identification of QTLs and environmental interactions associated with agronomic traits on chromosome 3A of wheat. Crop Sci. 43:1493–1505.

Churchill, G.A., and R.W. Doerge. 1994. Empirical threshold values for quantitative trait mapping. Genetics 138:963–971.

Cuthbert, J.L., D.J. Somers, A.L. Brule-Babel, P.D. Brown, and G.H. Crow. 2008. Molecular mapping of quantitative trait loci for yield and yield components in spring wheat (*Triticum aestivum* L.). Theor. Appl. Genet. 117:595–608.

Darvasi, A., A. Weinreh, V. Minke, J.I. Weller, and M. Soller. 1993. Detecting marker-QTL linkage and estimating QTL gene effect and map location using a saturated genetic map. Genetics 134:943–951.

Dhungana, P., K.M. Eskridge, P.S. Baenziger, B.T. Campbell, K.S. Gill, and I. Dweikat. 2007. Analysis of genotype-by-environment interaction in wheat using a structural equation model and chromosome substitution lines. Crop Sci. 47:477–484.

Ellis, M.H., W. Spielmeyer, K.R. Gate, G.J. Rebetzke, and R.A. Richards. 2002. Perfect markers for the Rht-B1b and Rht-D1b dwarfing genes. Theor. Appl. Genet. 105:1038–1042.

Guzman, P.S., B.W. Diers, D.J. Neece, S.K.S. Martin, A.R. LeRoy, C.R. Grau, T.J. Hughes, and R.L. Nelson. 2007. QTL associated with yield in three backcross-derived populations of soybean. Crop Sci. 47:111–122.

Hackett, C. 2002. Statistical methods for QTL mapping in cereals. Plant Mol. Biol. 48:585–599.

Haley, C., and L. Andersson. 1997. Linkage mapping of quantitative trait loci in plants and animals. p. 49–71. *In* P. Dear (ed.) Genome mapping: A practical approach. Oxford Univ. Press, New York.

Haley, C.S., and S.A. Knott. 1992. A simple regression method for mapping quantitative trait loci in line crosses using flanking markers. Heredity 69:315–324.

Hayden, M.J., P. Stephenson, A.M. Logojan, D. Khatkar, C. Rogers, J. Elsden, R.M.D. Koebner, J.W. Snape, and P.J. Sharp. 2006. Development and genetic mapping of sequence-tagged microsatellites (STMs) in bread wheat (*Triticum aestivum* L.). Theor. Appl. Genet. 113:1271–1281.

He, P., J.Z. Li, X.W. Zheng, L.S. Shen, C.F. Lu, Y. Chen, and L.H. Zhu. 2001. Comparison of molecular linkage maps and agronomic trait loci between DH and RIL populations derived from the same rice cross. Crop Sci. 41:1240–1246.

Hittalmani, S., N. Huang, B. Courtois, R. Venuprasad, H.E. Shashidhar, J.-Z. Zhung, K.-L. Zheng, G.-C. Wang, J.S. Sidhu, S. Srivantaneeyakul, V.P. Singh, P.G. Bagali, H.C. Prasanna, G. McLaren, and G.S. Khush. 2003. Identification of QTL for growth-and grain yield-related traits in rice across nine locations of Asia. Theor. Appl. Genet. 107:679–690.

Hori, K., K. Sato, N. Nankaku, and K. Takeda. 2005. QTL analysis in recombinant chromosome substitution lines and doubled haploid lines derived from a cross between *Hordeum vulgare* ssp. *vulgare* and *Hordeum vulgare* ssp. *spontaneum*. Mol. Breed. 16:295–311.

Joppa, L.R., D. Chengheng, G.E. Hart, and G.A. Hareland. 1997. Mapping gene(s) for grain protein in tetraploid wheat (*Triticum turgidum* L.) using a population of recombinant inbred chromosome lines. Crop Sci. 37:1586–1589.

Kaeppler, S.M. 1997. Quantitative trait locus mapping using sets of near-isogenic lines: Relative power comparisons and technical considerations. Theor. Appl. Genet. 95:384–392.

Kato, K., H. Miura, and S. Sawada. 2000. Mapping QTLs controlling grain yield and its component on chromosome 5A of wheat. Theor. Appl. Genet. 101:1114–1121.

Keurentjes, J.J.B., L. Bentsink, C. Alonso-Blanco, C.J. Hanhart, H.B.D. Vries, S. Effgen, D. Vreugdenhil, and M. Koornneef. 2007. Development of a near-isogenic line population of *Arabidopdsis thaliana* and comparison of mapping power with a recombinant inbred line population. Genetics 175:891–905.

Kosambi, D.D. 1944. The estimation of map distance from recombination values. Ann. Eugen. 12:172–175.

Kuchel, H., K. Williams, P. Langridge, H.A. Eagles, and S.P. Jefferies. 2007a. Genetic dissection of grain yield in bread wheat. II. QTL-by-environment interaction. Theor. Appl. Genet. 115:1015–1027.

Kuleung, C., P.S. Baenziger, and I. Dweikat. 2004. Transferability of SSR markers among wheat, rye and triticale. Theor. Appl. Genet. 108:1147–1159.

Kumar, N., P.L. Kulwal, H.S. Balyan, and P.K. Gupta. 2007. QTL mapping for yield and yield contributing traits in two mapping populations of bread wheat. Mol. Breed. 19:163–177.

Lander, E.S., and D. Botstein. 1989. Mapping Mendelian factors underlying quantitative traits using RFLP linkage maps. Genetics 121:185–199.

Lander, E.S., P. Green, J. Abrahamson, A. Burlow, M.J. Daly, S.E. Lincoln, and L. Newburg. 1987. Mapmaker an interactive computer package for constructing primary genetic linkage maps of experimental and natural populations. Genomics 1:174–181.

Law, C.N. 1966. The location of genetic factors affecting a quantitative character in wheat. Genetics 53:478–498.

Law, C.N., A.J. Worland, and B. Giorgi. 1976. The genetic control of ear emergence time by chromosome 5A and 5D in wheat. Heredity 36:49–58.

Lima, M. de L.A., C.L. de Souza, D.A.V. Bento, A.P. de Souza, and L.A.C.-Garcia. 2006. Mapping QTL for grain yield and plant traits in a tropical maize population. Mol. Breed. 17:227–239.

Lin, R., R.D. Horsley, N.L.V. Lapitan, Z. Ma, and P.B. Schwarz. 2009. QTL mapping of dormancy in barley using the Harrington/Morex and Chevron/Stander mapping populations. Crop Sci. 49:841–849.

Lizarazu, R., A. Mujeeb-Kazi, and M.D.H.M. William. 1992. Maize (*Zea mays* L.) mediated polyhaploid production in some Triticeae using a detached tiller method. J. Genet. Breed. 46:335–346.

Melchinger, A.E., H.F. Utz, and C.C. Schon. 1998. Quantitative trait locus (QTL) mapping using different testers and independent population samples in maize reveals low power of QTL detection and large bias in estimate of QTL effects. Genetics 149:383–403.

Morris, R. 1964–1984. Chromosomal locations of genes for wheat characters compiled from the literature. Ann. Wheat Newsl. Vol. 16–30.

Paterson, A.H., J.W. Deverna, B. Lanini, and S.D. Tanksley. 1990. Fine mapping of quantitative trait loci using selected overlapping recombinant chromosomes in an interspecies cross of tomato. Genetics 124:735–742.

Peterson, C.J. 1992. Similarities among test sites based on cultivar performance in the hard red winter wheat region. Crop Sci. 32:907–912.

Quarrie, S.A., A. Steed, C. Calestani, A. Semikhodskii, C. Lebreton, C. Chinoy, N. Steele, D. Pljevljakusic, E. Waterman, J. Weyen, J. Schondelmaier, D.Z. Habash, P. Farmer, L. Saker, D.T. Clarkson, A. Abugalieva, M. Yessimbekova, Y.

Turuspekov, S. Abugalieva, R. Tuberosa, M.-C. Sanguinetti, P.A. Hollington, R. Aragues, A. Royo, and D. Dodig. 2005. A high density genetic map of hexaploid wheat (*Triticum aestivum* L.) from Chinese Spring × SQ1 and its use to compare QTLs for grain yield across a range of environments. Theor. Appl. Genet. 110:865–880.

Robin, Y., A. Korol, M. Shtemberg, E. Nevo, and M. Soller. 2003. High-resolution mapping of quantitative trait loci by selective recombinant genotyping. Genetics 164:1657–1666.

SAS Institute. 1999. The SAS system for windows. Release 9.1. SAS Institute, Cary, NC.

Shah, M.M., P.S. Baenziger, Y. Yen, B. Moreno-Sevilla, and K. Halioglu. 1999a. Genetic analysis of agronomic traits controlled by wheat chromosome 3A. Crop Sci. 39:1016–1021.

Shah, M.M., K.S. Gill, P.S. Baenziger, Y. Yen, S.M. Kaeppler, and H.M. Ariyarathne. 1999b. Molecular mapping of loci for agronomic traits on chromosome 3A of bread wheat. Crop Sci. 39:1728–1732.

Sidhu, D., and K.S. Gill. 2004. Distribution of genes and recombination in wheat and other eukaryotes. Plant Cell Tissue Organ Cult. 79:257–270.

Somers, D.J., P. Isaac, and K. Edwards. 2004. A high-density microsatellite consensus map for bread wheat (*Triticum aestivum* L.). Theor. Appl. Genet. 109:1105–1114.

Song, Q.J., J.R. Shi, S. Singh, E.W. Fickus, J.M. Costa, J. Lewis, B.S. Gill, R. Ward, and P.B. Cregan. 2005a. Development and mapping of microsatellite (SSR) markers in wheat. Theor. Appl. Genet. 110:550–560.

Song, X., K. Wang, W. Guo, J. Zhang, and T. Zheng. 2005b. A comparison of genetic maps constructed from haploid and BC_1 mapping populations from the same crossing between *Gossypium hirsutum* L. and *Gossypium barbadense* L. 2005. Genome 48:378–390.

Torada, A., M. Koike, K. Mochida, and Y. Ogihara. 2006. SSR-based linkage map with new markers using an interspecific population of common wheat. Theor. Appl. Genet. 112:1042–1051.

Vales, M.I., C.C. Schön, F. Capettini, X.M. Chen, A.E. Corey, D.E. Mather, C.C. Mundt, K.L. Richardson, J.S. Sandoval-Islas, H.F. Utz, and P.M. Hayes. 2005. Effect of population size on the estimation of QTL: A test using resistance to barley stripe rust. Theor. Appl. Genet. 111:1260–1270.

Vargas, M., F.A. van Eeuwijk, J. Crossa, and J.M. Ribaut. 2006. Mapping QTLs and QTL × environment interaction for CIMMYT maize drought stress program using factorial regression and partial least squares methods. Theor. Appl. Genet. 112:1009–1023.

Wang, R.X., L. Hai, X.Y. Zhang, G.X. You, C.S. Yan, and S.H. Xiao. 2009. QTL mapping for grain filling rate and yield related traits in RILs of the Chinese winter wheat population Heshangmai X Yu8679. Theor. Appl. Genet. 118:313–325.

Wang, S., C.J. Basten, and Z.B. Zheng. 2006. Windows QTL Cartographer V2.5. Release September 2006. Program in Statistical Genetics, North Carolina State Univ., Raleigh, NC.

Xing, Y.Z., Y.F. Tan, J.P. Hua, X.L. Sun, C.G. Xu, and Q. Zhang. 2002. Characterization of main effects, epistatic effects and their environmental interactions of QTLs on the genetic basis of yield traits in rice. Theor. Appl. Genet. 105:248–257.

Yen, Y., and P.S. Baenziger. 1992. A better way to construct recombinant chromosome lines and their control. Genome 35:827–830.

Yue, B., K. Cui, S. Yu, W. Xue, L. Luo, and Y. Xing. 2006. Molecular marker-assisted dissection of quantitative trait loci for seven morphological traits in rice (*Oryza sativa* L.). Euphytica 150:131–139.

Zhu, H., G. Briceno, R. Dovel, P.M. Hayes, B.H. Liu, C.T. Liu, and S.E. Ulrich. 1999. Molecular breeding for grain yield in barley: An evaluation of QTL effects in a spring barley cross. Theor. Appl. Genet. 98:772–779.

Zhuang, J.Y., Y.Y. Fan, Z.M. Rao, J.L. Wu, Y.W. Xia, and K.L. Zheng. 2002. Analysis on additive effects and additive-by-additive epistatic effects of QTLs for yield traits in a recombinant inbred line population of rice. Theor. Appl. Genet. 105:1137–1145.