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Identification of QTLs and Environmental Interactions Associated with Agronomic Traits on Chromosome 3A of Wheat

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Identification of QTLs and Environmental Interactions Associated with Agronomic Traits on Chromosome 3A of Wheat

B. T. Campbell, P. S. Baenziger,* K. S. Gill, K. M. Eskridge, H. Budak, M. Erayman, I. Dweikat, and Y. Yen

ABSTRACT

Genetic analyses of complex traits in wheat (*Triticum aestivum* L.) are facilitated by the availability of unique genetic tools such as chromosome substitution lines and recombinant inbred chromosome lines (RICLs) which allow the effects of genes on single chromosomes to be studied individually. Chromosome 3A of 'Wichita' is known to contain alleles at quantitative trait loci (QTLs) that influence variation in grain yield and agronomic performance traits relative to alleles of 'Cheyenne'. To determine the number, location, and environmental interactions of genes related to agronomic performance on chromosome 3A, QTL and QTL × environment analyses of 98 RICLs-3A were conducted in seven locations across Nebraska from 1999 through 2001. QTLs were detected for seven of eight agronomic traits measured and generally localized to three regions of chromosome 3A. QTL × environment interactions were detected for some QTLs and these interactions were caused by changes in magnitude and crossover interactions. Major QTLs for kernels per square meter and grain yield were associated within a 5-centimorgan (cM) interval and appeared to represent a single QTL with pleiotropic effects. This particular QTL displayed environmental interactions caused by changes in magnitude, wherein the positive effect of the Wichita QTL allele was larger in higher yielding environments.

GRAIN YIELD AND AGRONOMIC PERFORMANCE are the most commonly measured, but poorly understood crop traits. Modern strategies for investigating the genetic basis of grain yield and agronomic performance were first established in the 1980s with the use of molecular markers to construct genetic linkage maps in discrete populations (Edwards et al., 1987; Lander and Botstein, 1989; Stuber et al., 1987; Tanksley et al., 1982). Information from genetic linkage maps and agronomic data collected from field experiments allowed the identification of QTL associated with agronomic trait variability. The aim of QTL studies is to provide a framework for understanding complex traits by identifying and measuring the relative impact of alleles at a mapped chromosomal region. The identified QTLs can also be used by plant breeders using marker assisted selection (MAS) to increase breeding efficiency (Dudley, 1993).

Scientists conducting QTL experiments in wheat have access to unique genetic resources, including chromosome substitution lines. Evaluating reciprocal chromosome substitution lines between two parental lines for complex traits allows for the identification of single chromosomes containing QTLs for those traits (Berke et al., 1992a,b; Cantrell and Joppa, 1991). Single reciprocal chromosome substitution lines can be targeted for development of RICLs that segregate only for genes on that chromosome (Shah et al., 1999a,b; Joppa et al., 1997). RICL populations present a powerful tool to conduct QTL studies, especially in wheat, which has the largest genome size of the cereals at 16 000 Mbp (Arumuganathan and Earle, 1991). Kaeppler (1997) documented the advantage of using RICL populations to detect QTLs in wheat, by showing the statistical power of 50 RICLs was equal to that of 200 recombinant inbred lines, when considering a Type I error rate of 5%. The power of 100 RICLs (0.98) exceeded that of 200 recombinant inbred lines (0.41) by a factor of 2.4 times, when considering a Type I error rate of 1%. Because of these advantages, RICL populations have been created to study grain yield, grain protein, and other agronomic traits in wheat (Araki et al., 1999; Joppa et al., 1997; Kato et al., 1999, 2000; Shah et al., 1999a,b).

The analysis of grain yield and agronomic traits controlled by genes on chromosome 3A in Nebraska was initiated in the 1980s. Berke et al. (1992a,b) evaluated a full set of reciprocal chromosome substitution lines between cv. Cheyenne (CNN) and cv. Wichita (WI) for grain yield and other agronomic traits and reported that chromosome 3A from WI increased grain yield 12 to 15% when placed in CNN background. This research led to the development of a set of 50 chromosome 3A recombinant inbred chromosome lines (RICLs-3A), derived from a cross between CNN and CNN (WI3A) (Shah et al., 1999a,b). Shah et al. (1999a,b) evaluated the 50 RICLs-3A lines for anthesis date, plant height, grain volume weight, grain yield, 1000-kernel weight, spikes per square meter, and kernels per spike. Anthesis date (*Eps*) was mapped as a single gene on the short arm of chromosome 3A and explained significant variation for 1000 kernel weight, kernels per spike, and plant height. Additional QTLs were detected for yield components and plant height elsewhere on the chromosome. However, QTLs for grain yield per se were not detected.

The inability to map QTLs for grain yield could be attributed to the interaction of yield component QTLs, hence no single grain yield locus could be identified. QTL × E interactions (QEI) of the crossover type could

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also influence the ability to detect QTLs for grain yield. Shah et al. (1999b) detected QTLs for grain yield in individual environments, but individual QTLs were not consistently detected across environments. Inconsistent QTL detection has been observed and attributed to QEI in other grain yield QTL studies in wheat (Araki et al., 1999; Kato et al., 2000) and other crop plants (Beavis and Keim, 1996; Hayes et al., 1993; Lu et al., 1997; Paterson et al., 1991; Sari-Gorla et al., 1997).

Often QEI are reported in terms of QTL detection in individual environments. Analysis of variance (ANOVA) procedures can be employed to detect statistically significant QEI (Sari-Gorla et al., 1997; Zhu et al., 1999). Another approach to study QEI, not currently reported, could be to extend the concept of stability analysis (Eberhart and Russell, 1966) to select for environmentally stable experimental lines in advanced, agronomic performance trials. Just as breeders attempt to select for environmentally stable experimental lines for cultivar release, utilization of MAS to select for environmentally stable QTLs is important to identify and select QTLs for MAS. Various stability statistics (Kang, 1993; Lin et al., 1986) also could be extended to evaluate the stability of lines within a mapping population by separating and comparing lines based on marker (QTL) genotype.

In addition to the biological explanations for the absence of grain yield QTLs on chromosome 3A of wheat (Shah et al., 1999b), the use of two- and three-replication, randomized complete block designs (RCBD) to measure grain yield could have resulted in insufficient statistical power to detect important, but small, trait variation among the lines. Shah et al. (1999a,b) suggested increasing both the number of RICLs-3A used for QTL mapping and the number of replications to decrease experimental error, thus providing more precise measurements of grain yield within and across environments.

On the basis of these recommendations, we evaluated a population of 98 RICLs-3A for grain yield and other agronomic traits in seven environments. An incomplete block design was used to enhance statistical precision. The objective of this study was to identify QTLs and QEI for eight agronomic traits [anthesis date (AD), plant height (PHT), grain volume weight (GVWT), grain yield (GYLD), 1000-kernel weight (TKWT), spikes per square meter (SPSM), kernels per spike (KPS), and kernels per square meter (KPSM)] present on chromosome 3A on the basis of agronomic evaluations in seven environments.

MATERIALS AND METHODS

Plant Materials and Trait Evaluations

A population of 98 chromosome 3A RICLs was used to study AD, PHT, GVWT, GYLD, TKWT, SPSM, KPS, and KPSM in wheat. Traits were measured following the procedures outlined by Shah et al. (1999a), with the exception that GYLD was measured by harvesting all four rows with a small plot combine and KPSM was calculated as plot yield divided by kernel weight. The development of the first 50 RICLs-3A

was previously described by Shah et al. (1999a,b), and the second 48 RICLs-3A by Yen and Baenziger (1992). The 98 lines, CNN, CNN (WI3A), three commonly grown cultivars (Arapahoe, Pronghorn, Jagger) and Wichita were grown in replicated field trials at Lincoln in 1999 to 2001, Mead in 2000 to 2001, and Sidney, NE, in 2000 to 2001 for a total of seven environments. The environments are diverse and representative of wheat producing areas of Nebraska (Peterson, 1992).

At Lincoln 1999, the 104 entries were evaluated in a RCBD with four replications. In 2000 and 2001, the 104 entries were evaluated in a four-replication, incomplete block design (ICBD), where each replication consisted of eight incomplete blocks of thirteen entries. Each entry was grown in a four-row plot that was 2.4 m long with 30 cm between rows. Seeding rate and plot management were in accordance with local practice. An application of Tilt (1-[[2-(2,4-dichlorophenyl)-4-propyl-1, 3-dioxlan-2-yl] methyl-1H-1, 2,4 trizole; Syngenta, Greensboro, NC) was applied according to the recommended rate approximately 1-wk postanthesis at Lincoln and Mead locations to control fungal diseases.

Field Data Analysis

Data for each trait were analyzed for normality by PROC UNIVARIATE (SAS Institute, 1999). An analysis of variance (ANOVA) was conducted in each environment by PROC GLM coupled with the RANDOM statement to test significant differences among the RICLs-3A, and between the parents, CNN and CNN (WI3A) (SAS, 1999). Homogeneity of variance tests were conducted to determine if data from individual environments (E) could be pooled to conduct a combined ANOVA across environments to evaluate GEI. For the combined analysis, genotypes and GEI were partitioned into relevant sources of variation, including RICLs-3A, CNN vs. CNN (WI3A), RICLs-3A × E, and CNN vs. CNN (WI3A) × E (Table 1). Phenotypic correlations for the 98 RICLs-3A were conducted in individual environments and pooled across environments by means of adjusted least squares means (LSMEANS) (SAS, 1999), with the objective of identifying traits that may be correlated and thus controlled by separate trait QTLs that are linked, or one QTL that is pleiotropic for those traits.

Molecular Marker and QTL Analysis

Genomic DNA was extracted from young leaves following the procedure described by Saghai-Maroof et al. (1984). Restriction fragment length polymorphism (RFLP) and microsatellite markers were used to construct a linkage map of chromosome 3A. Clones used in RFLP analyses were kindly provided by the USDA-ARS central probes repository, Albany, CA, Professor M. D. Gale, John Innes Centre, Norwich, UK, and Dr. A. Graner, Federal Center for Breeding Research on Cultivated Plants, Grünbach, Germany. Genomic DNA digestion, Southern blot analyses, probe labeling and purification, hybridization, and autoradiography were performed as described by Gill et al. (1991).

Microsatellite primer sequences from wheat were identified from Röder et al. (1998) and kindly provided by Dr. P. Cregan, USDA-ARS, Beltsville, MD. Polymerase chain reaction (PCR) reactions were conducted following the procedure outlined by Röder et al. (1998), with minor modifications. PCR products were size separated on 12% (w/v) polyacrylamide gels (37:1 acrylamide:bisacrylamide) in TAE buffer (40 mM Tris-acetate, 20 mM sodium acetate, 1 mM EDTA, pH 7.6) at 300 V for 4 h. Gels were stained in a 1 μg mL^{-1} ethidium

bromide solution for 30 min, destained in distilled water for 2 h, and visualized under UV light.

Heterogeneity of marker segregation in the first 50 RICLs-3A and second 48 RICLs-3A sub-populations was evaluated to determine if subpopulations could be pooled (Liu, 1997). Marker segregation in the combined RICLs-3A population was evaluated using goodness of fit tests using the expected 1:1 Mendelian segregation ratio (Liu, 1997). Linkage map construction was conducted by MAPMAKER/EXP 3.0 (Lincoln et al., 1992) with the distance unit set to recombination fractions. The GROUP command with a LOD threshold of 5.0 and an independent distance of 50 cM was used to assign markers to a linkage group. Repetitive use of the RIPPLE command identified the best order of markers within the linkage group.

Single marker analyses (SM) and composite interval mapping (CIM) QTL analyses were conducted in individual environments and across environments to detect the main effect of chromosomal regions associated with agronomic traits by the adjusted LSMEANS for the RICLs-3A entries and QTL Cartographer 1.30 (Basten et al., 2000). Initially, SM was conducted for each trait to identify markers associated with variation for that trait. Traits with significant marker associations ($P < 0.05$) as determined by SM were further evaluated by CIM with 2-cM intervals scanned for the presence of QTL. Three-hundred permutation tests ($P < 0.05$) were conducted for CIM to establish a significance threshold to control Type-I error. For CIM analyses, no more than five background markers were used to control background effects; a 1-cM window was used. Background markers were selected by means of forward-backward stepwise regression with thresholds of $P < 0.1$ for entering and $P < 0.1$ for remaining in the model.

Analysis of QTL × Environment Interactions

ANOVA was conducted following the procedures used by Zhu et al. (1999) and Sari-Gorla et al. (1997) to partition trait variance into sums of squares due to (i) environments, (ii) incomplete block effects nested within environments, (iii) marker genotype main effects (QTL), and (iv) marker × environment interactions (MEI). Genotype and GEI were included in the model to identify if significant residual genotype and GEI variation remained after main effect QTL and QEI were placed in the model. This procedure allowed for GEI (Table 1) to be partitioned into QEI, assuming that marker loci are closely linked to QTLs.

For each trait, marker main effects and interactions were selected for the model by evaluating the variation explained by a single marker at a time. Each statistically significant marker main effect ($P < 0.05$) and MEI were included in a model ordered from the largest to smallest sums of squares. Analyses were conducted in SAS by PROC GLM coupled with the RANDOM statement (SAS, 1999) to identify the best model of QTL and QEI to explain the variance for each trait. Sequential sums of squares (Type I) were used for marker and MEI effects. After each run, statistically insignificant main effect QTL or QEI were discarded from the model and a new model was constructed, until a final model was selected that contained all significant QTL and QEI for a given trait.

Stability Analysis

Stability parameters (Eberhart and Russell, 1966) were estimated, with the seven environments, by regressing genotype means on an environmental index. The environmental index was estimated as the mean of all genotypes at a specific environment minus the grand mean. The regression coefficient

Table 1. Analysis of variance of seven traits for CNN(WI3A) recombinant inbred chromosome lines combined over seven locations from 1999 to 2001.

Source	df	Anthesis Date (days after May 1) MS	df	Plant Height cm MS	Grain Yield Mg ha⁻¹ MS	Grain Volume Weight kg hL⁻¹ MS	1000 kernel weight g MS	Spike number m⁻² MS	Kernel number per spike MS	Kernel number m⁻² MS
Environment (E)	6	42 031.0***	6	50 346.0***	488.16***	2 940.3***	5 945.3***	7 570 931.0***	6 511.7**	3 809 413 966**
Blk (E)	187	11.3**	189	187.9***	1.28***	11.1***	24.3***	40 004.0***	63.5**	10 582 818***
Genotypes (G)	103	99.7***	103	373.3***	0.51***	5.0***	16.1***	12 733.0***	42.8**	7 422 253**
RICLS-3A	97	91.8***	97	190.6***	0.39***	3.2***	13.4***	11 301.2***	17.2**	4 848 250**
Checks	3	35.2***	3	3 355.8***	2.99***	44.5***	104.6***	66 000.9***	340.0**	63 689 672***
CNN vs. CNN(WI3A)	1	289.8***	1	366.8***	2.01***	14.4***	4.8	1 842.4	13.2	9 261 348**
RICLS-3A vs. Others	1	1 081.0***	1	5 638.0***	4.60***	17.2***	76.4***	2.7	1 067.5**	90 441 133**
Parents vs. Checks	1	566.3***	1	3 868.9***	1.55***	42.0***	5.3	32 613.6***	769.5**	18 082 199***
G × E	618	4.6***	618	33.7***	0.21***	2.1***	6.8***	6 890.1**	11.2**	2 614 062***
RICLS-3A × E	582	4.5***	582	30.2***	0.17***	1.8***	5.5***	6 113.7***	9.7**	2 033 422**
Checks × E	18	2.7**	18	106.3***	0.95**	4.5**	16.9***	16 592.1***	31.9**	8 944 417**
CNN vs. CNN(WI3A) × E	6	8.7**	6	33.0	0.21	4.9***	11.8***	8 652.3***	12.3	3 272 315*
RICLS-3A vs Others × E	6	13.4***	6	106.3***	1.52***	19.9***	60.9***	40 976.6***	73.0**	28 413 901**
Parents vs. Checks × E	6	7.4**	6	92.6***	0.34*	6.9***	42.9***	17 238.7***	39.7**	13 486 897**
Pooled Error	1789	1.4	1995	19.3	0.14	0.9	3.6	4 806.2	7.2	1 374 591
Mean RICLS-3A		26.2		105.0	3.42	76.9	32.8	406.6	26.7	10 471
Mean CNN(WI3A)		23.8		103.3	3.67	77.8	32.6	435.1	26.7	11 251
Mean CNN		28.6		108.4	3.27	76.7	32.0	424.0	25.7	10 341
CV		4.6		4.2	10.7	1.2	5.8	17.0	10.0	11.1

* Significant at the 0.05 level of probability.
** Significant at the 0.01 level of probability.

(b_i) and deviations from regression (S^2_d) were the parameters used to compare environmental responses of genotypes. GEI sums of squares was partitioned into sums of squares due to (i) regression of genotypes on the environmental index and (ii) pooled deviations from regression. Each partition was further broken down into sums of squares due to (i) among RICLs-3A, (ii) among check cultivars, and (iii) between CNN and CNN (WI3A) (Table 5). The GEI linear interaction mean square provided a test of genetic differences among genotypes for their response to linearly arrayed environmental productivity. The pooled deviation mean square provided a test of genetic differences among genotypes for their deviation from regression.

For an individual trait, the environmental stability of each marker detected as a main effect QTL or associated with QEI was evaluated by regressing marker genotype means on the environmental index described previously. Environmental response of each marker genotype (QTL genotype) was evaluated by means of the regression coefficient (b_i). Regression coefficients for the two possible genotypes of a marker were compared by an F-test, which used the sums of squares of the pooled deviations from regression as an error term. Significantly different b_i between the two RICLs-3A genotypes possible at a given marker locus indicated that the effect of marker genotypes differed in their linear response to the environmental index.

RESULTS AND DISCUSSION
Field Data Analysis

Significant differences were observed among the RICLs-3A for each of the eight traits. The two parents [CNN vs. CNN (WI3A)] differed for AD, PHT, GYLD, GVWT, and KPSM (Table 1), but not for TKWT, SPSM, and KPS. These results are in agreement with previous reports involving 50 RICLs-3A (Shah et al., 1999a), and the original chromosome 3A substitution lines (Berke et al., 1992a; Yen et al., 1997), with the exception that parents were different for TKWT in Shah et al. (1999a) and for GVWT in Berke et al. (1992a). Neither of these authors measured KPSM. RICLs-3A × E interactions were significant for all of the traits, whereas the CNN vs. CNN (WI3A) × E interactions were significant for AD, GVWT, TKWT, SPSM, and KPSM, but not for PHT, GYLD, and KPS. In contrast, Shah et al. (1999a) detected significant RICLs-3A × E for GYLD, TKWT, and SPSM only, and observed no significant CNN vs. CNN (WI3A) × E for any other traits. Differences between our results and those reported by Shah et al. (1999a) are likely due to our increased statistical power using 98 RICLs-3A versus 50 RICLs-3A, incomplete block field designs, and differences between environments evaluated in both studies.

Pooled phenotypic correlations among all traits for 95 RICLs-3A were calculated to identify associations among traits (Table 2). As expected, GYLD was positively correlated with SPSM, KPSM, and GVWT but negatively correlated with AD. Hence, earlier AD and higher values for the yield components SPSM and KPSM were most associated with higher GYLD. In contrast, TKWT and KPS were not correlated with GYLD. SPSM and KPSM were negatively correlated with TKWT, which was not unexpected given the well-known tendency for yield component traits to display compensatory effects. Highly significant phenotypic correlations between GYLD, SPSM, and KPSM are usually indicative of linked, but separate controlling genes, or pleiotropy of one common controlling gene.

Molecular Markers and Linkage Analysis

Twenty molecular markers were used to construct a linkage map of chromosome 3A. Three of the 98 RICLs-3A were determined to be heterozygous for chromosome 3A on the basis of the restriction pattern of several markers (presumably because of a univalent chromosome shift in their development). Inclusion of the heterozygous lines did not affect the ANOVA results. These three lines were not included in map construction or subsequent QTL analyses. Heterogeneity of marker segregation tests indicated that marker data (except for *Eps*) could be pooled over the two subpopulations. A Chi-square test ($P < 0.01$) indicated 1:1 segregation for 18 of the 20 markers, with the other two markers skewed somewhat toward the WI allele. These two markers were still included in the map, although their P-values were slightly below 0.01 because of a homogenous segregation within each subpopulation. Anthesis date (*Eps*) was not included as a marker in this study, as it did not show a homogeneous segregation in the RICLs-3A subpopulations. Shah et al. (1999a,b) mapped *Eps* as a single locus on the short arm of chromosome 3A on the basis of evidence of a bimodal (1:1 segregational) distribution of the 50 RICLs-3A, although there was a slight skewing toward earliness (WI allele). However, in the second subpopulation, the 45 RICLs-3A were highly skewed toward late anthesis (CNN allele). Differences in segregation between subpopulations were most

Table 2. Phenotypic correlations of 95 CNN (WI3A) recombinant inbred chromosome lines for eight traits pooled across seven Nebraska environments.

Trait†	PHT	GYLD	TKWT	SPSM	KPS	KPSM	GVWT
AD	0.54**	−0.20**	−0.27**	0.14**	−0.28**	0.01	0.06
PHT	–	0.02	−0.17**	0.18**	−0.17**	0.12**	−0.02
GYLD		–	0.02	0.58**	0.06	0.83**	0.16**
TKWT			–	−0.44**	0.08*	−0.50**	0.28**
SPSM				–	−0.59**	0.75**	0.04
KPS					–	0.00	−0.04
KPSM						–	0.03

* Significant at the 0.05 level of probability.
** Significant at the 0.01 level of probability.
† AD, anthesis date; PHT, plant height; GYLD, grain yield; TKWT, 1000 kernel weight; SPSM, spike number per square meter; KPS, kernel number per spike; KPSM, kernel number per square meter; GVWT, grain volume weight.

likely a result of unintentional selection bias during the development of each RICLs-3A subpopulation. Heterogeneity within the CNN genotype used to create the RICLs-3A in each subpopulation was doubtful because a common seed source was used to develop both subpopulations. Differences in AD segregation between subpopulations could also be due to segregation of more than one locus for AD, which has been suggested by Eskridge et al. (2000) and Miura et al. (1999).

QTL Identification and QTL × E Interactions

QTLs were detected for all traits except AD. QTL results from each environment and the combined analysis are summarized in Table 3. QTL scans for GYLD and KPSM within the individual and over the seven environments are shown in Fig. 1. A summary of QTLs detected across environments for all traits is shown in Fig. 2. For GYLD, we detected QTLs in four environments, for SPSM, KPSM, PHT, and TKWT in three environments, and for KPS and GVWT in two environments. Overall, three regions of chromosome 3A were detected as harboring QTLs for these traits. The regions were from *Xcdo549–Xtam055* (*Xtam61*) (Region 1), *Xcdo638–Xbcd366* (*Xcmwg680*) (Region 2), and *Xbcd366* (*Xcmwg680*)–*Xbcd1555* (Region 3). Region 1 contained QTLs for GYLD, KPSM, PHT, KPS, and TKWT. Region 2 contained QTLs for GYLD, KPSM, TKWT, and SPSM, and Region 3 contained QTLs for PHT, GVWT, and KPS. A single QTL for KPS was detected in Lincoln 2001 in a 4th region between *Xbcd141-Xbcd372* and a single QTL for GVWT in Lincoln 2000 was detected in a 5th region between *Xbcd361–Xgwm155*. In contrast, Shah et al. (1999b) were not able to detect QTLs for GYLD per se using

data from 50 RICLs-3A, but did detect QTLs for PHT, TKWT, SPSM, and KPS. In that study, the chromosomal region with the largest effect was the *Eps* region, while other chromosomal regions contributed minor effects. The QTLs detected by Shah et al. (1999b) in other chromosomal regions (aside from *Eps*) corresponded to the QTLs we detected in one or more environments.

Comparing GYLD QTL detection on the basis of 95 versus 50 RICLs-3A in the current experiment indicated the effects of GYLD QTLs were greater with an increased number of RICLs-3A lines. Hence, the evaluation of 95, as opposed to 50, RICLs-3A enhanced the ability to detect QTLs for GYLD. In addition, reevaluating the initial 50 RICLs-3A population by means of the updated genetic map of chromosome 3A and CIM analyses verified the absence of GYLD QTLs expressed in the environments evaluated by Shah et al. (1999a,b). Thus, differences between the set of environments used by Shah et al. (1999a,b) and those used in the current study were responsible for GYLD QTL detection differences between the two studies. Mean values for GYLD in individual environments ranged from 1.93 to 4.67 Mg ha^{-1} in the current study compared to 2.44 to 2.97 Mg ha^{-1} in the previous study.

Grain Yield

For GYLD QTLs, the WI allele always increased GYLD. The QTL with largest effect was located in Region 2 (*QGyld.unl.3A.2*) and was identified consistently in all four environments where GYLD QTLs were detected (Fig. 1, Table 3). On the basis of the combined analysis, *QGyld.unl.3A.2* explained 28.1% of the phenotypic variance and provided an additive effect of a 66 kg ha^{-1} increase in GYLD on the substitution of a WI

Table 3. Summary of QTLs identified by composite interval mapping for seven agronomic traits using 95 lines grown in seven individual environments and combined across environments.

Trait	QTL	Environment	R^2 (%)	Additive effect†
Grain yield	*QGyld.unl.3A.1*	Combined	6.7	+32 kg ha^{-1}
	QGyld.unl.3A.2	Lincoln 2000	12.8	+82
		Lincon 2001	17.6	+104
		Mead 2001	26.1	+204
		Sidney 2001	8.3	+82
		Combined	28.1	+66
Kernel per square meter	*QKpsm.unl.3A.1*	Combined	14.6	+170 kernels
	QKpsm.unl.3A.2	Lincoln 2000	15.0	+389
		Lincon 2001	8.4	+212
		Mead 2001	20.6	+591
		Combined	19.1	+195
1000-Kernel weight	*QTkwt.unl.3A.1*	Lincoln 2001	14.2	−0.38 g
		Mead 2001	8.6	−0.34
		Combined	12.7	−0.27
	QTkwt.unl.3A.2	Lincoln 2000	12.6	−0.63
Plant height	*QPht.unl.3A.1*	Lincoln 1999	10.1	−1.2 cm
	QPht.unl.3A.3	Mead 2000	30.4	−1.7
		Sidney 2001	17.1	−1.4
Grain volume weight	*QGvwt.unl.3A.3*	Lincoln 1999	25.8	+0.29 kg hL^{-1}
		Combined	43.1	+0.23
	QGvwt.unl.3A.5	Lincoln 2000	10.6	+0.18
Spikes per square meter	*QSpsm.unl.3A.2*	Lincoln 2001	12.6	+17.7 spikes
		Mead 2001	14.7	+19.5
	QSpsm.unl.3A.3	Sidney 2001	10.5	+7.2
		Combined	22.8	+10.3
Kernels per spike	*QKps.unl.3A.1*	Sidney 2001	12.8	+0.6 kernels
		Combined	15.5	+0.3
	QKps.unl.3A.4	Lincoln 2001	9.8	−1.3
		Combined	9.5	−0.3

† Additive effect represents the substitution of a WI allele for a CNN allele.
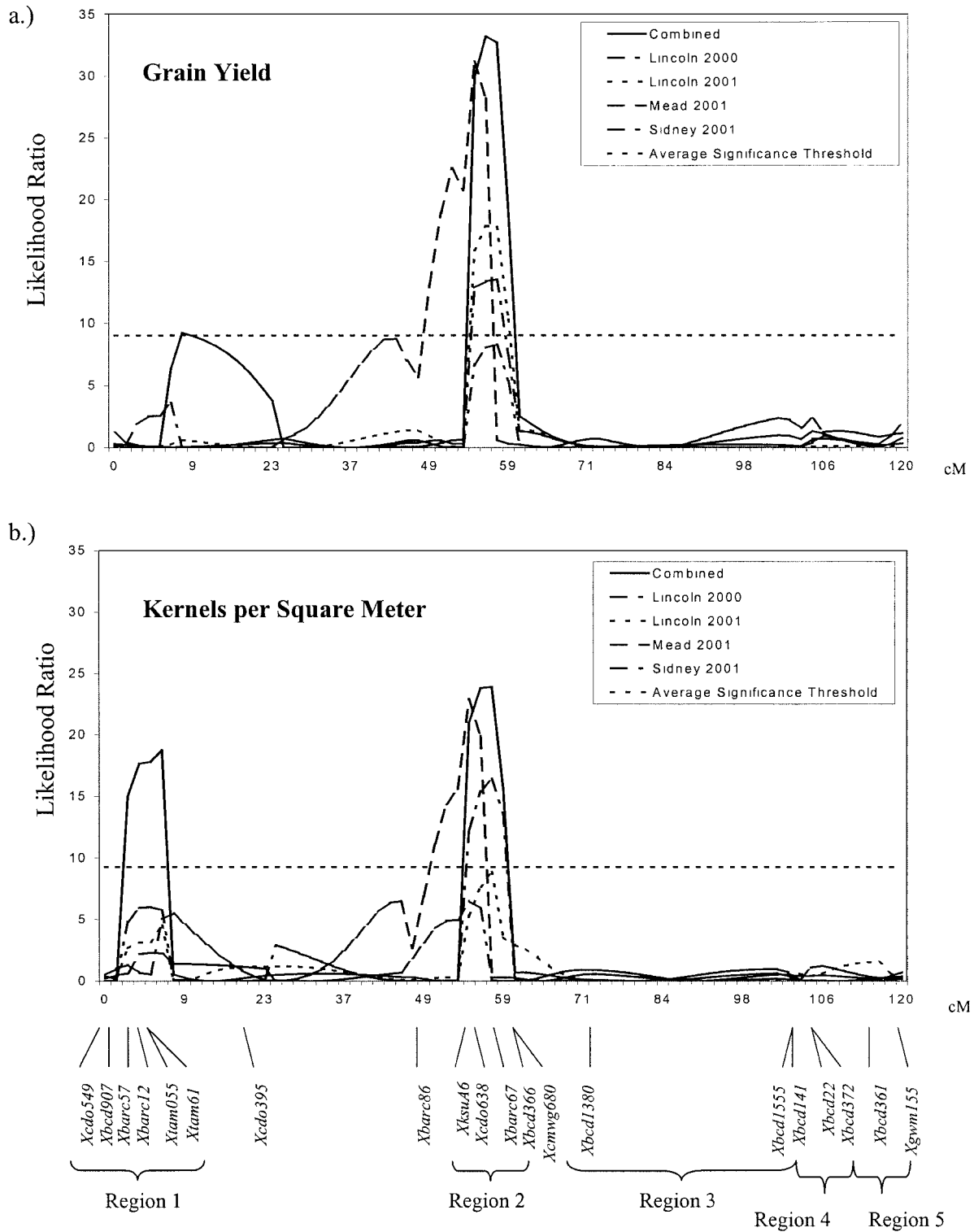
a.)

b.)

Chromosome 3A

Fig. 1. Composite interval mapping QTL scans along chromosome 3A showing the likely location of QTLs for (a.) grain yield and (b.) kernels per square meter using least square means from individual environments and combined across environments.

allele for a CNN allele. The minor QTL in Region 1 (*QGyld.unl.3A.1*) was detected in the combined analysis only and explained 6.6% of the phenotypic variance. Analysis of variance (Table 4) showed that *Xbarc67* × E was statistically significant, indicating *QGyld.unl.3A.2*

displayed sensitivity to the environment. Inability to detect the effect of *QGyld.unl.3A.2* in the remaining three environments was likely due to QEI. Overall, allelic differentiation at *QGyld.unl.3A.2* was greatest in higher yielding environments such as Mead 2001 and
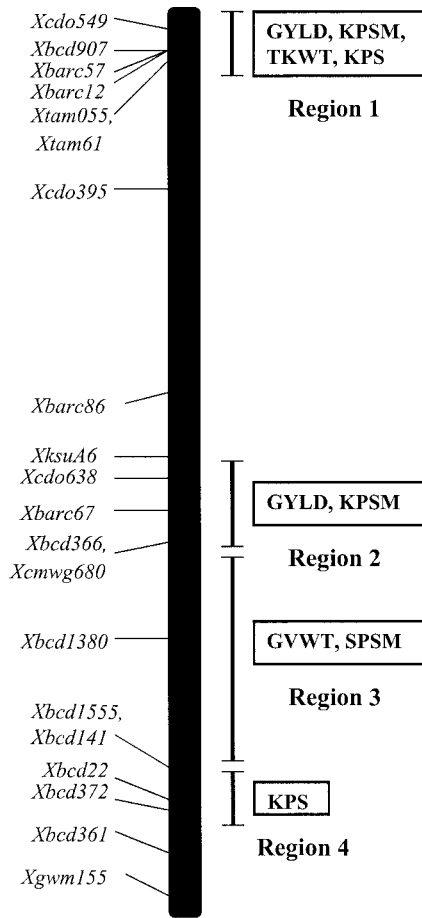
Fig. 2. Summary of the location of QTLs for grain yield (GYLD), 1000-kernel weight (TKWT), spikes per square meter (SPSM), kernels per spike (KPS), kernels per square meter (KPSM), and grain volume weight (GVWT) detected on chromosome 3A across environments using composite interval mapping.

Lincoln 2001, while absent or reduced in the lowest yielding environments of Lincoln 1999 and Sidney 2001, respectively.

Kernels per Square Meter

QTLs for KPSM were detected in three of seven environments, and were localized in Regions 1 and 2 (Fig. 1, Table 3). All QTLs for KPSM were coincident with QTLs for GYLD and the WI allele always increased KPSM. The QTL with largest effect was located in Region 2 (*QKpsm.unl.3A.2*) explaining 19.1% of the phenotypic variance. KPSM was increased by 195 kernels with the substitution of a WI allele for a CNN allele. The QTL in Region 1 (*QKpsm.unl.3A.1*) explained 14.6% of the phenotypic variance and provided an increase of 170 kernels with the substitution of a WI allele for a CNN allele. Identification of (near-)identical genomic positions with significant effects on KPSM and GYLD is consistent with a hypothesis of a single QTL with pleiotropic effects, or with the hypothesis of one (or two) QTLs for either (or both) trait(s). No line was detected with low KPSM and high GYLD or vice versa in graphs of GYLD vs. KPSM for the 95 lines, suggesting pleiotropy rather than linkage. Analysis of variance

Table 4. Analysis of variance for marker and marker × E interaction for grain yield (GYLD), 1000 kernel weight (TKWT), spikes per square meter (SPSM), kernels per spike (KPS), grain volume weight (GVWT), plant height (PHT), and kernels per square meter using 95 RICLs-3A across seven environments.

GYLD		TKWT		SPSM		KPS		GVWT		PHT		KPSM	
Source	MS	Source	MS	Source	MS	Source	MS	Source	MS	Source	MS	Source	MS
E	452.9**	E	5 226.9***	E	6 663 643***	E	5 048.1***	E	2 538.1**	E	38 577.4***	E	3 554 934 770**
Blk (E)	1.3***	Blk (E)	27.3***	Blk (E)	38 980***	Blk (E)	60.2***	Blk (E)	13.0***	Blk (E)	197.1***	Blk (E)	11 123 037***
Xbarc67	10.3***	Xbarc12	140.6***	Xbcd1555	164 082***	Xbarc12	169.1***	Xbcd1555	82.9***	Xbcd1380	2 621.6***	Xbarc67	85 599 926***
Xbcd366	1.0***	Xtam055	16.9*	Xbarc67	33 883***	Xbcd141	151.6***	Geno.	2.3***	Xbarc86	376.5***	Xbarc12	64 418 784***
Geno.	0.3***	Geno.	12.6***	Geno.	9 757***	Xbcd361	38.1***	Xbcd1380 × E	6.0***	XksuA6	85.4*	Geno.	3 370 077***
Xbarc67 × E	0.6***	Xbcd366 × E	17.5***	Xbcd366 × E	14 267***	Geno.	13.3***	Xbarc12 × E	5.3***	Geno.	166.8***	Xbarc67 × E	6 000 867***
Geno. × E	0.2**	Geno. × E	5.3***	Xtam055 × E	10 468***	XksuA6 × E	19.8*	Xbcd1555 × E	2.1***	Xbcd141 × E	66.3***	Xbcd1555 × E	3 371 557*
Error	0.1	Error	3.5	Geno. × E	6 339**	Xbarc12 × E	19.6*	Geno. × E	1.7**	Xbcd1555 × E	55.8***	Geno. × E	2 028 183***
				Error	4719	Geno. × E	9.5**	Error	0.9	Xcdo549 × E	58.1***	Error	1 349 036
						Error	7.1			Geno. × E	31.0***		
										Error	18.9		

* Significant at the 0.05 level of probability.
** Significant at the 0.01 level of probability.

(Table 4) indicated the effect of *Xbarc67* × E and *Xbcd1555* × E were statistically significant, indicating that *QKpsm.unl.3A.2* displayed sensitivity to different environmental conditions. A statistically significant QTL was not detected at *Xbcd1555*, but the significant *Xbcd1555* × E interaction indicated the effect of Region 3 on KPSM was very minor overall, yet sensitive to different environments.

1000-Kernel Weight

Two QTLs for TKWT were detected in three of seven environments and localized in Regions 1 and 2 (Table 3) with the WI allele always providing a decrease in TKWT (compared to increases in GYLD and KPSM). The QTL in Region 1 (*QTkwt.unl.3A.1*) was detected in two of the three environments in which QTLs were detected and in the combined analysis, and explained 12.7% of the phenotypic variance. *QTkwt.unl.3A.1* provided an additive effect of a 0.27 g decrease in TKWT on the substitution of a WI allele for a CNN allele. *QTkwt.unl.3A.2* was detected in one individual environment (Lincoln 2000) and analysis of variance (Table 4) indicated the *Xbcd366* (*Xcmwg680*) × E interaction was significant. This interaction would explain the failure to detect *QTkwt.unl.3A.2* in environments other than Lincoln 2000 if the interaction was of a skewed crossover type.

Plant Height

Statistically significant QTLs for PHT were not detected in the combined analysis. However, two QTLs for PHT were detected in three of seven individual environments, with the WI allele providing a lower value for PHT at each QTL (Table 3). *QPht.unl.3A.1* was identified only in Lincoln 1999, and *QPht.unl.3A.3* only in Mead 2000 and Sidney 2001. The inability to detect a main effect of *QPht.unl.3A.1* and *QPht.unl.3A.3* in the combined analysis and in other individual environments may have resulted from QEI detected in the analysis of variance (Table 4), with that QEI being the crossover type of interaction. Statistically significant *Xcdo549* × E, *Xbcd1555* × E, and *Xbcd141* × E interactions were detected and revealed that *QPht.unl.3A.1* and *QPht.unl.3A.3* displayed different effects across environments.

Grain Volume Weight

Two QTLs were detected for GVWT in two of seven environments, localized in Regions 3 (*QGvwt.unl.3A.3*) and 5 (*QGvwt.unl.3A.5*), with the WI allele always providing the higher value (Table 3). *QGvwt.unl.3A.3* was the only QTL detected in the combined analysis and explained 43.1% of the phenotypic variance, while providing an additive effect of increasing GVWT by 0.23 kg hL^{-1} with the WI allele. A QTL peak was revealed in two additional environments at *QGvwt.unl.3A.3*, but those peaks did not exceed the significance threshold as determined by the permutation test. The analysis of variance (Table 4) identified three statistically significant marker × E interactions, including *Xbcd1380* × E,

Xbarc12 × E, and *Xbcd1555* × E. *Xbarc12* × E indicated Region 1 was sensitive to environmental interactions and the effects of a QTL in Region 1 were below the level of detection for CIM, representing the effects of a very minor QTL. The *Xbcd1380* × E and *Xbcd1555* × E interactions indicated that the effect of Region 3 was different across environments, which may have prevented detection of *QGvwt.unl.3A.3* in more individual environments.

Spikes per Square Meter and Kernels per Spike

QTLs for SPSM were detected in three of seven environments and localized in Regions 2 (*QSpsm.unl.3A.2*) and 3 (*QSpsm.unl.3A.3*) (Table 3), with the WI allele always providing the higher value for SPSM. *QSpsm.unl.3A.3* was the only QTL detected in the combined analysis, explaining 22.8% of the phenotypic variance and providing a small increase of 10.3 SPSM with the WI allele. The effect of *QSpsm.unl.3A.2* was detected in two individual environments (Lincoln 2001, Mead 2001), but not the combined analysis. Analysis of variance revealed significant interactions for *Xbcd366* (*Xcmwg680*) × E and *Xtam055* (*Xtam61*) × E, indicating Regions 2 and 3 were sensitive to the environment for SPSM. For KPS, two QTLs (*QKps.unl.3A.1* and *QKps.unl.3A.4*) were detected in the combined analysis, with the WI allele providing the higher value at *QKps.unl.3A.1* and the lower value at *QKps.unl.3A.4*. Analysis of variance (Table 4) indicated the *Xbarc12* × E interaction was statistically significant, revealing that *QKps.unl.3A.1* displayed sensitivity to environmental interactions. A significant environmental interaction was also detected for *XksuA6* × E and revealed that the effect of Region 3 was sensitive to the environment.

Environmental Interactions and Genotype Stability

Partitioning GEI (linear) into RICLs-3A (linear), parents (linear), and checks (linear) revealed significant differences in slope (b_i) among the RICLs-3A (linear) for PHT, GVWT, and TKWT and between the parents (linear) for SPSM and KPSM (Table 5). Hence, genotypes within the RICLs-3A population responded dissimilarly to a low to high gradient of environmental indicies for PHT, GVWT, and TKWT. The parents [CNN and CNN (WI3A)] also responded dissimilarly over the same gradient and indicies for SPSM and KPSM.

Regressing QTL genotype means on an environmental index indicated that some QTL genotypes exhibited different responses across environmental conditions (Fig. 3). For GYLD, four markers [*Xbarc86*, *XksuA6*, *Xbarc67*, and *Xbcd366* (*Xcmwg680*)] showed differences in slope between marker genotypes and were localized in Region 2, where a major QTL for GYLD was detected. The difference in slope between the two marker genotypes, represented by *Xbarc67* in Fig. 3a, was due to a change in magnitude. The increasing phenotypic differential between the two *Xbarc67* genotypes was greater in more productive environments, with the

Table 5. Partitioning of genotype × environment interactions into linear and nonlinear components. Mean squares and significance levels of F-tests from the regression analysis of all traits for 98 RICLs-3A, check cultivars, parents, RICLs-3A vs. others, and parents vs. check cultivars combined over seven environments from 1999 to 2001.

Source	df	Anthesis date MS	df	Plant height MS	Grain yield MS	Grain volume weight MS	1000-kernel weight MS	Spike number m^{-2} MS	Kernel number per spike MS	Kernel number m^{-2} MS
Genotypes	103	30.7**	103	103.4**	0.14**	1.3**	4.4**	3 585**	12.5**	2 092 692**
Environment (linear)	1	63 435.4**	1	75 534.5**	732.18**	4 410.8**	8 918.1**	11 356 425**	9 768.3**	5 714 120 613**
G × E (linear)	103	0.5	103	15.4**	0.07	1.4**	4.3**	2 209	3.6	915 568**
RICLs-3A (linear)	97	0.5	97	13.0*	0.05	1.3**	2.9**	2 043	2.5	654 352
Checks (linear)	3	0.2	3	67.7**	0.34**	0.2	8.6**	2 610	27.3*	4 275 250**
Parents (linear)	1	0.2	1	0.1	0.14	0.6	4.5	9 800*	0.2	4 060 729*
RICLs-3A vs. Others (linear)	1	0.8	1	81.1**	0.91**	15.5**	76.3**	9 457*	23.2**	11 943 301**
Parents vs. Checks (linear)	1	0.6	1	40.7*	0.05	4.6**	47.5**	2 342	21.9**	2 001 602
Pooled deviations	520	1.6*	520	10.0	0.06	0.6	1.7	1 865	3.3	684 901
RICLs-3A dev.	490	1.6*	490	9.3	0.05	0.5	1.5	1 698	3.0	576 093
Checks dev.	20	2.0	15	24.5	0.24**	2.9**	4.8	6 072	10.1	3 483 517**
Parents dev.	10	1.3	5	12.7	0.04	0.2	1.6	1 611	4.8	419 248
Pooled Error	1 789	1.4	1 995	19.3	0.1	0.9	3.6	4 860	7.2	1 374 591

* Significant at the 0.05 level of probability.
** Significant at the 0.01 level of probability.

WI allele always providing a higher value than the CNN allele. Similarly, Berke et al. (1992b) found that differences between grain yield for CNN (WI3A) and CNN were greater in higher yielding environments.

Four markers localized in Region 1 displayed statistically different marker genotype slopes for PHT (*Xcdo549, Xbarc12, Xtam055* (*Xtam61*), and *Xcdo395*), and another marker (*Xbcd1380*) displayed statistically different marker genotype slopes for TKWT. For PHT and TKWT, differences in slope between marker alleles were due to crossover interactions, with the WI allele providing the higher value in environments conducive to shorter PHT and lower TKWT. Crossover interactions for the effects of marker genotypes on PHT and

TKWT QTL are represented by *Xcdo549* and *Xbcd1380*, respectively (Fig. 3b,c).

For KPS, three markers [*Xbarc12, Xtam055* (*Xtam61*), and *Xbcd141*] displayed differences in slope between marker genotypes and were localized in Regions 1 and 3. Differences in slope between marker genotypes for *Xbarc12, Xtam055* (*Xtam61*), and *Xbcd141* were due to changes in magnitude, with greater differences between genotypes in higher KPS environments, as illustrated by *Xtam055* (*Xtam61*) and *Xbcd141* (Fig. 3d). *Xbarc12* and *Xtam055* (*Xtam61*) always displayed higher values for KPS with the WI allele, but *Xbcd141* always displayed higher values for the CNN allele. These results indicate that alleles for these two QTLs were in repul-
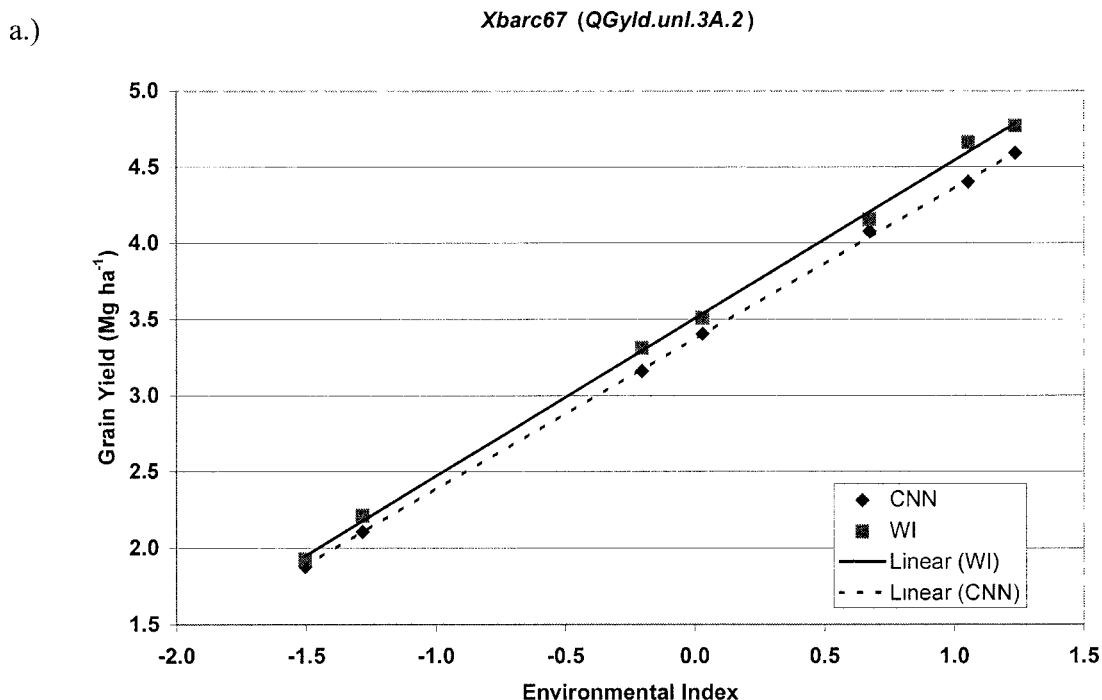
a.)

Fig. 3. Statistically significant regressions of marker genotype mean on an environmental index estimated from the mean of marker genotypes grown in each of seven Nebraska environments minus the grand mean for: a.) grain yield (GYLD), b.) plant height (PHT), c.) 1000-kernel weight (TKWT), and d.) kernels per spike (KPS).
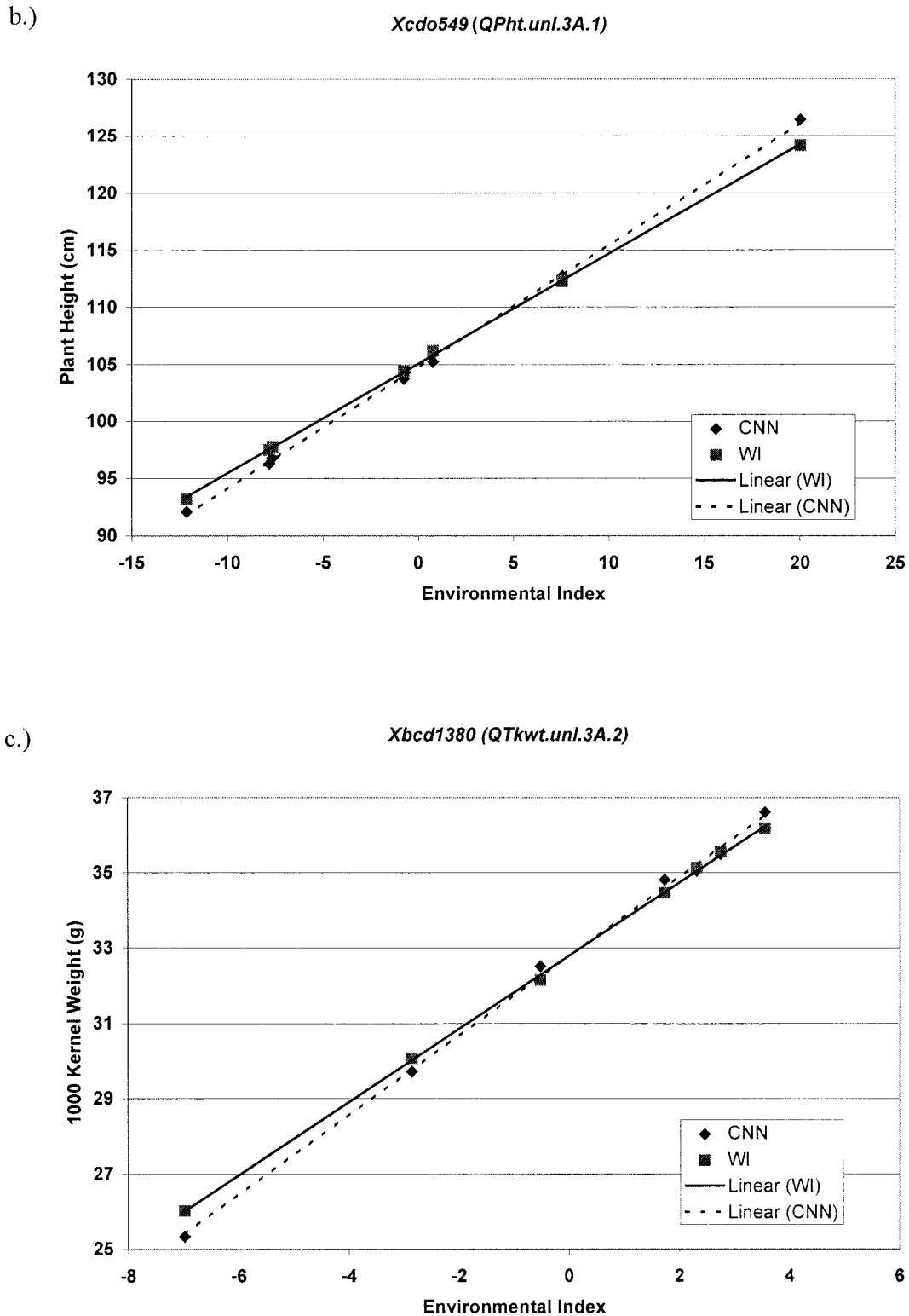
b.)

Xcdo549 (QPht.unl.3A.1)

c.)

Xbcd1380 (QTkwt.unl.3A.2)

Fig. 3. Continued.

sion phase. No statistically significant differences in marker genotype slopes were detected for KPSM, SPSM, and GVWT.

CONCLUSIONS

This experiment clearly shows that QTLs and QEI associated with agronomic performance can be detected on chromosome 3A of wheat by means of a population of 95 RICLs-3A. Although these conclusions apply to the present population of RICLs-3A and the Nebraska environments they were evaluated in, our goal was to provide a general idea of the nature of QTLs affecting agronomic performance on chromosome 3A and their interactions with the environment. QEI analyses indicated some QTLs were sensitive to different environ-

d.)

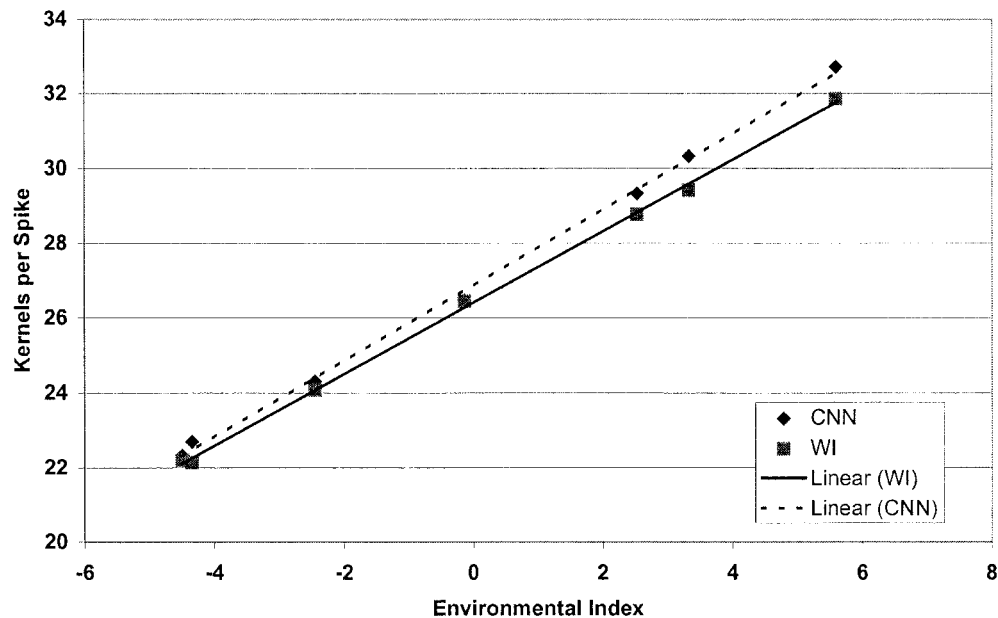**Xtam055 (QKps.unl.3A.1)**
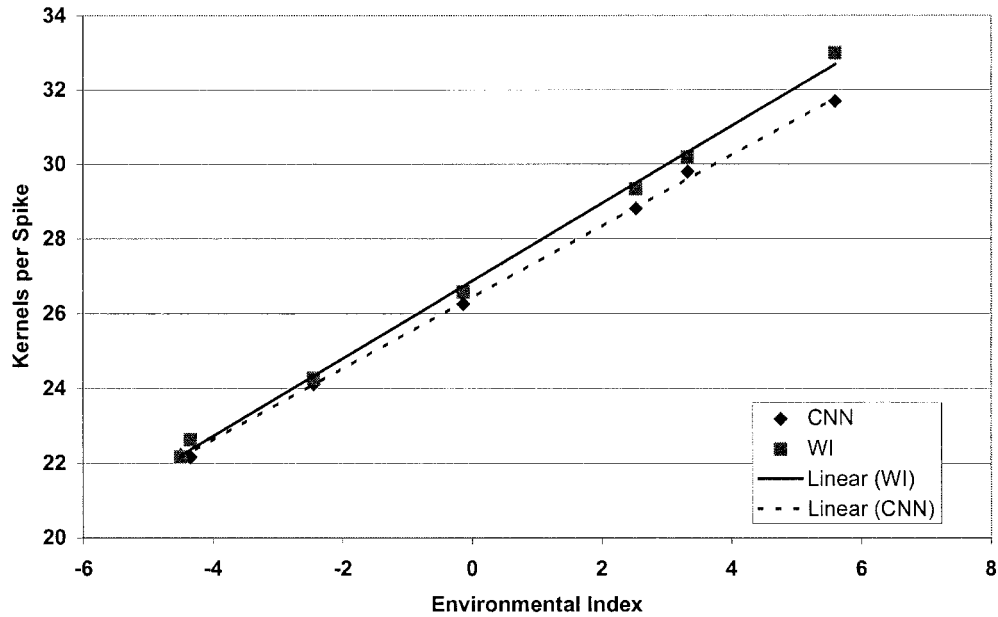
e.)

Xbcd141 (QKps.unl.3A.3)

Fig. 3. Continued.

mental conditions, displaying interactions caused by either changes in magnitude of the QTL effect and crossover interactions.

Major QTLs for GYLD and KPSM were identified in Region 2 [*Xcdo638– Xbcd366* (*Xcmwg680*)] and most likely represented a single, major QTL for KPSM displaying pleiotropic effects on GYLD. Other studies in wheat using RICLs for chromosomes 4A and 5A indicate that grain yield QTLs are always detected concurrently with QTLs for yield component traits or other

developmental traits (Araki et al., 1999; Kato et al., 2000). This implies that effects of QTLs detected for grain yield are simply due to the effects of QTLs for one or more yield component (and other) traits, which would be expected because of the complex nature of grain yield and common associations with other agronomic traits.

Overall, the analysis of variance approach used to detect QEI, coupled with regressing QTL genotype means on an environmental index, resulted in a better

understanding of QEI relative to comparing QTL detection across environments. One advantage of conducting the regression of QTL allelic means on an environmental index approach was that QEI could be assessed in terms of a magnitude difference (e.g.- *QGyld.unl.3A.2*) or crossover type (e.g.- *QPht.unl.3A.1*, *QTkwt.unl.3A.2*). Our approach at dissecting QEI revealed that expression of the favorable allele at the major GYLD QTL *QGyld.unl.3A.2* (WI allele) was greatest (in terms of magnitude) in higher yielding environments such as Lincoln 2001 and Mead 2001 and lowest or absent in lower yielding environments such as Lincoln 1999 and Sidney 2001. Identifying and understanding environmental differences contributing to *QGyld.unl.3A.2* expression differences highlights the importance of understanding QTL expression across environments before selecting for QTLs associated with higher grain yield in a breeding program.

In contrast to *QGyld.unl.3A.2*, QEI detected for PHT and TKWT were due to crossover interactions, as the WI allele provided the higher value in lower PHT and TKWT environments and the lower value in higher PHT and TKWT environments, but apparently not having an appreciable effect on grain yield interaction. The crossover type of interactions for these PHT and TKWT QTLs limited their detection across environments and led to a nonsignificant QTL main effect in the combined analysis. Large GEI and QEI for PHT was not surprising, as Budak et al. (1995) reported difficulty in selecting consistently tall, non-semidwarf genotypes in eastern Nebraska for western Nebraska. WI, CNN, CNN (WI3A), and the RICLs-3A are conventional height, non-semidwarf lines. The environmentally sensitive QTLs for PHT and TKWT detected in this study clearly illustrate the importance of determining if QEI are due to changes in magnitude or crossover interactions before using MAS to select for QTLs, because identifying and selecting the proper allele at QTLs with crossover interactions requires careful selection in target environments. Inappropriate allele identification or selection could result in the indirect selection of QTL alleles with detrimental effects in some target environments.

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