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Mapping QTLs controlling grain yield and its components on chromosome 5A of wheat

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Abstract Chromosome 5A of wheat is known to carry a number of genes affecting adaptability and productivity. To localize quantitative trait loci (QTLs) controlling grain yield and its components, an RFLP map was constructed from 118 single-chromosome recombinant lines derived from the F_1 between Chinese Spring (Cappelle-Desprez 5A) and Chinese Spring (*Triticum spelta* 5A). The map was combined with the field-trial data scored over 3 years. A total of five regions in chromosome 5A contributed effects on yield traits. Increases in grain yield, 50-grain weight and spikelet number/ear were determined by complementary QTL alleles from both parents. The effects associated with the vernalization requirement gene *Vrn-A1* or a closely linked QTL were significant only in the favorable growing season where the later-flowering *vrn-A1* allele from Cappelle-Desprez 5A produced a higher tiller number/plant and spikelet number/ear. The effects of the ear morphology gene *q* or closely linked QTL(s) were detected for grain yield and ear grain weight. Three other QTLs with minor effects were dispersed along chromosome 5A. These QTLs had large interactions with years due to changes in the magnitude of the significant response. The alleles from *T. spelta*, however, conferred a higher yield performance.

Key words *Triticum aestivum* · Grain yield · Yield components · QTLs · Single-chromosome recombinant lines

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Introduction

Grain yield in cereals is generally controlled by a number of quantitative trait loci (QTLs) and is affected by environmental factors, making it difficult to manipulate and improve breeding programs. Grain yield can be dissected into a number of component traits such as spike number per plant, ear grain weight, spikelet number per ear, and 1000-grain weight. These component traits are also under QTL control and the effects of individual QTLs on phenotypic variation are relatively small (Yano and Sasaki 1997). Some of them, however, are less environmentally sensitive and have higher heritabilities than grain yield itself (Bezant et al. 1997; Yano and Sasaki 1997). Therefore, while looking for QTLs controlling grain yield, QTLs for yield components should also be determined to provide more useful information.

The advent of molecular markers, and in particular restriction fragment length polymorphisms (RFLPs), have greatly facilitated the detection of QTLs controlling yield traits and the relationship between grain yield and its components. Using molecular-linkage genetic maps, it is possible to estimate the number of loci controlling genetic variation in a segregating population and to characterize these loci with regard to map position, gene action, phenotypic effects, pleiotropic effects and epistatic interactions with other QTLs (Xiao et al. 1996). It has been demonstrated that correlated, or components of plant yield, traits often have QTL mapping at similar locations. This has been observed in maize (Abler et al. 1991; Veldboom et al. 1994; Austin and Lee 1996), tomato (Paterson et al. 1991), rice (Xiao et al. 1996) and barley (Tinker et al. 1996; Bezant et al. 1997).

In hexaploid wheat (*Triticum aestivum* L.), however, QTL analyses of grain yield and its components using molecular marker systems are more complex than for diploids like barley and rice, and hence are currently limited (Hyne et al. 1994; Araki et al. 1999). Chromosome 5A of wheat is known to carry a number of genes affecting adaptability and productivity (Law and Worland 1973; Snape et al. 1985; Miura and Kuroshima

1996). A gene that has received detailed attention is the vernalization requirement gene, *Vrn-A1*, which is one of the main determinants of the winter/spring growth-habit polymorphism. The ear morphology gene *q*, the frost-resistant gene *Fr1* (Galiba et al. 1995), and a QTL response to drought stress (Quarrie et al. 1994) have all been located on the long arm of 5A. Snape et al. (1985) reported pleiotropic effects of *Vrn-A1* and *q* on plant yield and some yield components. In addition to these two major gene loci, further QTLs affecting productivity have been postulated on this chromosome (Snape et al. 1985; Roberts 1989; Miura and Kuroshima 1996).

To identify QTLs for agronomically and economically important traits on chromosome 5A, we developed a homozygous population of single-chromosome recombinant lines and constructed a genetic linkage map locating major gene loci and RFLP markers (Kato et al. 1998, 1999a, b). This paper describes the detection and location of QTLs controlling grain yield and its components using the linkage genetic map and the homozygous recombinant lines.

Materials and methods

Experimental methods, mapping population, RFLP marker loci, major gene loci (*Vrn-A1*, *q* and *B1*) and statistical QTL analysis were as described in Kato et al. (1998, 1999a, b). A homozygous population of 118 single-chromosome recombinant lines (SCRs) was produced from F_1 plants of a cross between substitution lines for chromosome 5A from a spring accession of *Triticum spelta* and a French winter-wheat cultivar 'Cappelle-Desprez' into a 'Chinese Spring' (CS) background, using the technique first described by Law (1966). Initially, the F_1 hybrid was crossed as male parent to a CS monosomic-5A line. In the resulting progeny monosomic plants were identified by cytological examination of mitotic chromosomes in root-tip preparations. These were selfed, and disomic recombinants were selected by cytological examination of progeny. Extracted disomics were grown to maturity and allowed to self-pollinate. Since chromosome 5D of CS carries the dominant *Vrn-D1* allele promoting the spring growth habit (Pugsley 1972; Law et al. 1976), all SCRs and parental substitution lines used here were of the spring habit.

Spring-sown trials were conducted at the experimental field of Obihiro University of Agriculture and Veterinary Medicine over 3 years, 1993, 1994 and 1996. The SCR population and the two parental lines, CS (Cappelle-Desprez 5A) and CS (*T. spelta* 5A), were sown in late April using a randomized complete block design with five replicate blocks. Each plot contained a single 1-m row of 11 plants of each line. Rows were spaced 30-cm apart. At maturity, five leading tillers of five random plants were taken from each plot and used for evaluating single-tiller yield components (ear grain weight, spikelet number/ear) and 50-grain weight. The remainder of each plot was harvested. Grain yield and tiller number were calculated for each plot.

In each trial, analyses of variance (ANOVA) were performed to detect differences between the parental genotypes. To identify QTLs controlling yield traits, the Simple Interval Mapping (SIM) and simplified Composite Interval Mapping (sCIM) procedures were carried out using the software package MQTL (Tinker and Mather 1995) which detects both QTLs and QTL×environment interaction. The linkage group was scanned at 5-cM-interval test statistics. Nine evenly spaced background markers were specified for sCIM. Except for multi-environment sCIM analysis, where a precise test statistic is not computable, type-I 5% significant thresholds were established with 1000 permutations. The significance of QTL regions is reported as test statistics [TS=n ln(RSSr/RSSf)] where n is the number of observations, RSSf is the residual sum of squares for the full model, and RSSr is the residual sum of squares from the model without the effect being tested. This test statistic is similar to the likelihood ratio and approximately equals the F statistic. For a single environment, TS can be converted to a LOD computed by MAPMAKER/QTL by multiplying by 0.22 or dividing by 2 ln(10). Detected QTL regions were grouped in a multi-locus linear model which estimates the overall phenotypic variance explained by the model.

Results

Analysis of yield traits

The mean performance for plant yield and four component traits of the parental lines in each of the 3 years are presented in Table 1. All traits except 50-grain weight were significantly different between the parental lines. Compared to CS (Cappelle-Desprez 5A), CS (*T. spelta* 5A) had a higher grain yield and component yield excluding tiller number. The plant yield of CS (*T. spelta* 5A) was higher than that of CS (Cappelle-Desprez 5A) by more than 70% in the 1994 and 1996 trials, and by about 30% in the 1993 trial, respectively. These large differences were mainly ascribable to differences in ear grain weight.

Table 1 Mean performance and range of grain yield and its components of the parental lines and the mapping population measured in the three trials

Trial	Line	Plant yield (g)	Tiller number/ plant	Ear grain weight (g)	50-grain weight (g)	Spikelet number/ ear
1993	CS (Cappelle-Desprez 5A)	5.19*	7.3	1.37*	1.88	15.3*
	CS (*T. spelta* 5A)	6.88	8.8	1.58	1.77	17.3
	Mapping mean	5.11	7.1	1.40	1.76	15.7
	population range	2.19–7.14	5.1–10.1	0.78–1.70	1.45–2.01	12.1–18.5
1994	CS (Cappelle-Desprez 5A)	6.13*	12.2	0.72***	1.51	19.2
	CS (*T. spelta* 5A)	10.66	11.2	1.28	1.53	18.4
	Mapping mean	8.97	11.9	1.09	1.49	19.3
	population range	3.83–14.42	8.5–17.0	0.53–1.46	1.16–1.59	16.8–21.1
1996	CS (Cappelle-Desprez 5A)	4.15*	15.4*	0.48***	1.57	6.5***
	CS (*T. spelta* 5A)	7.27	12.3	0.89	1.67	10.0
	Mapping mean	6.38	14.7	0.75	1.54	9.2
	population range	2.45–10.32	9.8–18.8	0.42–1.11	1.23–1.72	6.1–12.2

*, *** significantly different from CS (*T. spelta* 5A) at P=0.05–0.01 and P<0.001, respectively

Table 2 Phenotypic correlation coefficients averaged across 3 years among ear emergence time (EET), plant height (HT), culm length (CL), ear length (EL), grain yield (YLD), tiller number/plant (TN), grain weight per ear (GWE), 50-grain weight (FGW) and spikelet number per ear (SNE) for 118 SCRs from the cross CS (Cappelle-Desprez 5A)×CS (*T. spelta* 5A)

Item	EET	HT	CL	EL	YLD	TN	GWE	FGW
HT	–0.17*							
CL	–0.01	0.97**						
EL	–0.64**	0.60**	0.39**					
YLD	–0.38**	0.63**	0.53**	0.67**				
TN	0.47**	0.10	0.19*	–0.26**	0.29**			
GWE	–0.60**	0.53**	0.41**	0.65**	0.77**	–0.15		
FGW	–0.52**	0.53**	0.44**	0.57**	0.67**	–0.22*	0.95**	
SNE	–0.39**	0.67**	0.54**	0.76**	0.77**	0.06	0.61**	0.49**

*, **, correlation was significant at the 0.05 and 0.01 probability level, respectively

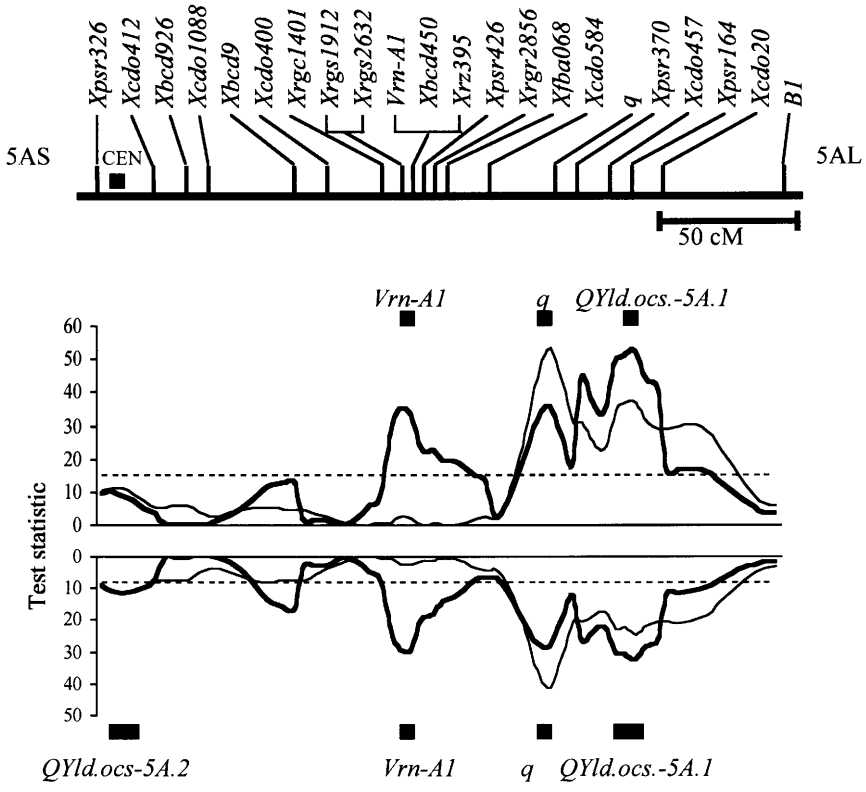

Fig. 1 Effect and position of QTLs for grain yield. Both the QTL main effect (upper) and the QTL×years interaction (lower) were calculated by SIM (*normal line*) and sCIM (*bold line*). The *dotted line* indicates the 5% significant threshold level for SIM

The frequency distribution of each phenotype trait over 3 years in the SCR population showed that all traits approximately fit normal distributions (data set is not shown). ANOVA revealed highly significant differences between SCRs, and SCR×year interaction for each trait, showing that genes on chromosome 5A controlling yield traits segregate in the population and that the expression of these genes was not consistent between years. SCRs having phenotypic values greater than the higher parent and smaller than the lower parent (i.e. transgressive segregants) were observed for all traits (Table 1).

Trait correlations

The correlation coefficients among all traits including ear emergence time, plant height, culm length and ear length (Kato et al. 1999a) are presented in Table 2. Grain yield and its components showed positive correlations. In addition, ear emergence time, culm length and ear length were significantly correlated with grain yield and its components.

Plant yield

A total of four regions were found to have effects on plant yield (Fig. 1) and both parents carried QTL alleles which increased phenotypic values (Table 3). The effect associated with *Vrn-A1* or a closely linked QTL was detected in the 1994 trial by sCIM, and the high-yielding allele with an additive effect of 1.43 g (1994) came from 'Cappelle-Desprez' (Table 3). The effect of *q* or a closely linked QTL was detected in the 1994 and 1996 trails.

Table 3 Location and multi-locus estimates of QTLs controlling grain yield and its components

Trait	Year	Locus	Peak	TS[a]	Threshold[b]	R^2	Additive[c]
Grain yield	1994	*q*	*q*	37.1	8.7	0.27	2.18 S
		Vrn-A1	*Xrgs1912, Xrgr2632*	30.3	8.7	0.08	1.43 C
		QYld.ocs-5A.1	*Xpsr164/Xcdo20*	27.2	8.7	0.21	1.06 S
		[multi-locus model[d]]				0.39	
	1996	*q*	*q*	30.4	8.7	0.23	1.52 S
		QYld.ocs-5A.2	*Xpsr326/Xcdo412*	15.6	8.7	0.12	1.07 S
		[multi-locus model]				0.30	
Tiller number /plant	1993	*Vrn-A1*	*Xrgs1912, Xrgr2632*	9.0	8.8	0.07	0.49 C
	1994	*Vrn-A1*	*Vrn-A1, Xbcd450, Xrz395*	55.4	8.8	0.37	2.15 C
		QTn.ocs.5A.1	*Xpsr370/Xcdo457*	12.6	8.8	0.10	0.42 C
		[multi-locus model]				0.41	
	1996	*QTn.ocs-5A.1*	*Xpsr370*	25.4	8.6	0.19	1.23 C
		QTn.ocs-5A.2	*Xcdo1088/Xbcd9*	12.9	8.6	0.10	0.68 C
		[multi-locus model]				0.24	
Ear grain weight	1994	*q*	*q*	64.6	8.9	0.42	0.16 S
		QEgw.ocs-5A.1	*Xpsr164/Xcdo20*	53.7	8.9	0.37	0.15 S
		QEgw.ocs.5A.2	*Xcdo1088/Xbcd9*	23.0	8.9	0.18	0.12 S
		QEgw.ocs-5A.3	*Xpsr326/Xcdo412*	12.1	8.9	0.10	0.09 S
		[multi-locus model]				0.61	
	1996	*q*	*q*	21.6	8.6	0.17	0.09 S
		QEgw.ocs-5A.2	*Xcdo1088/Xbcd9*	20.1	8.6	0.16	0.07 S
		QEgw.ocs-5A.3	*Xpsr326/Xcdo412*	19.9	8.6	0.16	0.10 S
		[multi-locus model]				0.32	
50-grain weight	1993	*QFgw.ocs-5A.1*	*Xcdo457/Xpsr164*	24.6	8.5	0.19	0.12 C
	1994	*Vrn-A1*	*Xcdo400/Xrgc1401*	13.1	8.4	0.11	0.04 S
	1996	*QFgw.ocs-5A.1*	*Xcdo457/Xpsr164*	14.4	8.3	0.11	0.06 C
Spikelet number /ear	1993	*QSpn.ocs-5A.1*	*Xcdo457/Xpsr164*	59.0	8.3	0.39	1.97 S
	1994	*Vrn-A1*	*Vrn-A1, Xbcd450, Xrz395*	79.7	8.5	0.49	1.41 C
	1996	*QSpn.ocs-5A.1*	*Xcdo457/Xpsr164*	35.2	8.9	0.26	1.51 S
		QSpn.ocs-5A.2	*Xcdo1088/Xbcd9*	17.5	8.9	0.14	0.53 S
		QSpn.ocs-5A.3	*Xpsr326/Xcdo412*	21.1	8.9	0.16	1.10 S
		[multi-locus model]				0.41	

[a] TS: indicates test statistic
[b] Threshold: indicates the threshold for type-I error rate of 5% by simple main effect
[c] Additive: indicates an additive SIM main effect of the parent contributing the higher value allele, where c=CS (Cappelle-Despres 5A) and s=CS (*T. spelta* 5A)
[d] Multi-locus model: indicates the value of variance QTL main effect/phenotypic variance

A '*T. spelta*' allele of this region producing a speltoid ear had additive effects of 2.18 g (1994) and 1.52 g (1996) and accounted for 27% and 23% of the phenotypic variance, respectively. A QTL, designated *QYld.ocs-5A.1*, was mapped within the 11.0-cM *Xpsr164/Xcdo20* interval, where again the '*T. spelta*' allele had an additive effect of 1.06 g (1994) on yield increase which accounted for 21% of the phenotypic variance. A QTL, designated *QYld.ocs-5A.2*, was mapped within the 24.7-cM centromeric region flanked by *Xpsr326* and *Xcdo412*, where the '*T. spelta*' allele had an additive effect of 1.07 g (1996) on yield increase which accounted for 12% of the phenotypic variance. The phenotypic expressions of the four QTLs varied over years. Significant QTL×year interactions corresponding to QTL main effects were identified mainly due to effects of the 1993 trial when temperatures were lower.

Tiller number/plant

Three loci were detected for tiller number/plant by both SIM and sCIM (Fig. 2). At these three loci, tillers were increased by the alleles from 'Cappelle-Desprez'. *Vrn-A1* or a closely linked QTL had additive effects of 0.49 (1993) and 2.15 (1994), and accounted for 7% (1993) and 37% (1994) of the phenotypic variance, respectively. A QTL, *QTn.ocs-5A.1*, identified within the *Xpsr370/Xcdo457* segment, and closely linked to *q* by about 10 cM, had additive effects of 0.42 (1994) and 1.23 (1996), and accounted for 10% (1994) and 19% (1996) of the phenotypic variance, respectively. A QTL, *QTn.ocs-5A.2*, identified by marker *Xbcd9*, had additive effects of 0.68 (1996), and accounted for 10% of the phenotypic variance. A QTL×year interaction was detected within the same marker interval of the significant QTL main effects, due to changes in the magnitude of response.

Ear grain weight

Four loci, with '*T. spelta*' contributing all the alleles for increasing ear grain weight, were detected by both SIM and sCIM in 1994 and 1996 (Fig. 3). The largest effect was associated with *q* or a closely linked QTL which had additive effects of 0.16 g (1994) and 0.09 g (1996), and

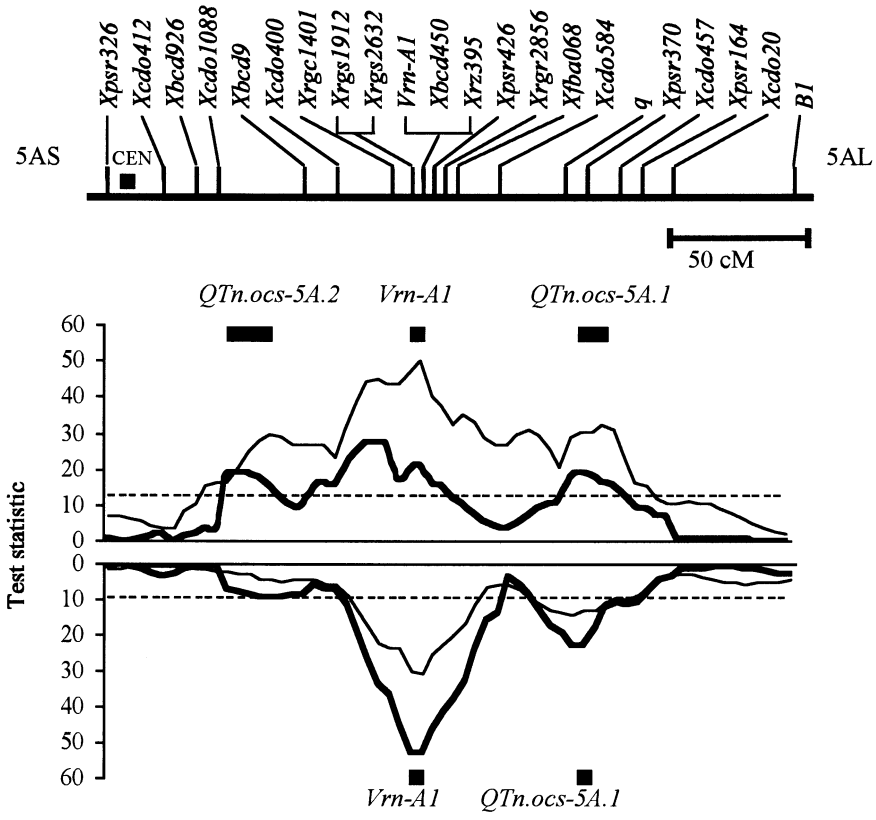

Fig. 2 Effect and position of QTLs for tiller number/plant. Both the QTL main effect (upper) and the QTL×years interaction (lower) were calculated by SIM (*normal line*) and sCIM (*bold line*). The *dotted line* indicates the 5% significant threshold level for SIM

accounted for 42% (1994) and 17% (1996) of the phenotypic variance. Similar to grain yield, this increasing effect by the '*T. spelta*' allele did not appear in the 1993 trial, resulting in a significant QTL×year interaction with a greatly exceeded magnitude over the QTL main effect. At the other three QTLs, designated as *QEgw.ocs-5A.1* which mapped to the *Xpsr164/Xcdo20* interval, *QEgw.ocs-5A.2* in the *Xcdo1088/Xbcd9* interval and *QEgw.ocs-5A.3* in the *Xpsr326/Xcdo412* interval, tillering was increased by the '*T. spelta*' alleles and significant QTL×year interactions were detected. A close linkage of *QEgw.ocs.1* with *q* suggests that this putative QTL is presumably equivalent to a QTL proposed by Snape et al. (1985) on either side of *q*. The grain yield effect associated with *Vrn-A1* was not detected for this trait in any year.

50-grain weight

Two loci affecting 50-grain weight were detected by both SIM and sCIM (Fig. 3). In 1994, *Vrn-A1* or its adjacent region had an additive effect of 0.04 g, increasing by the '*T. spelta*' allele, and accounted for 11% of the phenotypic variance. In the unfavorable seasons of the 1993 and 1996 trials, a QTL (*QFgw.ocs-5A.1*) was identified in the *Xcdo457/Xpsr164* interval. The increasing allele at *QFgw.ocs-5A.1* came from 'Cappelle-Desprez'.

Spikelet number/ear

Four QTLs were detected for spikelet number/ear (Table 3). The *Vrn-A1* region had a major effect in the 1994 trial accounting for half of the phenotypic variance such that the later-flowering *vrn-A1* from 'Cappelle-Desprez' increased spikelet number/ear by 1.41. In the unfavorable seasons of 1993 and 1996, a QTL (*QSpn.ocs-5A.1*) was detected within the *Xcdo457/Xpsr164* interval with additive effects of 1.97 (1993) and 1.51 (1996). In the 1996 trial, two other minor QTLs, *QSpn.ocs-5A.2* and *QSpn.ocs-5A.3*, were identified in the *Xcdo1088/Xbcd9* and *Xpsr326/Xcdo412* intervals, respectively. At both QTLs, '*T. spelta*' alleles increased spikelet number and had additive effects of 0.53 and 1.10 which accounted for 14% and 16% of the phenotypic variance, respectively. The significant QTL×year interactions were detected at the three loci except for the *Vrn-A1* region, due to the reduction or disappearance of the significant effects in at least 1 year.

Discussion

Many quantitative traits can be partitioned between smaller components of a quantitative and/or qualitative nature. The present study identified five chromosomal regions controlling grain yield and its components QTLs on chromosome 5A, and confirmed that these grain-yield QTLs were correlated with QTLs for yield components and found at the same map positions.

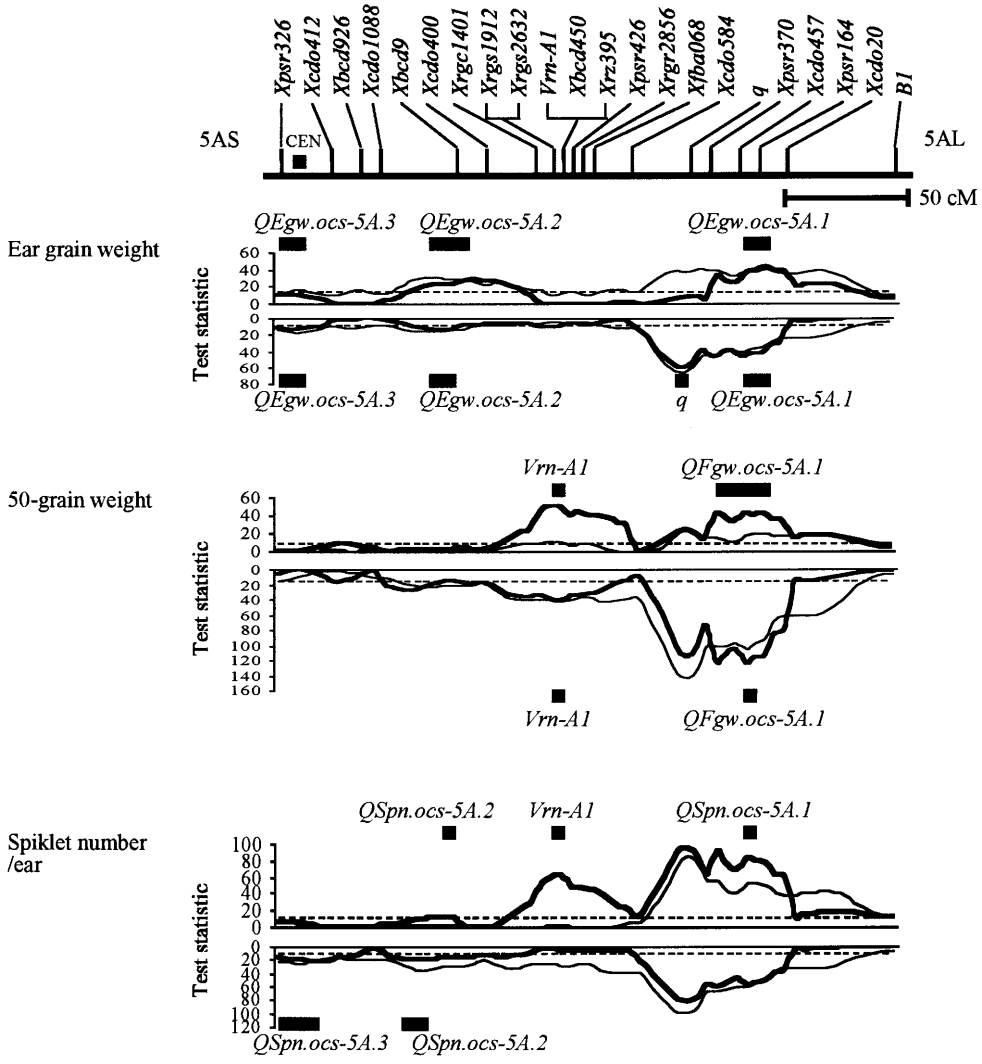

Fig. 3 Effect and position of QTLs for yield components. Both the QTL main effect (upper) and the QTL×years interaction (lower) were calculated by SIM (*normal line*) and sCIM (*bold line*). The *dotted line* indicates the 5% significant threshold level for SIM

Trait correlations may also reflect a consequence of patterns of plant growth and development. In general, plant yield is increased by factors that allow longer periods of grain fill (e.g. Worland 1996). The effects associated with *Vrn-A1* on tiller number and spikelet number were revealed in the favorable conditions of the 1994 trial where an increased number of tillers and spikelets were associated with the later-flowering *vrn-A1* allele from 'Cappelle-Desprez'. For ear grain weight, however, there was no effect of the *Vrn-A1* locus. The same result was reported by Snape et al. (1985). A possible explanation is that an increase in spikelet numbers by the *vrn-A1* allele was affected adversely by reductions in grain size. Such a complementary effect was found for the photoperiod response gene *Ppd-D1* on chromosome 2D. Worland (1996) demonstrated that the insensitive *Ppd-D1* genotypes with a shortened life cycle showed significant increases in spikelet fertilities that more than compensated for reductions in spikelet numbers and promoted an overall increase in the number of grains setting in the ear. If this is true for *Vrn-A1*, a yield advantage associated with *vrn-A1* should rely upon an increase in fertile tillers and spikelets by means of a response to the longer periods of growth.

In the previous QTL analysis of chromosome 5A on the control of flowering time, we have shown that *Vrn-A1* and *QEet.ocs-5A.1* are major determinants of variation. Both loci are comparable in the direction and magnitude of their additive effect and the amount of variance accounted for (Kato et al. 1999a). *QEet.ocs.1*, positioned distal to marker *Xcdo584* by some 20 cM and proximal to *q* by less than 10 cM, was presumed to be a QTL for earliness *per se* (Snape et al. 1985; Kato et al., unpublished data). In most situations earlier-flowering plants tend to reduce yield simply due to their shortened life cycle. However, because of a loose genetic linkage with *Vrn-A1* (about 40 cM) and no effect on grain yield and its components, *QEet.ocs.1* can have breeding potential as a promising target for changing ear emergence time without yield reductions. The third flowering QTL, *QEet.ocs-5A.2*, mapped within the *Xcdo412/Xbcd9* interval, and the *T. spelta* allele had an effect on early ear

emergence time by about 3 days only in a CS (Cappelle-Desprez 5A) background (Kato et al. 1999c). The adjacent region identified by *Xbcd9* had minor effects on tiller number, ear grain weight and spikelet number/ear, where the later-flowering 'Cappelle-Desprez' allele had the effects of increasing tiller number (*QTn.ocs.2*), and reducing both ear grain weight (*QEgw.ocs.2*) and spikelet number/ear (*QSpn.ocs.2*). Hence, there are at least two patterns of correlations between flowering time and yield traits, due to (1) the pleiotropic effects of *Vrn-A1* and *QEet.ocs.2* or the effects of closely linked loci and (2) independent effects of *QEet.ocs.1*. A better understanding of such patterns of trait correlations could contribute to breeding strategies aimed to improve adaptability and productivity. In the future, fine-structure mapping of these regions will be conducted.

The evaluation of homozygous mapping populations in multiple environments presents additional challenges and opportunities for QTL analysis. Paterson et al. (1991) suggested that the studies conducted in a single environment are likely to underestimate the number of QTLs which can influence a certain trait. The positions of QTLs are presumably constant within a genome but the effects of QTLs may vary among environments due to QTL×environment interaction. These concepts were confirmed in the present experiment. It is also possible to identify environmentally sensitive QTLs, meaning that the expression of the QTLs will occur under certain environments (e.g. a particular range of temperatures). For such an environment-specific QTL, one would only be able to identify the QTL at a location where these environmental conditions are satisfied. Although most QTL×year interactions in the current study were due to changes in the magnitude of the significant response, it is of interest to note that a high *q*×year interaction appeared for yield components especially for ear grain weight and 50-grain weight. The effect of *q* on ear grain weight was variable across the 3 years. A significant *q*×year interaction was due to the favorable *q* allele that was either not significant or else decreased its effect under the cool weather of 1993 and 1996. In these two seasons 50-grain weight was increased by the *Q* allele but spikelet number/ear was increased by the alternative *q* allele, probably due to competing demands for limited photosynthate in those adverse seasons. Consequently it was probable that the compensating effects of the *q* locus on these two traits reduced the significant effect on grain weight. This demonstrates interactions between the increase in one of the two components and a decrease in another by a QTL in the same location. On the other hand, why these effects associated with *q* were not significant in the 1994 season was uncertain, as was other QTLs like *QFgw.ocs.1* and *QSpn.ocs.1*.

For genetic analysis of wheat, the present investigation demonstrates the power of SCRs as a tool for locating and identifying QTLs controlling important quantitative traits. For grain yield, four QTLs including *Vrn-A1* and *q* were detected on chromosome 5A, and both parental substitution lines were found to possess favorable QTL alleles. The occurrence of such transgression could be directly associated with the inheritance of complementary QTL alleles from the two parents. As mentioned above, two QTLs with minor effects were dispersed from the centromeric region flanked by *Xpsr326* and *Xcdo412* to the 11.0-cM *Xpsr164/Xcdo20* QTL interval, the vicinity of the 4A/5A break-point on the long arm. The dispersed nature of the yield QTLs and flowering time QTLs on this chromosome would mean that recombinant 5A chromosomes can be selected which increase the variation of productivity and adaptability over that of both parental homologues.

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