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In an elite cross of maize a major quantitative trait locus controls one-fourth of the genetic variation for grain yield

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Abstract Quantitative trait loci (QTLs) for grain yield, dry matter content and test weight were identified in an F_2 segregating population derived from a single cross between two elite maize lines (B73 and A7) and testcrossed to two genetically divergent inbreds. Most of the QTLs inferred were consistent across locations, indicating that the expression of the genes influencing the traits under investigation was largely independent of the environment. By using two different tester lines we found that QTLs exhibited by one tester may not necessarily be detected with the second one. Only loci with larger effects were consistent across testers, suggesting that interaction with tester alleles may contribute to the identification of QTLs in a specific fashion. Analysis across both testers revealed four significant QTLs for grain yield that explained more than 35% of the phenotypic variation and showed an overall phenotypic effect of more than 2 t/ha. The major QTL for grain yield, located in the proximity of the Nucleolus Organiser Region, accounted for 24.5% of the phenotypic variation for grain yield and showed an average effect of allele substitution of approximately 1 t/ha. Marker-assisted introgression of the superior A7 allele at this locus in the B73 genetic background will not differ from qualitative trait introgression and will eventually lead to new lines having superior testcross performance.

Key words RFLP markers · Heterosis · QTL mapping · Testcross performance · *Zea mays* L.

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Introduction

Quantitative variation is of importance for adaptative evolution and selective improvement of crop species. However, little is known about the genetic basis of quantitative variation, although a model for the simultaneous segregation of many independent loci, called polygene loci or quantitative trait loci (QTLs; Mather 1941; Thompson and Thoday 1974), each with small effects, works well to describe the major features of quantitatively inherited traits (Falconer 1989). Therefore, a more precise identification of genetic factors contributing to quantitative traits should provide information on their relative contribution to continuous variation and on genome organisation.

Genetic markers linked to factors affecting metric traits have been used to study quantitative inheritance. These include morphological markers (Sax 1923), chromosome substitution lines (Snape et al. 1977), and isozyme loci. Although the usefulness of morphological and isozyme markers for identifying and locating QTLs has been described (see Paterson et al. 1991; Stuber 1992 for a review), their number is insufficient for many applications in plant breeding.

DNA markers, particularly restriction fragment length polymorphisms (RFLPs), are almost unlimited, allow the construction of dense linkage maps in several crop species (for review see Paterson et al. 1991; Gebhardt and Salamini 1993), and make possible the dissection of quantitative variation into Mendelian factors (Paterson et al. 1988a, b; Lander and Botstein 1989).

In maize detailed linkage maps exist (Coe et al. 1990; Helentjaris 1987; Burr et al. 1988). In this species studies carried out with elite lines adapted to the US Corn Belt (Smith et al. 1990; Melchinger et al. 1991; Livini et al. 1992) indicate that RFLPs can be used for assigning maize inbreds to heterotic groups and for detecting pedigree relationships among lines. The existence and mapping of QTLs has been also documented for grain yield, yield components, abiotic stresses and insect resist-

ance (Reiter et al. 1991; Schön et al. 1993; Edwards et al. 1992; Stuber et al. 1992; Walton and Helentjaris 1987).

Grain yield is a trait with complex inheritance and low heritability. Because of this, the use of molecular markers could greatly enhance the efficiency of selection for this trait. However, the development of markers to assist the selection of a trait is recommended only for QTLs controlling large fractions of the total genetic variation. The objectives of the study presented here were to identify QTLs affecting grain yield and other grain-related traits in testcrosses of maize, to estimate the magnitude of QTL effects, to investigate the consistency of QTLs across testers and to explore the possibility of marker-assisted selection for grain yield.

Materials and methods

Plant material

This was developed by crossing the inbred lines B73 and A7, respectively related to the "Stiff Stalk Synthetic" (BSSS) and "Lancaster Sure Crop" (LSC) heterotic groups. The two lines are polymorphic at several molecular marker loci (Livini et al. 1992). Two-hundred and thirty-two F_3 lines were developed, each tracing back to an individual F_2 plant. In the 1990 breeding nursery at Bergamo, Italy, 10 plants of each of the 232 F_3 lines were testcrossed to the two tester lines A1 and Mo17, which represent, respectively, the BSSS and LSC germ plasms.

Field trials

Each set of testcrosses was divided into three subsets and evaluated in adjacent randomised complete block (RCB) experiments with two replications at Bergamo and Brescia, Northern Italy, in 1992. Each RCB experiment comprised 79 entries, including 77 F_3 testcrosses and 2 testcrosses of the parent lines as checks. We used two-row plots, 5 m long, with plant densities of 53,000 plants/ha at Bergamo and 56,000 plants/ha at Brescia. At each location, the level of fertilisation and weed control practices were those currently used to grow maize hybrids. Irrigation was applied throughout the summer to avoid water stress. Testcrosses and checks were evaluated for grain yield (t/ha at 15.5% grain moisture), dry matter content (% dry matter in grain at harvest) and test weight (kg/hl measured at harvest moisture with GAG-2 grain analysis instrument).

RFLP assays

From each of the 232 F_3 lines, 15–20 seedlings were grown and leaf tissues harvested and bulked. RFLP assays were performed as in Livini et al. (1992). A total of 72 genomic maize clones that reveal polymorphic loci on specific maize chromosomes were selected from those available from the Brookhaven National Laboratory, the University of Missouri Columbia and Pioneer Hi-Bred Int. to provide a uniform coverage of the entire genome. In addition, 15 RAPD markers were used (Ajmone-Marsan et al. 1993).

Statistical analyses

Each RCB experiment was analysed separately. To obtain means unbiased by the effects of the three sub-experiments per tester-location combination, entry means were adjusted according to the overall mean of individual RCBs, considering each subset of testcrosses as a random sample from the entire testcross population. Error mean squares for the complete set of testcrosses were estimated by pooling the error variances over the three sub-experiments per tester-location combination.

Adjusted entry means and pooled error mean squares of single locations were used for the analyses of variance across locations. The normal distribution of entry means of individual locations and across locations was checked using Shapiro and Wilk's (1965) W-test. Estimates of variance components for genotypes (σ_g^2), genotype-location interaction (σ_g^2) and error (σ_e^2) of F_3 lines and their standard errors were estimated from the expected mean squares as described by Searle (1971). The effects of locations and genotypes were considered to be random. Heritability (h^2) on a progeny-mean basis was estimated for each trait by dividing the genotypic variance by the phenotypic variance (see Hallauer and Miranda 1988). Confidence intervals ($P < 0.10$) of heritability estimates were calculated according to Knapp et al. (1985). Coefficients of phenotypic (r_p) and genotypic (r_g) correlation between the testcross performance of F_3 lines with both testers were estimated using the formula of Mode and Robinson (1959).

Expected segregation ratios (1:2:1) and allelic frequencies ($p = q = 0.5$) at individual marker loci were tested using chi-square tests (Weir 1990). A linkage map of the 72 RFLP markers was assembled using the MAPMAKER computer programme (Lander et al. 1987). To declare significant linkage between markers, a LOD threshold of 3.0 and a maximum recombination frequency of 0.4 were chosen. Map distances between marker loci were estimated using Haldane's (1919) mapping function.

The mapping of the QTLs and estimation of their genetic effects were performed according to the method of interval mapping described by Lander and Botstein (1989) using the computer package MAPMAKER/QTL (Lander et al. 1987; Lincoln and Lander 1990). QTL analyses were performed on entry means from individual environments and on entry means across environments.

Following Cowen (1988), we used a purely additive genetic model for the analysis of our testcross progenies. Genetic effects of putative QTLs were estimated as an average effect of substituting an allele from parent P1 by an allele of parent P2 in the testcrosses. The corresponding model can be written as follows:

$$y_j = \mu_{P1} + k_j a^T + e_j$$

Here, y_j = phenotypic trait value of testcrosses of line j; μ_{P1} = mean phenotypic trait value of testcrosses carrying the allele from P1 at the putative QTL; $k_j = 0, 0.5$ or 1 if the parental F_2 plant is homozygous P1, heterozygous or homozygous P2, respectively; a^T = average effect of substituting allele P1 by P2 at the QTL; and e_j = variation not controlled by QTL.

We used a LOD threshold of 2.5 to declare the presence of a significant QTL. When the marker density used is into account a LOD of 2.5 corresponds approximately to a probability of $P < 0.05$ for declaring a single false QTL in the entire genome. QTLs were considered to be identical for both testers when their support intervals were overlapping. Endpoints of the support intervals were determined by a decrease in the LOD score of 1.0 relative to the maximum LOD score. Estimates of the total phenotypic variance (σ_p^2) explained and the total LOD score were calculated by fitting a model including all putative QTLs for the respective trait simultaneously. When the LOD curve showed two nearby peaks, indicating two linked QTLs, the significance of the QTL with the smaller LOD score was tested by re-scanning the chromosome, keeping the QTL with the greater LOD fixed. According to Stuber et al. (1992), an increase of LOD 2.0 can be considered to be diagnostic for the presence of two linked QTLs.

Results

Agronomic traits

Grain yield of F_3 testcrosses with both tester lines was higher at Bergamo (Table 1). At Bergamo, testcrosses of

Table 1 Means for grain yield, dry matter content, plant height and test weight averaged over testcross progenies of 232 F_3 lines derived from cross P1 × P2 crossed to tester Mo17 (Exp. 1) and A1 (Exp. 2) and evaluated at two locations

Experiment	Location	Grain yield (t/ha)	Dry matter content (%)	Test weight[a] (kg/hl)
1	Bergamo	10.42 ± 0.06[b]	72.58 ± 0.06	68.02
	Brescia	8.76 ± 0.05	74.65 ± 0.04	–
2	Bergamo	9.84 ± 0.05	74.38 ± 0.07	69.04
	Brescia	8.94 ± 0.05	75.89 ± 0.07	–

[a] Measured at one location only
[b] Standard errors are attached

tester Mo17 (Exp. 1) showed a higher yield, whereas at Brescia, testcrosses of tester A1 (Exp. 2) performed better. Dry matter content was higher at Brescia for both testers. At both locations, values for dry matter content of A1 testcrosses exceeded those of Mo17. The test weight of the A1 testcrosses was slightly higher than of Mo17 testcrosses.

Testcross performance of parents P1 and P2 with tester Mo17 differed significantly for grain yield ($P < 0.01$) and test weight ($P < 0.05$) (Table 2). For tester A1, the testcross means of the two parental lines were significantly different for all traits except test weight ($P < 0.01$ and 0.05, respectively). The comparison between the testcross performance of F_3 lines and parents with tester Mo17 yielded significant differences for dry matter content ($P < 0.01$), the parents' mean being higher for the former.

For all traits, genotypic differences among F_3 lines were highly significant for both testers (Table 1). For tester Mo17 (Exp. 1), genotype-by-location interaction (σ^2_{gl}) was highly significant ($P < 0.01$) for the traits that were evaluated at both locations, while for tester A1 (Exp. 2), σ^2_{gl} was significant for dry matter content only ($P < 0.05$). In all cases, the estimates σ^2_{gl} were significantly lower than those of genotypic variance.

Broad-sense heritabilities were moderately high for all traits and both testers. For the traits evaluated at both locations, estimates ranged from 0.58 (grain yield) to 0.76 (test weight) for tester Mo17 and from 0.62 (grain yield) to 0.73 (test weight) for tester A1.

Genotypic correlations (r_g) between the testcross performance of F_3 lines with testers Mo17 and A1 were moderately high for dry matter content, while for grain yield, correlation was only weak (Table 3).

RFLP linkage map

The segregation of 72 probes was assessed on the 232 F_3 lines. The genetic map is shown in Fig. 1 with distances

Table 2 Means, variance components, and heritabilities of testcross progenies from parent lines (P1 and P2) and 294 F_3 lines derived from cross P1 × P2 and crossed to Mo17 (Exp. 1) and A1 (Exp. 2) for four quantitative traits measured at two locations

Experiment	Parameter	Grain yield (t/ha)	Dry matter content (%)	Plant height (cm)	Test weight[a] (kg/hl)
1	Testcross means				
	P1 (3)[b]	9.18 ± 0.207[c]	73.76 ± 0.177	257.52 ± 2.118	68.85 ± 0.466
	P2 (3)	10.04 ± 0.207	74.16 ± 0.177	261.36 ± 2.118	67.53 ± 0.446
	$\bar{P}$ (6)	9.61 ± 0.147	73.96 ± 0.125	259.30 ± 1.498	68.19 ± 0.316
	F_3 (294)	9.59 ± 0.030	73.62 ± 0.026	263.22 ± 0.250	68.02 ± 0.056
	Variance components				
	σ^2_g	0.545 ± 0.085**	0.403 ± 0.060**	36.867 ± 7.406**	1.862 ± 0.209**
	σ^2_{gl}	0.258 ± 0.066**	0.189 ± 0.049**	26.918 ± 6.975**	–[d]
	σ^2_e	1.090 ± 0.064	0.708 ± 0.042	115.024 ± 6.724	1.196 ± 0.089
	Heritability				
	h^2	0.58	0.60	0.47	0.76
	90% C.I. on h^2[e]	0.48–0.65	0.51–0.67	0.39–0.56	0.66–0.83
2	Testcross means				
	P1 (3)	9.10 ± 0.085[c]	75.47 ± 0.172	242.42 ± 0.911	69.57 ± 0.431
	P2 (3)	9.65 ± 0.085	74.96 ± 0.172	226.83 ± 0.911	69.63 ± 0.431
	$\bar{P}$ (6)	9.38 ± 0.060	75.21 ± 0.122	234.63 ± 0.644	69.90 ± 0.305
	F_3 (294)	9.39 ± 0.026	75.14 ± 0.038	236.94 ± 0.296	69.04 ± 0.052
	Variance components				
	σ^2_g	0.388 ± 0.055**	0.825 ± 0.114**	51.501 ± 8.719**	1.528 ± 0.177**
	σ^2_{gl}	0.053 ± 0.039	0.178 ± 0.078*	4.984 ± 7.347	
	σ^2_e	0.862 ± 0.050	1.544 ± 0.090	168.182 ± 9.808	1.115 ± 0.088
	Heritability				
	h^2	0.62	0.63	0.54	0.73
	90% C.I. on h^2[e]	0.54–0.69	0.55–0.70	0.43–0.62	0.63–0.81

** Mean square associated with variance component estimate significant at the 0.01 probability level based on the F-test
[a] Measured at one location only
[b] Number of entries
[c] Standard errors are attached
[d] No estimate
[e] Confidence intervals on h^2 were calculated using the method of Knapp et al. (1985)

Table 3 Phenotypic (r_p) and genotypic (r_g) correlation coefficients between testcrosses of 294 F_3 lines crossed to tester Mo17 (Exp. 1) and A1 (Exp. 2) and evaluated at two locations for grain yield, dry matter content, plant height, and test weight

Trait	(r_p)	(r_g)
Grain yield	0.20**	0.28 ± 0.11[b]
Dry matter content	0.44**	0.69 ± 0.09[b]
Plant height	0.35**	0.63 ± 0.12[b]
Test weight[a]	0.46**	–[c]

** Significant at the 0.01 level of significance
[a] Only one environment
[b] Estimate greater than twice its standard error
[c] No estimate

Fig. 1 Genetic linkage map obtained from segregation analysis of 87 molecular markers in 232 F_3 families derived from cross B73 × A7. □ Probes used for QTL analysis, [XXX] probes not mapping in accordance with the Maize Genetics Cooperation Newsletter map, ●,●● probes deviating significantly from Hardy-Weinberg equilibrium ($P < 0.05$; $P < 0.01$), *,** Probes with allelic frequencies significantly different from 0.5 ($P < 0.05$; $P < 0.01$)

given in centiMorgans (cM). The linear order of the markers on the chromosomes was in good agreement with previously published RFLP maps in maize (Burr et al. 1988; Coe et al. 1990) with the following exceptions: UMC026, UMC042B and UMC010 on the long arm of chromosome *3* showed a reversed order; the two tightly linked probes BNL 8.39 and BNL 14.07 on the short arm of chromosome 7 mapped several cM apart on our map; BNL 13.05 on chromosome *8* was expected to map in a more proximal position than that found in the present study.

For 10 (13%) of the 72 marker loci assayed, the chi-square test revealed deviations from Mendelian segregation ratios (1:2:1) and/or from the expected allelic frequencies ($p = q = 0.5$) of an F_2 population. However, as suggested by Edwards et al. (1987), loci with deviant ratios should not affect QTL identification. The segregation of 15 RAPD markers was assessed on 45 progenies randomly chosen among the 232 F_3 lines analysed with RFLP markers.

The B73 × A7 F_2 linkage map based upon the 87 markers spans 1,600 cM with an average spacing of 18.3 cM between markers leaving, however, 11 gaps larger than 40 cM.

QTL analyses

Most QTLs found for the traits under investigation were consistent across locations (data not shown). Therefore, results from QTL analyses are only presented on means across environments.

Grain yield

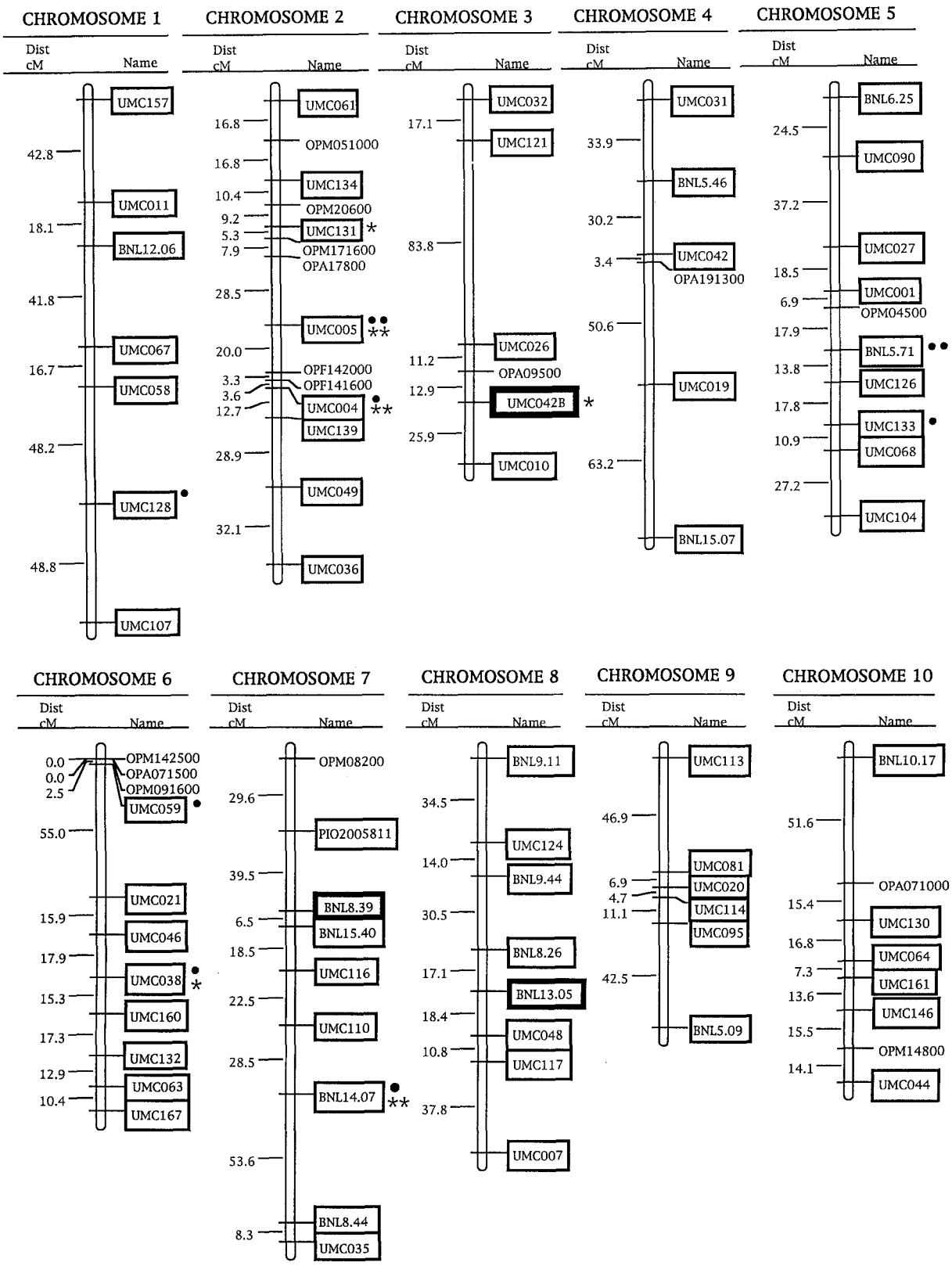
QTL analyses for grain yield revealed two significant QTLs for tester Mo17, one on the long arm of chromosome *4* and the other on the short arm of chromosome *6* (Fig. 2a). The corresponding LOD scores were 3.2 and 6.1, respectively (Table 4). In the testcrosses of A1, the short arm of chromosome *6* and the long arms of chromosomes *9* and *10* showed highly significant effects with LOD scores of 2.9, 5.4, and 2.9, respectively. Only the QTL on chromosome *6*, which accounted for the highest amount of the phenotypic variation, was found to be located in the same map position. Simultaneous fit of all putative QTLs accounted for 21.7% of the phenotypic variance among the progeny of Mo17, while the three QTLs found for tester A1 accounted for 25.2% of the phenotypic variance for grain yield (Table 4). In the combined analysis across both testers, three genomic regions, located on *4L*, *6S* and *10L* significantly affected grain yield (Table 4). Corresponding LOD scores ranged from 2.6 to 7.4. Overall, 35.4% of the phenotypic variance for grain yield was explained by the three QTLs. It was interesting to note that the QTL on the short arm of chromosome *6* (LOD 7.4) accounted for 24.5% of the total phenotypic variation detected for grain yield, and it alone showed an average effect of allelic substitution of 1 t/ha. While B73 contributed the superior allele at the QTL on chromosome *4*, for all remaining QTLs detected, the alleles carried by A7 lead to an increase in grain yield (Table 4). The sum of the absolute effects of allelic substitutions at all QTLs identified in the testcrosses to Mo17 and to A1 and across both testers was 2.04, 2.14 and 2.01 t/ha, respectively. Effects of the putative QTLs revealed in both testcross series and confirmed in the combined analysis across testcrosses showed a consistent direction, i.e., the superior allele was consistently contributed by the same parental line.

Dry matter content

Analysis of Mo17 testcross data for dry matter content revealed two regions on chromosomes *1* and *2* with LOD scores of 4.8 and 4.9, respectively (Fig. 2b). The two loci together accounted for 22.7% of the phenotypic variance (Table 4). Analysis of A1 testcross data confirmed the presence of the QTL on chromosome *2* and suggested a second QTL on chromosome *8*. Together they explained 22.5% of the phenotypic variance. The regions on chromosomes *1* and *2* were confirmed in the combined analysis across testers. The corresponding LOD scores were 3.6 and 8.9, respectively. In total, 26.4% of the phenotypic variance were explained by the two QTLs.

Test weight

For test weight, six significant QTLs located on chromosomes *1*, *2*, *3*, *5*, and *9* were detected in the Mo17



= Probes used for QTL analysis

XXX = Probes not mapping in accordance with Maize Genetics Cooperation News Letter map

● ●● = Probes deviating significantly from Hardy-Weinberg equilibrium (P<0.05; P<0.01)

* ** = Probes with allelic frequencies significantly different from 0.5 (P<0.05; P<0.01)

testcrosses (Fig. 2c). They explained between 6.2% and 16.7% of the phenotypic variance. All QTLs together accounted for 41.1% of the total phenotypic variation. QTL analyses of tester A1 revealed only two QTLs on chromosomes *2* and *9* that were both identical with the regions found in the testcrosses with Mo17. Combined analyses across both testers yielded three significant QTLs located on chromosomes *1*, *2* and *9* that explained 38.8% of the phenotypic variance.

Fig. 2a–c RFLP map showing QTL for **a** grain yield, **b** dry matter content, and **c** test weight. QTL bars are placed at the maximum LOD score position. *Bar length* is proportional to the percentage of phenotypic variance explained (nearby *digit*) by each locus

Discussion

In different plant species, including maize, recent studies have identified marker-linked chromosome regions that affect a wide range of traits (Landry et al. 1987; Nienhuis et al. 1987; Paterson et al. 1988; Keim et al. 1990; Beavis et al. 1991; Stuber et al. 1992). This has been confirmed in our experiments in which grain yield, in particular was considered.

Although variation was observed in the magnitude of the LOD scores for individual locations, most of the QTLs found were consistent across locations. This supports the conclusion that the expression of genes influencing yield and related traits was largely independent of environmental factors. In this sense our data represent a significant confirmation of the results reported by Stuber et al. (1992), who found little evidence for genotype-by-environment interaction for most QTLs associated with grain yield in a cross between the maize lines B73 and Mo17.

The experimental mating design adopted in our experiments was based on two different tester lines. As expected, we found that QTLs revealed by one tester may not be detected with the second one; however, QTLs with larger effects were consistent across testers. These results indicate that the allelic composition of a tester line may either allow or not allow the detection of QTLs segregating in a population. Consequently, QTL data averaged over two testers, while supporting the existence of a relevant QTL allele, contributed by null or negative counterparts in both testers, may decrease the significance of a LOD score when the QTL is detectable only in one of the two testcrosses. The identification of a QTL in a testcross progeny can also be hampered by masking effects of dominant tester alleles at the QTL. From this point of view, it can be stressed, in agreement with theoretical indications proposed by Hull (1945), that the most efficient tester for evaluating maize lines would be the one that is homozygous recessive at all loci and that homozygosity for dominance alleles at any locus should be avoided. Further experiments involving different genetic materials are warranted to verify the distribution in different tester lines of QTL alleles at relevant QTL loci.

In the present study, we found a total of four QTLs significantly affecting grain yield. They are located on chromosomes *4*, *6*, *9* and *10*. Three of them were confirmed by the analysis averaged across testers and showed an overall phenotypic effect of more than 2 t/ha, accounting for approximately 35% of the phenotypic variation for grain yield. The number of QTL identified in our study is lower than that found by Stuber et al. (1992). They identified at least six to eight QTLs, depending on the experimental progenies analysed, which accounted for approximately 60% of the phenotypic variation in grain yield. However, it may be stressed that for detection, a QTL must be tightly linked to adjacent marker loci, its genetic effect must be sufficiently large and the detection must not be limited by the degree of polymorphism in the cross under study. In fact, no contribution to the genetic variance can be expected if two loci with effects of similar size are closely linked in a repulsion phase or if the parents of a cross carry the same alleles at a given locus.

Although the comparison of different sets of data may not lead to definitive conclusions, due to the use of different markers and the uncertainty of QTL positions, QTLs for grain yield found on chromosomes *9* and *10* in our study have overlapping support intervals with QTLs for grain yield found by Stuber et al. (1992) in cross B73 × Mo17. These authors, however, evaluated performance of backcross families, whereas in the present study testcross performance was measured.

In our study, the QTL in the vicinity of marker UMC051 on chromosome *6* accounted for approximately 25% of the phenotypic variation in grain yield. At this locus, the substitution of the B73 allele with the superior A7 allele gave, on average, a gain in yield of 1 t/ha. This QTL is located in the vicinity of the maize nucleolus organiser region. Rocheford et al. (1990) observed in a maize population selected for grain yield that the rDNA intergenic spacer-length variants and/or associated loci were influenced by selection for increased grain yield. Similarly, Cluster et al. (1987) observed changes in the rDNA spacer-length composition of *Drosophila melanogaster* populations that had undergone recurrent cycles of selection for development rate. Additionally, Frankham et al. (1980) also reported that selection response to alter the number of bristles in Drosophila is associated with genetic variation in the number of copies of the rRNA locus. A better understanding of the nature and linkage relationship of this QTL is being currently addressed in our laboratory.

Up to six QTLs significantly affected test weight, explaining a considerable amount of the phenotypic variation among testcrosses. This finding is in good agreement with the results of Schön et al. (1994), who detected between six and eight QTLs for kernel weight in a maize testcross population. On the basis of their support intervals, at least three of the QTLs found in our

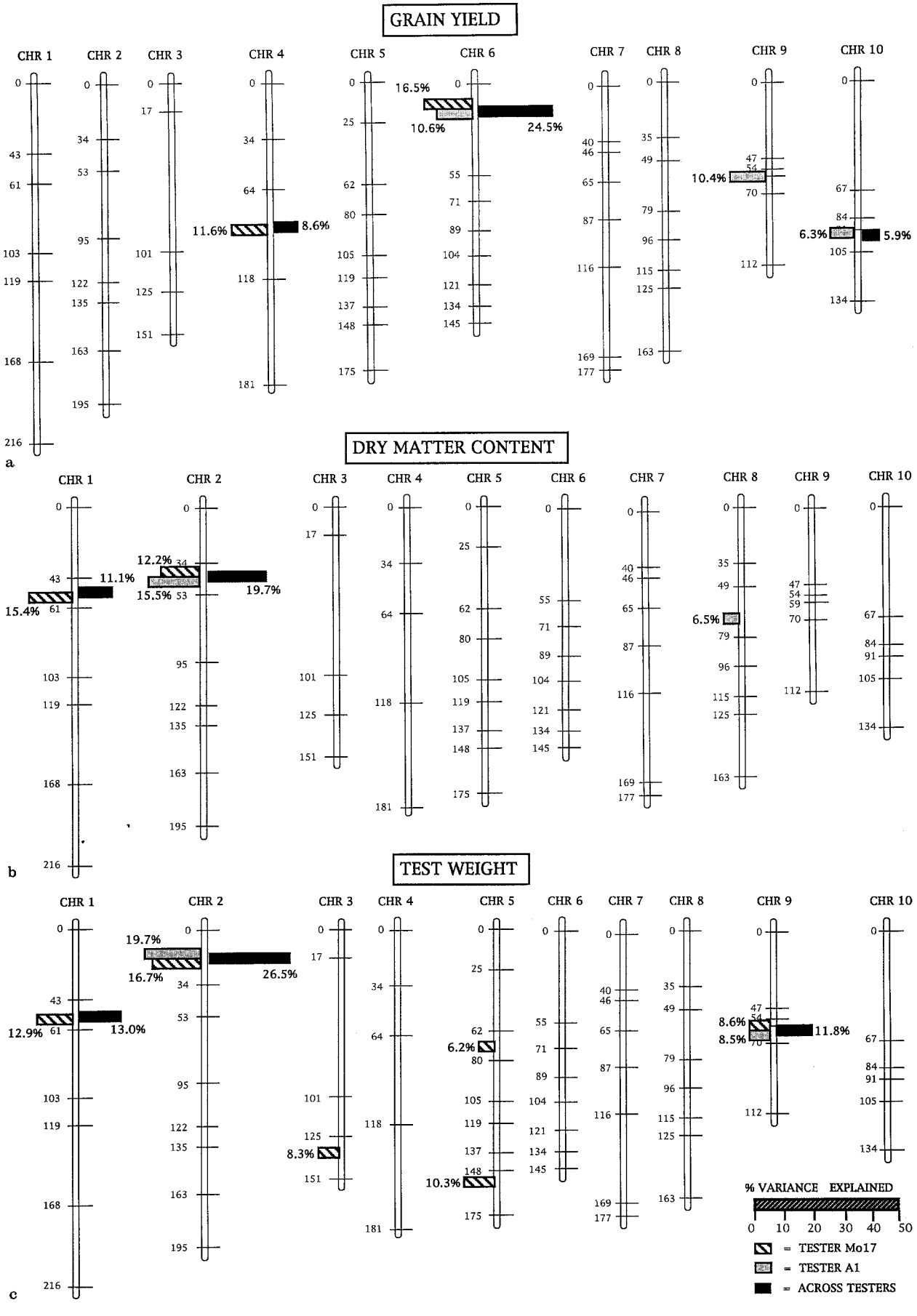

GRAIN YIELD
CHR 1
CHR 2
CHR 3
CHR 4
CHR 5
CHR 6
CHR 7
CHR 8
CHR 9
CHR 10
16.5%
10.6%
24.5%
11.6%
8.6%
10.4%
6.3%
5.9%
a
DRY MATTER CONTENT
12.2%
11.1%
15.5%
19.7%
15.4%
6.5%
b
TEST WEIGHT
19.7%
16.7%
26.5%
12.9%
13.0%
8.6%
8.5%
11.8%
6.2%
8.3%
10.3%
c
% VARIANCE EXPLAINED
0 10 20 30 40 50
= TESTER Mo17
= TESTER A1
= ACROSS TESTERS

Table 4 Biometrical parameters of putative QTL affecting grain yield, dry matter content and test weight in the testcross trials of 232 F_3 families of maize

Chromosome	RFLP markers flanking the QTL[a]		Maximum LOD score			Phenotypic variance			Genotypic class means					
									Mo17		A1		Combined	
	Mo17	A1	Mo17	A1	Combind	Mo17	A1	Combind	μAT	μBT	μAT	μBT	μAT	μBT
Grain yield									t/ha					
4	UMC042–UMC019	–	3.2	–	2.6	11.6	–	8.6	11.04	10.15	–	–	10.35	9.81
6	UMCO59–UMC021	UMC059–UMC021	6.1	2.9	7.4	16.5	10.6	24.5	9.09	10.24	8.96	9.75	9.01	10.00
9	–	UMC114–UMC095	–	5.4	–	–	10.4	–	–	–	8.96	9.72	–	–
10	–	UMC161–UMC146	–	2.9	2.8	–	6.3	5.9	–	–	9.08	9.67	9.29	9.77
	Total[c]		7.9	11.2	12.9	21.7	25.2	35.4	2.04[a]		2.14		2.01	
Dry matter content									%					
1	BNL12.06–UMC067	–	4.8	–	3.6	15.4	–	11.1	74.95	74.05	–	–	75.47	74.70
2	UMC134–UMC131	UMC134–UMC131	4.9	7.3	8.9	12.2	15.5	19.7	74.85	74.03	76.97	75.69	75.91	74.86
8	–	BNL9.44–BNL8.26	–	2.7		–	6.5	–	–	–	76.65	77.44	–	–
	Total		8.8	10.7	11.7	22.7	22.5	26.4	1.72		2.07		1.82	
Test weight[d]									Kg/hl					
1	BNL12.06–UMCO67	–	4.7	–	4.2	12.9	–	13.0	70.25	68.66	–	–	70.28	69.02
2	UMC061–UMC134	UMC061–UMC134	5.7	7.6	9.4	16.7	19.5	26.5	70.58	68.75	71.59	69.81	71.12	69.30
3	UMC042B–UMC010	–	3.1	–	–	8.3	–	–	67.21	68.52	–	–	–	–
5	UMC027–UMC001	–	2.6	–	–	6.2	–	–	67.25	68.35	–	–	–	–
5	UMC068–UMC104	–	3.9	–	–	10.3	–	–	67.15	68.58	–	–	–	–
9	UMC114–UMC095	UMC095–BNL5.09	4.0	4.3	5.9	8.6	8.5	11.8	69.80	68.52	70.66	69.52	70.20	69.01
	Total		19.6	11.2	17.3	41.1	24.6	38.8	8.53		2.92		4.27	

[a] QTL with overlapping support intervals were considered to be identical for both testers
[b] Percentage of phenotypic variance explained by QTL
[c] Estimates of total LOD score and total variance explained obtained from simultaneous fit of all putative QTL for the respective trait
[d] Sum of absolute effects, i.e. regardless of their direction
[e] Only one environment

material located on chromosomes 5 and 9 are likely to be located on the chromosomal regions described by these authors.

In conclusion, although further investigation will be required to verify the consistency of the effects detected in other genetic backgrounds, our results demonstrate the value of RFLP markers for identifying and localising genetic factors (QTL or specific genomic regions) that should be useful for marker-facilitated breeding programmes including intrapopulation selection or transfer of desired factors to other germplasms. Research involving marker-facilitated breeding approaches is currently being addressed in our laboratory.

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