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Comparison of QTLs mapped in RILs and their test-cross progenies of tropical maize for insect resistance and agronomic traits

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Abstract

Quantitative trait loci (QTL) affecting resistance to south-western corn borer *Diatraea grandiosella* (SWCB) and sugarcane borer *Diatraea saccharalis* (SCB) have been identified previously in $F_{2,3}$ lines and recombinant inbred lines (RILs) of tropical maize using restriction fragment length polymorphism (RFLP) analyses. Our objective was to determine whether QTLs identified in these generations are also expressed in test-crosses (TC) of RILs. A population of 166 TC progenies was developed by crossing RILs from the cross CML131 (susceptible) × CML67 (resistant) with the unrelated, susceptible tester line CML216. Resistance to first-generation SWCB, measured as leaf-feeding damage (LFD) under artificial infestation, and other agronomic traits were evaluated in two environments for the TC progenies and three environments for 183 RILs. The correlation between line *per se* and TC performance was low for LFD and intermediate for most agronomic traits. Estimates of the genotypic variance and heritabilities were smaller in the TC progenies than in the RILs for all traits. Quantitative trait loci were identified using an RFLP linkage map with 136 loci. For LFD, four QTLs were detected in the TC progenies, of which two were in common with nine QTLs previously mapped in the RILs. Few QTLs for agronomic traits were common to the two types of progeny, because of the low consistency of QTL positions for all traits in RIL and TC progenies, the use of TC progenies should be considered in QTL mapping studies as the first step for marker-assisted selection in hybrid breeding.

Key words: *Diatraea grandiosella* — *Zea mays* — host plant resistance — line *per se* performance — QTL mapping — RFLP — test-cross performance

Two corn borer species, the south-western corn borer *Diatraea grandiosella* Dyar (SWCB) and the sugarcane borer *Diatraea saccharalis* Fabricius (SCB) can cause severe damage in maize production in Central and Latin America. Breeding for multiple borer resistance as a means of effective and environmentally safe control has been a major research objective in the CIMMYT maize programme (Smith et al. 1989). Resistance to SWCB and SCB in tropical maize germplasm was found to be quantitative with mainly additive gene action for first-generation leaf-feeding damage (Hinderliter 1983, Thome et al. 1992). Resistant populations were developed by S_1 recurrent selection and inbred lines with high levels of resistance were derived.

With increasing cultivation of hybrids in many tropical production areas, the test-cross performance of lines in hybrids is the primary goal rather than their performance *per se*. Correlations between line *per se* and test-cross performance are low for most traits in maize (Hallauer and Lopez-Perez 1979), indicating that selection based on line *per se* performance alone has a low efficiency. Little information is available regarding the correlation between line and hybrid performance for borer resistance in tropical maize. Thome et al. (1992) showed that resistance in the parental lines was not a reliable predictor for resistance of their hybrids.

Mapping of quantitative trait loci (QTL) using molecular markers such as restriction fragment length polymorphisms (RFLPs) can provide information about the number, position and gene action of the Mendelian factors involved in the inheritance of quantitative traits and is the first step in marker-assisted selection (MAS). Mapping of QTLs for SWCB and SCB resistance in tropical maize was performed in two populations of $F_{2,3}$ lines (Bohn et al. 1996, 1997, Khairallah et al. 1997) and recombinant inbred lines (RILs) derived from the same two crosses (Groh et al. 1997). Up to nine QTLs distributed across the genome were found to be involved in borer resistance.

Cowen (1988) suggested the use of test-cross (TC) progenies in mapping studies to detect differences in the heterotic effects of two parental lines relative to an unrelated tester line. Beavis et al. (1994) compared QTL positions for morphological traits in $F_{2,4}$ lines and TC progenies derived from the same $F_{2,3}$ lines and found very few QTLs in common, even though some traits showed relatively high phenotypic correlations between $F_{2,4}$ lines and TC progenies.

In the application of MAS for improving insect resistance in hybrids, it is important to know whether QTLs mapped for line *per se* performance are also expressed in hybrids produced from nearly homozygous lines. We mapped QTLs for SWCB resistance and agronomic traits in TC progenies derived from 166 RILs previously evaluated for their *per se* performance (Groh et al. 1998). The objectives of our study were to (1) estimate correlations between line *per se* performance and TC performance of RILs for leaf feeding resistance and other agronomic traits, (2) identify and characterize QTLs responsible for leaf feeding resistance and agronomic traits in 166 TC progenies derived from RILs, (3) investigate whether QTLs affecting agronomic traits are closely linked to QTLs for leaf-feeding resistance, and (4) determine the consistency of QTLs for leaf-feeding resistance and agronomic traits across RILs, $F_{2,3}$ lines and TC progenies of RIL.

Materials and Methods

Mapping populations: The parental lines used in this study have been described in detail by Bohn et al. (1996). A cross was made between CML131, a highly susceptible line out of CIMMYT's population 42 and CML67, a highly resistant line from Antigua Group 2. Three different types of progeny were derived from F_2 plants and used in QTL mapping studies. First, 215 $F_{2:3}$ lines were developed and used for QTL mapping of borer resistance and agronomic traits (Bohn et al. 1996). Second, 187 RILs in generation $F_{7:8}$ were generated by single-seed descent without selection (Groh et al. 1998). Third, test-cross (TC) progenies were produced by crossing 10 plants from a random subset of 166 RILs with tester CML216, an unrelated, susceptible line with good general combining ability for agronomic traits. Seed was harvested from all plants for each RIL and bulked to evaluate the TC progenies.

RFLP assays: The procedure for the RFLP assays of the RILs has been described by Groh et al. (1998). A total of 108 RFLP probes producing 136 marker loci were used for genotyping the 187 RILs. The same RFLP data set was used in the QTL analyses of the TC progenies because they were derived from a subsample of these RILs.

Field trials: The TC progenies were evaluated for insect resistance and agronomic traits during winter season, 1996A, and summer season, 1996B, at CIMMYT's experimental station in Tlaltizapán, Morelos, Mexico (18°N, 940 m elevation). A total of 176 entries, including the 166 TC progenies of the RILs, TC progenies of the parents CML131 and CML67, the susceptible control CML131 × Ki3, the resistant controls CML67 × CML139 and CML67 × CML135 and a high-yielding elite hybrid control with intermediate resistance were grown in a 16 × 11 alpha lattice design with two replications. Plots consisted of two rows of 2.5 m length and 0.75 m space between rows, containing 10 plants each.

Resistance to first-generation SWCB was evaluated as leaf-feeding damage (LFD) under artificial infestation. All 10 plants of the first row of each plot were infested 3–4 weeks after planting at the five- to six-leaf stage with about 60 laboratory-reared neonate SWCB larvae per plant, using a mechanical dispenser (Mihm 1983). Three to four weeks after infestation, ratings of LFD were taken for each infested plant using a 1 (no visible damage) to 10 (dead plant) rating scale. The second row of each plot was protected with an insecticide. In 1996A, plants had to be reinfested 1 week after the first infestation date owing to high larval mortality. Because insect supply was not sufficient for the complete trial, one replication was infested with SWCB and one with SCB larvae.

Agronomic traits were measured in both seasons in the protected rows. Male and female flowering were recorded in days from planting after 50% of the plants showed pollen or silks, respectively. Anthesis-silking interval (ASI) was calculated as the interval between male and female flowering. For grain yield, all ears per row were harvested by hand, dried for 3 days, shelled, and the grains were weighted separately. The total grain weight per plot was divided by the number of harvested plants to adjust for different plant numbers per row and to calculate the grain yield in g/plant. Plant height was measured in cm from the soil level to the first tassel branch.

A total of 183 RILs was grown in three seasons in Tlaltizapán (1994B, 1995A, 1995B) under SWCB infestation and under protection. The field design and evaluation of resistance was described by Groh et al. (1998). Days to male flowering, ASI, grain yield and plant height were measured in protected rows as described for the TC progenies.

Data analysis: Analyses of variance were performed for the 183 RILs and 166 TC progenies for each trial separately. Each year–season combination was considered as an environment. Orthogonal contrasts were calculated between means of the two parents and between the means of midparent ($\bar{P}$) and RIL. In the TC progenies, orthogonal contrasts were performed between TC means of parental lines, between resistant and susceptible controls and between TC means of $\bar{P}$ and RIL. Adjusted entry means and effective error mean squares were used to compute combined analyses of variance across environments. Estimates of the genotypic variance (σ_g^2), the genotype × environment interaction variance (σ_{ge}^2), the error variance (σ^2) and the phenotypic variance (σ_p^2) as well as heritabilities (h^2) and their exact 90% confidence intervals were calculated as described in detail by Bohn et al. (1996). Phenotypic ($\hat{r}_p$) and genotypic ($\hat{r}_g$) correlations between traits were calculated for TC progenies and RILs on an entry-mean basis. Genotypic correlations were calculated only if $\hat{\sigma}_g^2$ was significant for both traits. Correlations between line *per se* and TC performance were estimated using means across environments of the 166 TC progenies and their corresponding RILs.

QTL mapping: QTL analyses were performed on a subset of 170 RILs for which genotypic and phenotypic data were available applying the composite interval mapping approach of Zeng (1994). Entry means of each environment were used to perform a joint analysis according to the method of Jiang and Zeng (1995). QTL analyses of the 166 TC progenies were performed using the same statistical model:

$$y_{ij} = b_i + b_i^* x_j^* + \sum_k b_{ik} x_{jk} + e_{ij}. \quad (1)$$

For the RILs, the model has been described in detail by Groh et al. (1998). For the TC progenies, y_{ij} = the phenotypic value of TC progeny j in environment i; b_i = the mean phenotypic value of TC progenies of RILs with genotype qq at the putative QTL and mm at the markers used as cofactors in environment i; b_i^* = the substitution effect of allele q with allele Q at a putative QTL in environment i; x_j^* = variable taking values 0, 0.5 and 1 (compared with 0, 1 and 2 in RILs) with probabilities depending on the genotype of the RIL at the flanking markers in the interval under search (0.5 only if TCs were derived from heterozygous RILs); b_{jk} = the partial regression coefficient of the phenotype on the marker k; x_{jk} = variable taking values 0, 0.5 and 1 depending on the allele at the selected marker k; and e_{ij} = the residual variable of TC progeny j in environment i.

The hypothesis for the presence of a QTL was tested using three different models. Model III corresponds to simple interval mapping and was employed for selection of markers closely linked to putative QTLs to be used as cofactors; Model II corresponds to composite interval mapping using only unlinked markers as cofactors; Model I corresponds to composite interval mapping using all selected cofactors, plus markers flanking the target interval with a minimum map distance (window size) of 30 and 20 cM. The presence of a QTL was declared when the likelihood ratio (LR) exceeded the critical threshold (LR = 13.8 and 15.9 for two and three environments, respectively, equivalent to a comparison-wise significance level of $\alpha' = 0.0032$) in Model II and a peak was also detected in Model I at the same position. The peak in Model I did not need to exceed the threshold in order to confirm the QTL detected in Model II. However, if a significant LR peak was detected in Model II but was not confirmed by a peak in Model I, we rejected the hypothesis of the presence of a QTL. If the LR was significant only in Model I, a QTL was declared regardless of whether a peak was present in Model II (e.g. due to linked QTLs) or not. Two peaks for the same trait on one chromosome were accepted as two different QTLs when they were separated by at least two markers and a minimum distance of 20 cM. Otherwise, the higher peak was selected to represent the QTL position.

QTL × environment (QTL × E) interactions were tested at the 0.05 and 0.01 significance level. The presence of digenic epistatic interactions between the detected QTL was tested applying the regression approach of Haley and Knott (1992) based on stepwise regression and adding epistatic effects to the main effects in the model, as described by Lübberstedt et al. (1997).

For RILs, the additive effect of a QTL for one environment ($\hat{b}_i^*$) and across environments ($\hat{b}^*$) was obtained under the assumption of Model I (window size 30 cM). For TC progenies, $\hat{b}_i^*$ and $\hat{b}^*$ denote the substitution effect of the allele from parent CML131 with the allele from parent CML67 in combination with the tester allele in environment i and across environments, respectively. The phenotypic variance explained by QTL k was calculated from its estimated effect as

$R_k^2 = \hat{b}^{*2}/\hat{\sigma}_p^2$ across environments. The proportion of $\hat{\sigma}_p^2$ explained by all QTLs (R^2) was obtained from a multiple regression of entry means across environments on markers closely linked to all detected QTLs. The total genotypic variance explained by all QTLs was calculated as $Q^2 = R^2/\hat{h}^2$.

QTLs for the same trait detected in the RIL and TC progenies were declared as 'common' when they were located within the same 20 cM interval in the RIL linkage map and their gene effects had the same sign. Approximate positions of QTLs in the corresponding $F_{2:3}$ lines were compared with the QTLs in the RIL and TC progenies using the same criteria.

Results

Segregation and linkage of RFLPs

The results of the RFLP analyses have been presented previously (Groh et al. 1998). The linkage map for the 187 RILs from cross CML131 × CML67 with 136 marker loci had a total length of 1564 cM and an average spacing of 11.5 cM (Fig. 1).

Phenotypic data

TC progenies

Ratings of LFD for the TC progenies of the RILs ranged from 3.8 to 6.0 in 1996A and from 5.9 to 8.2 in 1996B (Table 1). The resistant control CML67 × CML139 had a significantly lower LFD than the susceptible control CML131 × Ki3 in both environments ($P < 0.05$). The TC progenies of CML67 had lower LFDs than the TC progenies of CML131 but differences were small ($P < 0.1$). The variance among TC progenies ($\hat{\sigma}_g^2$) for LFD was significant in 1996A but was not significant in 1996B and across environments, resulting in a very low estimate of h^2.

The susceptible control CML131 × Ki3 had higher grain yields than the resistant control CML67 × CML139 (Table 2). In contrast, the TC progeny of the susceptible parent CML131 had lower grain yields than the TC progeny of the resistant parent CML67. The elite control had higher grain yields than the other standards, but some TC progenies of the RILs were superior in both grain yield and LFD. The TC progenies of the RILs had higher grain yields than the TC progenies of $\bar{P}$. Estimates of $\hat{\sigma}_g^2$ were highly significant for all agronomic traits and $\hat{\sigma}_{ge}^2$ was significant except for grain yield. Heritabilities were intermediate for grain yield ($\hat{h}^2 = 0.43$) and greater for the other traits ($0.63 < \hat{h}^2 < 0.82$). Leaf-feeding damage showed a significant positive correlation with plant height but was not associated with any other trait (Table 4).

RILs

The susceptible parent, CML131, was superior to the resistant parent, CML67, for female flowering, grain yield and plant height (Table 3). Means of $\bar{P}$ were higher than means of RIL for grain yield and female flowering. Estimates of σ_g^2 and σ_{ge}^2 were highly significant for all traits. Heritabilities were high for all traits ($0.72 < \hat{h}^2 < 0.94$). Agronomic traits were not significantly correlated with LFD (Table 4).

Correlations between line *per se* performance and TC performance were low for LFD ($\hat{r}_p = 0.25$) and intermediate ($0.58 < \hat{r}_g < 0.77$) for female flowering, ASI and plant height (Table 4). No significant correlation between line *per se* and TC performance was found for grain yield.

QTL detection

TC progenies

For LFDs, four QTLs were detected on chromosomes 1, 3 and 7 (two QTLs, Table 5). With the exception of the QTL on chromosome 3, all QTLs showed no significant QTL × E interactions and the resistance alleles originated from the resistant parent CML67. A simultaneous fit of all QTLs explained 25.2% of the phenotypic variance ($\hat{\sigma}_p^2$).

Six QTLs were detected for female flowering on chromosomes 3 (two QTL), 6, 7, 8 and 9, with four displaying significant QTL × E interactions. For all QTLs except one, the alleles from CML131 contributed to early flowering. A simultaneous fit of all QTL explained 27.2% of $\hat{\sigma}_p^2$ and 32.4% of the genotypic variance ($\hat{\sigma}_g^2$). For ASI, six QTLs were detected on chromosomes 1, 2, 3, 4, 5 and 8. Half of the QTL showed significant QTL × E interactions. Alleles from both parents contributed to shorter ASI. A simultaneous fit of all QTLs explained 37.3% of $\hat{\sigma}_p^2$ and 59.2% of $\hat{\sigma}_g^2$. Only one QTL on chromosome 7, explaining 14.4% of $\hat{\sigma}_p^2$ and 29.4% of $\hat{\sigma}_g^2$ was detected for grain yield with the allele from CML131 increasing yield in both environments. Seven QTLs were found for plant height on chromosomes 2, 3, 4, 5, 7, 8 and 10. All QTLs except one were consistent across both environments. Both parents contributed alleles increasing plant height. The total proportion of $\hat{\sigma}_p^2$ and $\hat{\sigma}_g^2$ explained in a simultaneous fit of all QTLs was 42.8% and 51.6%, respectively.

RILs

For female flowering, three QTLs were detected on chromosomes 3 (two QTLs) and 9, with two of them displaying significant QTL × E interactions (Table 6). Both parents contributed alleles contributing to early flowering. A simultaneous fit with all QTLs explained 17.0% of $\hat{\sigma}_p^2$ and 20.2% of $\hat{\sigma}_g^2$. For ASI, six QTLs were found on chromosomes 1 (two QTLs), 3 (two QTLs), 5 and 10. Four QTLs showed significant QTL × E interactions. The total proportion of $\hat{\sigma}_p^2$ and $\hat{\sigma}_g^2$ explained by all QTL was 34.1 and 47.4%, respectively. Three QTLs were detected for grain yield on chromosomes 2, 6 and 10. Only one QTL displayed significant QTL × E interactions, with alleles from CML67 having a positive effect. A simultaneous fit of all QTLs explained 19.4% of $\hat{\sigma}_p^2$ and 23.7% of $\hat{\sigma}_g^2$. For plant height, only two QTLs were detected on chromosomes 3 and 5 which explained 12.1% of $\hat{\sigma}_p^2$ and 12.9% of $\hat{\sigma}_g^2$ in a simultaneous fit.

No significant ($P < 0.05$) digenic epistatic effects were found between the QTLs detected for all traits in both RIL and TC progenies.

Discussion

Field trials

Mean values for LFD of the TC progenies differed greatly between growing seasons 1996A and 1996B. This could be explained by different infestation levels in the two seasons. In 1996A, LFD was low owing to the high insect mortality after the first infestation date at the five- to six-leaf stage. Plants were reinfested 1 week later at the seven- to eight-leaf stage when they were already more vigorous and the resulting LFD was low, even for the susceptible controls. Data were combined across both replications although they were infested with two different *Diatraea* spp., SWCB and SCB. This was justified because both insects showed a very similar response to leaf-feeding resistance in this specific cross in previous experiments with $F_{2:3}$ lines and RILs (Bohn et al. 1997, Groh et al. 1998).

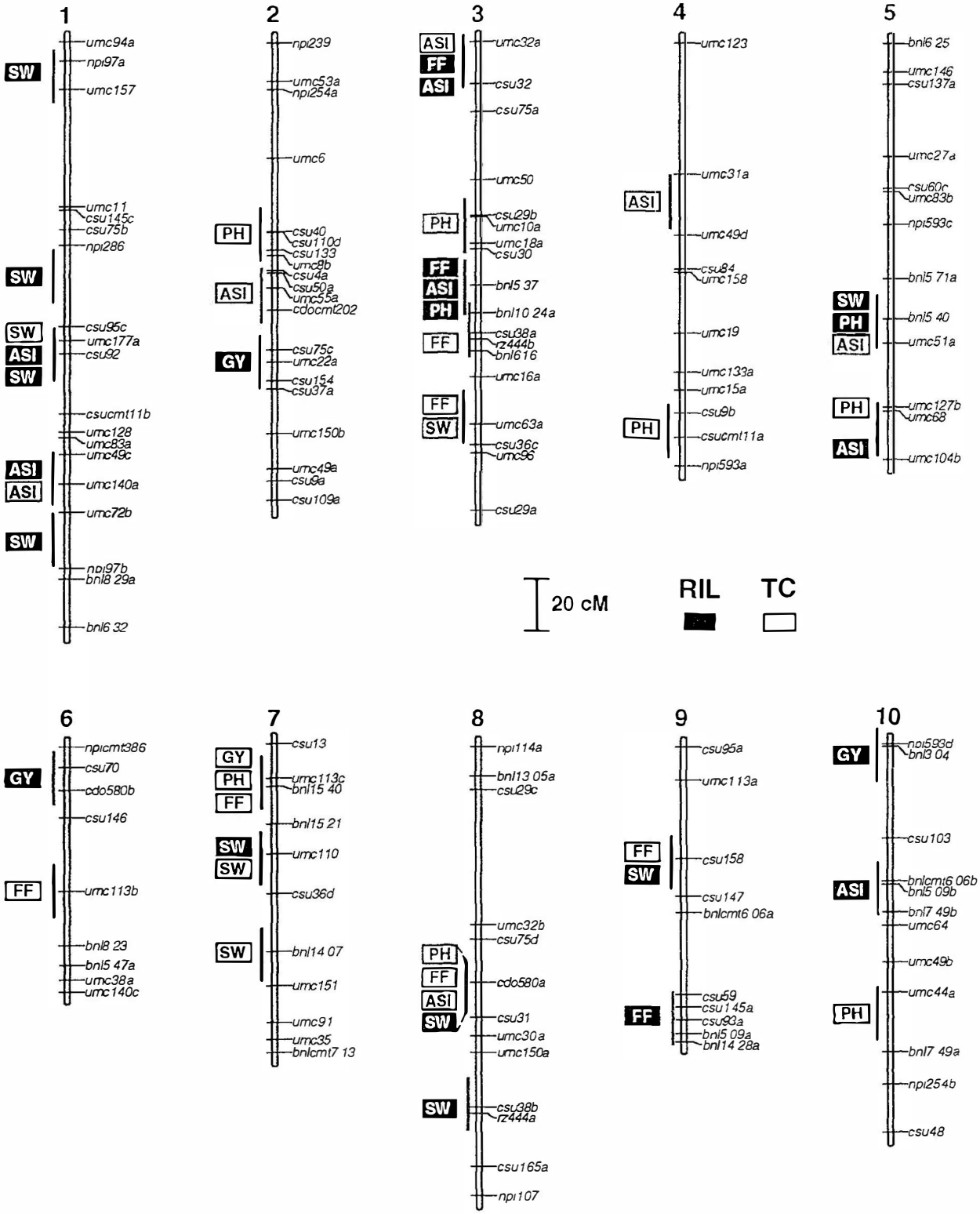

Fig 1 Linkage map with 136 RFLP marker loci based on 187 RILs from cross CML131 x CML67 Approximate positions of QTLs for SWCB leaf-feeding damage (SW) (Groh et al 1998), female flowering (FF), anthesis–silking interval (ASI), and grain yield (GY) detected using joint composite interval mapping in the RILs and their test-cross progenies are shown within common 20 cM intervals (indicated by bars)

Table 1: Means of control hybrids and test-cross progenies of parental lines, midparent ($\bar{P}$) and 166 RILs from cross CML131 × CML67, range and estimates of variance components of test-cross progeny of RILs for leaf-feeding damage in 1996A, 1996B and combined across environments and heritability, with 90% confidence interval across environments

Parameter	n[1]	Leaf feeding damage (1–10 scale) 1996A	1996B	Combined
Means of controls				
Elite hybrid	1	4.9 ± 0.4[2]	7.0 ± 0.4	6.0 ± 0.3
CML131 × Ki3	2	5.2 ± 0.3	7.8 ± 0.3	6.5 ± 0.2
CML67 × CML139	2	4.1 ± 0.3	6.0 ± 0.3	5.1 ± 0.2
Test-cross means				
CML131	2	5.0 ± 0.3	7.5 ± 0.3	6.3 ± 0.2
CML67	2	4.5 ± 0.3	7.0 ± 0.3	5.8 ± 0.2
$\bar{P}$	4	4.8 ± 0.2	7.3 ± 0.2	6.1 ± 0.1
RILs	166	4.8 ± 0.03	7.1 ± 0.03	6.0 ± 0.02
Range		3.8–6.0	5.9–8.2	5.1–6.8
$\hat{\sigma}_g^2$		0.051 ± 0.024*	0.012 ± 0.040	0.019 ± 0.021
$\hat{\sigma}_{ge}^2$		–	–	0.002 ± 0.022
$\hat{h}^2$		–	–	0.19
90% C.I.[3] of $\hat{h}^2$		–	–	(–0.04; 0.36)

* Variance component significant at P = 0.05.
[1] Number of entries.
[2] Standard errors are attached.
[3] Confidence interval according to Knapp et al. (1985).

However, the infestation with the less aggressive feeder, SCB, was presumably an additional reason for the lower LFD in this season. In 1996B, the infestation was conducted at an early growing stage when most plants had less than six leaves. The resulting LFD was high, possibly because resistance components, such as cell wall components, were not yet fully effective.

Genotypic variance and $\hat{h}^2$ were smaller for TC progenies in both seasons compared with the RILs, as expected by quantitative genetic theory. In contrast to the low $\hat{h}^2$ for LFD, estimates of h^2 for agronomic traits were intermediate to high. Consequently, it can be ruled out that seed mix-up, plot heterogeneity or germination and growth problems in the field experiment were responsible for the low $\hat{h}^2$ of LFD. We therefore conclude that the masking effect of the tester was the most important cause for the small $\hat{\sigma}_g^2$ in the TC progenies.

QTL detection

A low number of QTLs was detected for most agronomic traits in both types of progeny. In the RILs, the proportion of $\hat{\sigma}_p^2$ and $\hat{\sigma}_g^2$ explained by all QTLs for agronomic traits ranged from 12.1 to 34.1% and 12.9 to 47.4%, respectively, for two to six QTLs. In contrast, nine QTLs were detected for SWCB and SCB LFD in the same population, explaining about 52% of $\hat{\sigma}_p^2$ and 72% of $\hat{\sigma}_g^2$ (Groh et al. 1998). The low number of QTLs for agronomic traits in the RILs could be explained by the fact that parents, CML131 and CML67, represent extremes for resistance to corn borers but not for the agronomic traits. Because QTLs with dominance effects cannot be detected in homozygous lines, it is also possible that fewer QTLs were detected in the RILs for traits with dominant gene action, such as most agronomic traits, than for insect resistance displaying primarily additive gene action.

In contrast to our study, more QTLs for agronomic traits explaining a larger proportion of $\hat{\sigma}_p^2$ were detected in 171 $F_{2:3}$ lines from the same cross (Bohn et al. 1996). Small proportions of $\hat{\sigma}_p^2$ explained by QTLs for grain yield and yield components were also reported by Austin and Lee (1996) using 186 $F_{6:7}$ lines from a cross between elite lines, while QTLs with generally greater effects were detected using $F_{2:3}$ lines from the same cross. However, it should be pointed out that comparisons between different studies must be regarded with caution because different QTL mapping approaches were used.

In the TC progenies, one to seven QTLs were found for the agronomic traits, explaining 14.4 to 42.8% of $\hat{\sigma}_p^2$ and 29.4 to 59.2% of $\hat{\sigma}_g^2$. In contrast to the RILs, the number of QTLs and total amount of $\hat{\sigma}_p^2$ explained for LFD was not greater than for the agronomic traits. Quantitative trait loci for LFD in the TC progenies were mapped, although $\hat{\sigma}_g^2$ was not significant in the

Table 2: Means of control hybrids and test-cross progenies of parental lines, midparent ($\bar{P}$) and 166 RILs from cross CML131 × CML67, range and estimates of variance components of testcross progeny of RILs and heritabilities, with 90% confidence intervals for four agronomic traits evaluated in two environments

Parameter	Female flowering (days)	Anthesis-silking interval (days)	Grain yield (g/plant)	Plant height (cm)
Means of controls				
Elite hybrid	75.7 ± 0.7[1]	0.5 ± 0.6	166.7 ± 10.1	237.7 ± 4.8
CML131 × Ki3	71.4 ± 0.5	1.6 ± 0.5	152.2 ± 7.2	203.3 ± 3.6
CML67 × CML139	74.2 ± 0.5	0.0 ± 0.5	121.6 ± 7.2	205.4 ± 3.6
Test-cross means				
CML131	77.0 ± 0.5	2.5 ± 0.5	142.8 ± 7.2	225.8 ± 3.6
CML67	77.8 ± 0.5	1.6 ± 0.5	158 4 ± 7.2	229.5 ± 3.6
$\bar{P}$	77.4 ± 0.4	2.1 ± 0.3	150.6 ± 5.1	227.7 ± 2.5
RILs	77.5 ± 0.1	2.1 ± 0.1	158.6 ± 1.0	228.6 ± 0.8
Range	72.6–81.8	–0.8–4.3	118.6–201.2	203.0–255.3
$\hat{\sigma}_g^2$	2.09 ± 0.28**	0.60 ± 0.11**	77.9 ± 22.3**	96.8 ± 13.1**
$\hat{\sigma}_{ge}^2$	0.19 ± 0.12*	0.21 ± 0.09**	–6.2 ± 27.7	8.1 ± 5.4*
$\hat{h}^2$	0.82	0.63	0.43	0.82
90% C I.[2] of $\hat{h}^2$	(0.76; 0.85)	(0.53; 0.71)	(0.28; 0.56)	(0.78; 0.87)

*, ** Variance component significant at P = 0.05 and P = 0.01, respectively.
[1] Standard errors are attached.
[2] Confidence interval according to Knapp et al. (1985).

Table 3: Means of parental lines, midparent ($\bar{P}$) and 183 RILs from cross CML131 × CML67, range and estimates of variance components of RILs and heritabilities, with 90% confidence intervals for four agronomic traits evaluated in three environments

Parameter	Female flowering (days)	Anethesis-silking interval (days)	Grain yield (g/plant)	Plant height (cm)
Means				
CML131	68.9 ± 1.3[1]	0.7 ± 0 9	53.2 ± 6.3	142.7 ± 4.4
CML67	72.3 ± 1.5	0.6 ± 1.0	38.2 ± 7.0	97.8 ± 5.1
$\bar{P}$	70.6 ± 1.1	0.7 ± 0.8	45.7 ± 5.1	120.3 ± 3.7
RILs	73.2 ± 0.3	0.3 ± 0.1	31.8 ± 1.1	117.5 ± 1.3
Range	64.9–80.9	–5.5–5.4	3.4–77.5	59.7–166.6
$\hat{\sigma}^2_g$	9.23 ± 1.17**	2.15 ± 0.32**	187.7 ± 24.1**	300.3 ± 33.5**
$\hat{\sigma}^2_{ge}$	2.85 ± 0.44**	0.96 ± 0.22**	74.0 ± 3.6**	25.7 ± 4.8**
$\hat{h}^2$	0.84	0.72	0.82	0.94
90% C.I.[2] of $\hat{h}^2$	(0.80; 0.87)	(0.65; 0.77)	(0.78; 0.85)	(0.93, 0.95)

** Variance component significant at P = 0.01.
[1] Standard errors are attached.
[2] Confidence interval according to Knapp et al. (1985).

Table 4: Phenotypic ($\hat{r}_p$) and genotypic ($\hat{r}_g$) correlations between SWCB leaf-feeding damage and agronomic traits, measured for 166 test-cross progenies across two environments (above diagonal) and 183 RILs from cross CML131 × CML67 across three environments (below diagonal), and phenotypic and genotypic correlations between performance of testcross progenies and RILs (diagonal, in bold face)

Trait	Parameter	LFD	FF	ASI	GY	PH
Leaf feed. damage	$\hat{r}_p$	**0.25****	0.04	0.11	0.08	0.23**
(LFD)	$\hat{r}_g$	–[1]	–	–	–	–
Female flowering	$\hat{r}_p$	0.07	**0.48****	0.35**	0.01	0.21**
(FF)	$\hat{r}_g$	0.11$^+$	**0.58**$^{++}$	0.34^{++}	0.08	0.22^{++}
Anthesis-silking int.	$\hat{r}_p$	–0.07	0.43**	**0.45****	–0.02	0.01
(ASI)	$\hat{r}_g$	–0.12$^+$	0.44^{++}	**0.67**$^{++}$	0.13	0.05
Grain yield	$\hat{r}_p$	–0.15	–0.53**	–0.15	**0.04**	0.33**
(GY)	$\hat{r}_g$	–0.16$^+$	–0.57^{++}	–0.15$^+$	**0.07**	0.41^{++}
Plant height	$\hat{r}_p$	0.04	–0.20**	–0.06	0.30**	**0.68****
(PH)	$\hat{r}_g$	0.04	–0.19^{++}	–0.07	0.31^{++}	**0.77**$^{++}$

** Phenotypic correlation was significant at P = 0.01.
$^+$, $^{++}$ Genotypic correlation exceeded once or twice its standard error, respectively.
[1] Genotypic correlation was not estimated because $\hat{\sigma}^2_g$ was not significant for one trait.

analysis of the phenotypic data across environments. Using the joint CIM method of Jiang and Zeng (1995), QTLs were analysed on an entry-mean basis using data from single environments. Because $\hat{\sigma}^2_g$ was significant in one environment, QTL detection was possible but had a low power.

While we detected seven QTLs for plant height in the TC progenies, Lübberstedt et al. (1997) found 16 QTLs for the same trait in 380 TC progenies derived from a cross between two elite inbred lines, explaining about 62% of $\hat{\sigma}^2_p$ and 71% of $\hat{\sigma}^2_g$. Their results showed that QTL mapping using TC progenies can be highly efficient. According to theory (Moreno-Gonzalez 1993), TC progenies of both RIL and $F_{2\,3}$ lines can be used efficiently to detect differences in heterotic effects in combination with an inbred tester. In our study, tester CML216 was superior over both parental lines for most agronomic traits and probably masked the differences between the parental alleles.

Association between insect resistance and agronomic traits

The goal of MAS is to introduce genomic regions affecting insect resistance from a donor line into a susceptible elite line without changing the agronomic performance of the latter. Marker-assisted selection using QTL-marker associations for LFD closely linked to QTLs for agronomic traits could have a negative effect on yield when the allele increasing agronomic performance originates from the susceptible parent. In both types of progeny, LFD was not correlated with agronomic traits or showed very small correlations (Table 4). In the RILs, only one common region on chromosome 1 was found between QTLs for ASI and LFD, with the allele from CML131 reducing ASI, and one QTL for plant height on chromosome 5 was closely linked to a QTL for LFD, with the allele from CML67 increasing plant height. In the TC progenies, one common QTL on chromosome 3 was found between LFD and female flowering, with the allele from CML131 accounting for early flowering.

Anthesis–silking interval was reported to be highly correlated with grain yield under drought conditions in tropical maize (Ribaut et al. 1996). Because QTLs for ASI were consistently expressed across different stress levels, these authors suggested the use of QTL-marker associations for ASI in MAS as an indirect trait for grain yield under drought. Three QTLs for ASI on chromosomes 1, 5 and 10 in the RILs and three QTLs on chromosomes 1, 2 and 8 in the TC progenies were detected in regions common with QTLs mapped in the study of Ribaut et al. (1996). Several of the QTLs for ASI in the TC progenies

Table 5: Parameters associated with QTLs significantly affecting leaf-feeding damage and agronomic traits, estimated from phenotypic data of 166 test-cross progenies of RILs from cross CML131 × CML67, evaluated in 1996A and 1996B and in a joint analysis across two environments

Trait	Chromosome	QTL position (cM)	Marker interval	QTL effect[1] 1996A	1996B	Joint	Likelihood ratio QTl detection	QTL × E interaction	Phenot. variance expl. (%)
Leaf feeding damage (1–10 scale)									
	1	121	*csu92-csu11#2*	0 26[4]	0 18[4]	0 22[4]	23.1	1 2	6.5
	3	152	*umc63a-csu36c*	–0 26[4]	0.00	–0 12[4]	18.3[3]	7.2**	2.1
	7	40	*bnl15 21-umc110a*	0 18[4]	0 22[4]	0.20[4]	16.5	0.1	5.1
	7	77	*csu36#3-bnl14 07*	0.12	0 30[4]	0 20[4]	21.6	3.7	5 1
	Total[2]								25.2
Female flowering (days)									
	3	115	*rz5444b-bnl6 16*	–1 74[4]	–0.92[4]	–0 90[4]	33.8	13 0**	6 0
	3	142	*umc16a-umc63a*	–1.42[4]	–0 74	–0.72[4]	15.5[3]	7.4**	3 9
	6	56	*csu146-umc113b*	0 98[4]	0 86[4]	0.86[4]	17.5[3]	0 4	5.6
	7	26	*bnl15 40-bnl15 21*	0 00	–0 56[4]	–0 50[4]	15 6	5 9**	1.8
	8	90	*csu75#2-cdo580a*	–1.50[4]	–1 14[4]	–1 16[4]	16 3	1 6	10.0
	9	44	*csu158-csu147*	–0 28	–0.80[4]	–0 76[4]	17.5	4.7*	4.2
	Total								27 2
Anthesis–silking interval									
	1	172	*umc140a-umc72b*	–0 38	–0 72[4]	–0 52[4]	19 0	3.6	5 5
	2	94	*csu50-umc55a*	–0 38	–0 72[4]	–0 52[4]	16 1[3]	3.2	5.7
	3	27	*csu32-csu75*	0 66[4]	0.26	0.46[4]	15.2	5.4*	4.5
	4	60	*umc31a-umc49d*	0.06	0 84[4]	0 40[4]	19 8	12.6**	3 4
	5	120	*umc51a-umc127b*	–0 90[4]	–0 74[4]	–0 84[4]	29.6	0.6	13.4
	8	98	*cdo580a-csu31*	0 98[4]	0 50	0 74[4]	38 9	6 1*	11.5
	Total								37.3
Grain yield (g/plant)									
	7	8	*csu13-umc113c*	7 2	10 6[4]	9.0[4]	16 5	1 1	14.4
Plant height (cm)									
	2	74	*csu110d-csu133*	–5 2	–5 8[4]	–5 4[4]	15 3	0 2	4 9
	3	62	*umc50-csu29b*	6.4[4]	4.0	5 2[4]	18 1	2.6	4 4
	4	147	*csu9b-csu11#1*	8 2[4]	5 6[4]	6.8[4]	28.5	3.6	7 8
	5	144	*umc68-umc104b*	6 2[4]	0 8	3 4[4]	16 7	11.6**	1.9
	7	17	*umc113c-bnl15 40*	6.8[4]	6.6[4]	6 6[4]	19.7	0 0	7 3
	8	83	*csu75#2-cdo580a*	–9.2[4]	–5 6[4]	–7 4[4]	18.9	3 2	8 9
	10	110	*umc44a-bnl7.49a*	–6.6	–7 0[4]	–6 8[4]	18 4	0.1	7 7
	Total								42 8

*, ** QTL × E interaction was significant at P = 0 05 and 0.01, respectively
[1] A positive value means that the allele from CML131 increases the numeric value of the trait
[2] Estimates were obtained from a simultaneous fit of all putative QTLs affecting the trait.
[3] Likelihood ratio was estimated under Model I with window size 30 cM
[4] QTL effect was significant in the respective environment.

were close to QTLs for LFD in the RILs and the same was observed for female flowering. This suggests a possible association between insect resistance and characters affecting flowering.

Surprisingly, the TC progeny from the resistant parent had higher grain yield than the TC progeny from the susceptible parent, even though CML131 was superior to CML67. This was also reflected at the QTL level. At several QTLs for agronomic traits, the allele from CML67 contributed to increased agronomic performance. Thus, the transfer of QTLs for LFD into a recipient line should not have a negative influence on agronomic traits. However, CML131 does not represent an elite line because it was chosen for its susceptibility and results apply only to this specific cross. When using an elite line instead of CML131, it is questionable whether alleles from CML67 would still contribute to increased agronomic performance.

Several TC progenies combined insect resistance with relatively high grain yield. Our results showed that CML67 could be used in hybrid breeding for insect resistance without decreasing yield. Lines with good resistance and agronomic performance *per se* and in hybrid combinations are promising candidates for the improvement of insect resistance without reducing agronomic performance.

Comparison of QTLs across different types of progeny

The biometric model applied for QTL analysis of the RILs was modified for the TC progenies to take into account that TC progenies of the two marker classes show half the difference compared with RILs. In RILs, a QTL is detected when the additive effect between lines homozygous for the alleles from one parent at a marker locus and lines homozygous for the allele from the other parent is significant. TC progenies carry only one allele from either parent in combination with the tester allele. A QTL is detected when the substitution effect of replacing the allele from one parent with the allele from the other parent is significant. The possible interaction of parental alleles with the tester allele has to be kept in mind when comparing different types of progeny.

In maize breeding, the TC performance of lines is more important than their performance *per se*. Therefore, the main objective of our study was to compare QTLs mapped in $F_{2,3}$ lines, RILs and TC progenies in order to investigate the usefulness of different

Table 6. Parameters associated with QTLs significantly affecting agronomic traits, estimated from phenotypic data of 170 RILs from cross CML131 × CML67, measured in 1994B, 1995A and 1995B and in a joint analysis across three environments

Trait	Chromosome	QTL position (cM)	Marker interval	QTL effect[1] 1994A	1995A	1995B	Joint	Likelihood ratio QTL detection	QTL × E	Phenot Variance expl (%)
Female flowering (days)										
	3	36	*csu75-umc50*	0 66	0 18	0.98[3]	0 87[3]	16 8	8 4*	7 2
	3	90	*csu30-bnl5 37*	−1.07[3]	−1 56[3]	−0.91[3]	−0 94[3]	18 8	3.7	8 3
	9	106	*csu93a-bnl5 09*	−0 51	−1.48[3]	−0 71	−0.66[3]	15.9[4]	9.1*	4 1
	Total[2]									17.0
Anthesis-silking interval										
	1	123	*csu92-csu11#2*	−0 40[3]	−1 10[3]	−0.38[3]	−0.45[3]	33 3	12 3**	6 3
	1	168	*umc49c-umc140a*	−0 47[3]	−0 62[3]	−0 58[3]	−0 52[3]	24 7	0 7	8 4
	3	44	*csu75-umc50*	0.08	−0 16	0.54[3]	0 26[3]	15 9[4]	12.1**	2 1
	3	94	*csu30-bnl10.24a*	−0 13	0 38	−0.45[3]	−0.21[3]	16 5[5]	14 2**	1 4
	5	159	*umc68-umc104b*	−0 42	−0 58	−0 47[3]	−0 45[3]	18.6	0 7	6 4
	10	57	*bnl5.09#2-bnl7 49b*	−0 02	0.7	0.02	0 05[3]	17 1[4]	16.9**	0 0
	Total									34.1
Grain yield (g/plant)										
	2	116	*cdo202-csu75#4*	−4 1	−3 9[3]	−4 2[3]	−3 9[3]	18.3	0.1	7 3
	6	16	*csu70-cdo580b*	−4 4[3]	−4 6[3]	−2 0	−2.8[3]	27 2	7 0*	3 7
	10	2	*bnl3 04-umc51a*	−5 0[3]	−4 5[3]	−4 6[3]	−4.5[3]	23 2	0.3	9.4
	Total									19.4
Plant height (cm)										
	3	100	*bnl5 37-bnl10 24a*	6.9[3]	4 9[3]	4.7[3]	4.6[3]	20 0	7.2*	6 7
	5	113	*bnl5 40-umc51a*	−3 9	−3.2	−5 2[3]	−4 1[3]	17 5	6.2*	5 2
Total										12 1

*, ** QTL × E interactions were significant at P = 0.05
[1] A positive value means that the allele from CML131 increases the numeric value of the trait
[2] Estimates were obtained from a simultaneous fit of all putative QTLs affecting the trait.
[3] QTL effect was significant in the respective environment.
[4] Likelihood ratio was estimated under Model I with window size 30 cM
[5] Likelihood ratio was estimated under Model I with window size 20 cM

types of progeny in QTL identification In theory, RILs have a higher power of QTL detection than TC progenies for QTLs with additive gene action (Gallais and Rives 1993). In agreement with this expectation, we detected a greater number of QTLs for LFD accounting for a larger proportion of $\hat{\sigma}_p^2$ in the RILs compared with the TC progenies, probably owing to the low $\hat{h}^2$ in the TC progenies. However, a good agreement of QTL positions between lines and their TC progenies is essential for MAS when QTL mapping is conducted in F_2-derived lines with the final goal of using the improved inbred lines in hybrid combination. Thus, the identification of QTLs in RILs can only be efficient if these QTLs are still expressed in their hybrids.

Comparing RILs with TC progenies, correlation coefficients between line *per se* and TC performance, as well as the presence of common QTLs, can be used as indicators of consistency between types of progeny. In the present study, the correlation between line *per se* and TC performance was very low for LFD Two QTLs on chromosomes 1 and 7 were common with two out of nine QTLs in the RILs. In both regions, Bohn et al. (1997) also detected QTLs for LFD in $F_{2,3}$ lines from the same cross (Fig. 1). However, most QTLs from the RILs or $F_{2,3}$ lines could not be recovered in the TC progenies, including the QTLs on chromosome 9, which explained the greatest proportion of $\hat{\sigma}_p^2$ in the RIL and $F_{2,3}$ lines (Groh et el. 1998, Bohn et al. 1997). The QTL effect at this position was negative even in the TC progenies (data not shown). One QTL was detected on chromosome 3 in the TC progenies and not in the RILs or $F_{2,3}$ lines. At this QTL, the allele from the susceptible parent, CML131, contributed to increased insect resistance, suggesting that an allele for increased vigour from the agronomically superior line, CML131, in combination with the tester allele, had a positive effect on resistance.

We expected to find several common QTLs for LFD in all three types of progeny because gene action estimated in the $F_{2,3}$ lines was mainly additive (Bohn et al. 1996). As pointed out previously, the low estimate of h^2 for LFD in the TC progenies resulted in a low power of QTL detection and was probably the main reason for the small number of QTLs detected for this type of progeny. Furthermore, TC progenies, RILs and $F_{2,3}$ lines were evaluated for LFD in different environments and differences between QTLs for LFD for line *per se* and TC performance could be caused by QTL × E interactions. However, no significant QTL × E interactions were found for most QTLs in all three types of progeny and, thus, it appears to be of minor importance for insect resistance.

However, discrepancies could be caused by genetic effects, when the tester carried a dominant allele over both parental alleles and differences between TC progenies could not be detected even though additive effects were significant In addition, it is possible that different resistance mechanisms are responsible for leaf-feeding resistance in inbred lines compared with hybrids. In a previous study using the RILs (Groh et al. 1998), we found that QTLs for SWCB LFD and SCB LFD were highly associated with QTLs for leaf protein concentration. Resistant RILs had lower leaf protein concentration than susceptible ones, presumably providing insufficient protein for the development of neonate larvae (Bergvinson et al 1997). It might well be that in hybrids, protein concentration is not a limiting factor for larvae, but further research is needed to investigate this hypothesis.

For agronomic traits, few QTLs were common between the TC progenies and the RILs, although correlations between line *per se* and TC performance were intermediate for most traits. The highest correlation was found for plant height but no common QTL was detected. In a comparison between $F_{2:4}$ lines and TC progenies for several traits, Beavis et al. (1994) also found only a few QTLs in common, even when correlations were intermediate to high. Inconsistencies between types of progeny were expected to a certain extent because agronomic traits are highly influenced by dominance effects. It is very likely that the tester carried dominant alleles over both parental alleles and masked the differences between the parents. Furthermore, the dominance relationships between parental alleles and the tester allele might have been the same for both parents, with the result that differences between them could not be detected and, thus, QTLs mapped in the RILs could not be found in the TC progenies. In addition, the relatively small proportion of $\hat{\sigma}_g^2$ explained by all QTLs for most agronomic traits suggested that several QTLs with minor effects were not detected in both types of progeny. Thus, different sets of QTLs may have been detected in the RIL and TC progenies owing to sampling effects, causing the observed inconsistencies.

Another possible explanation for the differences between types of progeny is the presence of epistatic effects. Differences between means of midparent and population of the RIL and TC progenies for grain yield indicated the presence of epistasis. However, no significant digenic epistatic effects were found for grain yield in the RILs, while the identification of epistasis in the TC progenies was not possible because only one QTL was detected. Because tests considered only digenic epistasis and were performed at QTL positions only, they are not representative for the entire genome.

The choice of the tester in QTL mapping studies appears to be of great importance because a strong tester could mask differences between the RILs and result in nonsignificant estimates of $\hat{\sigma}_g^2$. This was shown in other studies when different testers were compared. Ajmone-Marsan et al. (1995) used two TC populations from F_3 lines crossed to two testers to detect QTLs for yield and yield components and found only QTLs with large effects consistent across testers. Schön et al. (1994) evaluated QTLs for protein content, kernel weight and plant height in two TC populations from 380 F_3 lines crossed to two testers. They also found only some QTLs in common across testers and concluded that genetic effects of QTLs found in TC populations are confounded by interactions with tester alleles.

To summarize, most QTLs found in the $F_{2:3}$ lines and RILs for all traits were not consistent with the QTLs detected in the TC progenies. This, and the low phenotypic correlations, especially for LFD, showed that selection based on line *per se* performance will not be efficient in hybrid breeding in either conventional selection or MAS. The development and evaluation of test-crosses during line improvement is a standard procedure in conventional selection. It would also be necessary in MAS during line improvement when QTLs detected in lines are not consistent with QTLs active in TC progenies. For traits with equal efficiency of both methods of selection, MAS is superior to conventional selection if the evaluation of molecular markers is faster and cheaper than the phenotypic evaluation in each cycle of selection. If QTLs are mapped in F_2-derived lines and TC progenies have additionally to be developed and tested to verify the QTL locations and effects in hybrids, the possible advantage of MAS over conventional selection with regard to savings in time and phenotypic evaluation is lost. Although RILs and $F_{2:3}$ lines detected more QTLs, explaining a greater proportion of $\hat{\sigma}_p^2$, these QTLs were not reliable predictors of QTLs in TC progenies. Hence, with regard to hybrid breeding, QTL mapping using TC progenies seems to be indispensable. However, a high precision of phenotypic data is essential in QTL mapping for subsequent applications in MAS. A greater number of test environments might be necessary for TC progenies compared with RIL or $F_{2:3}$ lines to obtain the same power of QTL detection owing to the reduced $\hat{\sigma}_g^2$ caused by masking effects of the tester.

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