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Genetic mapping in maize with hybrid progeny across testers and generations: plant height and flowering

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Abstract DNA markers were used to identify quantitative trait loci (QTLs) for plant height, ear height, and three flowering traits in hybrid progeny of two generations ($F_{2:3}$, $F_{6:8}$) of lines from a Mo17×H99 maize population. For both generations, testcross (TC) progeny were developed by crossing the lines to three inbred testers (B91, A632, B73). The hybrid progeny from the two generations were evaluated at the same locations but in different years as per an early generation testing program. QTLs were identified within each TC population and for mean testcross (MTC) performance. Overall, more QTLs were detected in the $F_{6:8}$ than the $F_{2:3}$ generation. Totalled over all five traits, 41 (B91) to 69% (B73) of the QTLs for tester effects and 67% of the QTLs for MTC detected in the $F_{2:3}$ generation were verified in the $F_{6:8}$ generation. Although differences in relative rank of the QTL effects across generations were observed, especially for the flowering traits, parental contributions were nearly always consistent. Several (8–11) QTLs were identified with effects for all three tester populations and for all traits except the anthesis-silk interval, which had only two such regions. Over all five traits, previous evaluations in this population identified 26 QTLs with consistent effects for two ($F_{2:3}$, $F_{6:8}$) inbred-progeny evaluations, and 20 (77%) were also associated with MTC in at least one of the generations evaluated herein. In all instances of common inbred and TC QTLs, parental contributions were the same.

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Introduction

The improvement of complex, quantitatively inherited traits in maize breeding programs involves the identification and selection of superior lines on the basis of the performance of their hybrid progeny throughout the inbred development process (Hallauer 1990). The majority of quantitative trait locus (QTL) mapping studies, however, have evaluated simple progeny types such as single plants or lines derived from selfing or backcrossing. QTLs identified with inbred progeny reflect within-population additive and dominance effects, whereas QTLs for hybrid performance reflect the interaction of the population's parental alleles with those of the tester. Because of the potential masking effects of favorable dominant alleles in the testers, lines with superior hybrid performance may not necessarily have a high frequency of favorable alleles for inbred per se performance (Smith 1986). Therefore, QTL studies evaluating hybrid progeny are necessary to determine if the same or different QTLs are responsible for inbred and hybrid performance.

Previous studies investigating QTL detection across testcross (TC) progeny of different testers have indicated that consistency of detection is trait-dependent and varies based on the relationship of the testers. For grain yield and morphological traits, Guffey et al. (1988, 1989) reported that genetic background had a large effect on QTL detection across three testcross populations. Schön et al. (1994) reported highly consistent QTL locations across two tester populations for kernel weight and plant height but not for protein content. Ajmone-Marson et al. (1995) evaluated grain yield, dry matter content, and test weight in two divergent populations of hybrid progeny and reported that the QTLs exhibited by one population were not necessarily detected with the second population, but QTLs with larger effects were consistent across populations. Lübberstedt et al. (1997a, b) reported consistent QTL detection across tester populations for dry matter content, plant height, protein concentration and protein yield, but not for dry matter yield and four forage quality traits. In an evaluation of progeny from two diverse testers, Kerns et al (1999) reported few common marker-trait associations.

Recently, QTLs for three tester populations (same materials utilized herein) and the mean testcross (MTC) performance were reported for grain yield and moisture (Austin et al. 2000). For these two traits, the choice of tester was shown to greatly affect the perception of QTL numbers, locations, and effects. Consistency of QTL regions across testers was low for grain yield with only one QTL having significant effects for all three testers, whereas eight such QTLs were detected for grain moisture. Grain moisture had a higher number of QTLs detected, a greater consistency of QTLs across generations, and a greater consistency QTLs across testers, which is most likely due to its higher heritability compared to grain yield.

In agreement with the low correlations observed between per se and testcross performance, previous studies have reported little evidence of common QTLs across the two progeny types. Beavis et al. (1994) reported few common QTLs between per se and testcross progeny (single tester) for grain yield and several morphological traits. Groh et al. (1998) reported some consistency of QTLs across progeny types for leaf feeding resistance; however, few QTLs for agronomic traits were common to the two progeny types. In studies which made comparisons using more than one tester (Guffey et al. 1988, 1989; Schön et al. 1994), inconsistent QTL detection between inbred per se and testrcoss progeny was observed. Kerns et al. (1999) reported that the number of common marker-trait associations between inbred per se and testcross progeny varied by tester (two testers evaluated) and trait (six traits evaluated). Based on the results of these studies, QTLs controlling inbred per se performance, in general, are not highly related to those controlling hybrid performance.

In the present study, $F_{2:3}$ and $F_{6:8}$ progeny from a cross between inbred lines Mo17 and H99 were crossed to three inbred testers. Similar to an early generation breeding program, the TC progeny from the two generations were evaluated for five morphological traits at the same locations but in different years. The first objective was to compare performance and QTL detection between TC progeny of early ($F_{2:3}$) and late ($F_{6:8}$) generations. The second objective was to compare the detection of QTLs across the three testers. QTLs for MTC were also compared to QTL results from $F_{2:3}$ and $F_{6:7}$ inbred per se evaluations of morphological traits in the same population (Austin 1997).

Materials and methods

Population and progeny development

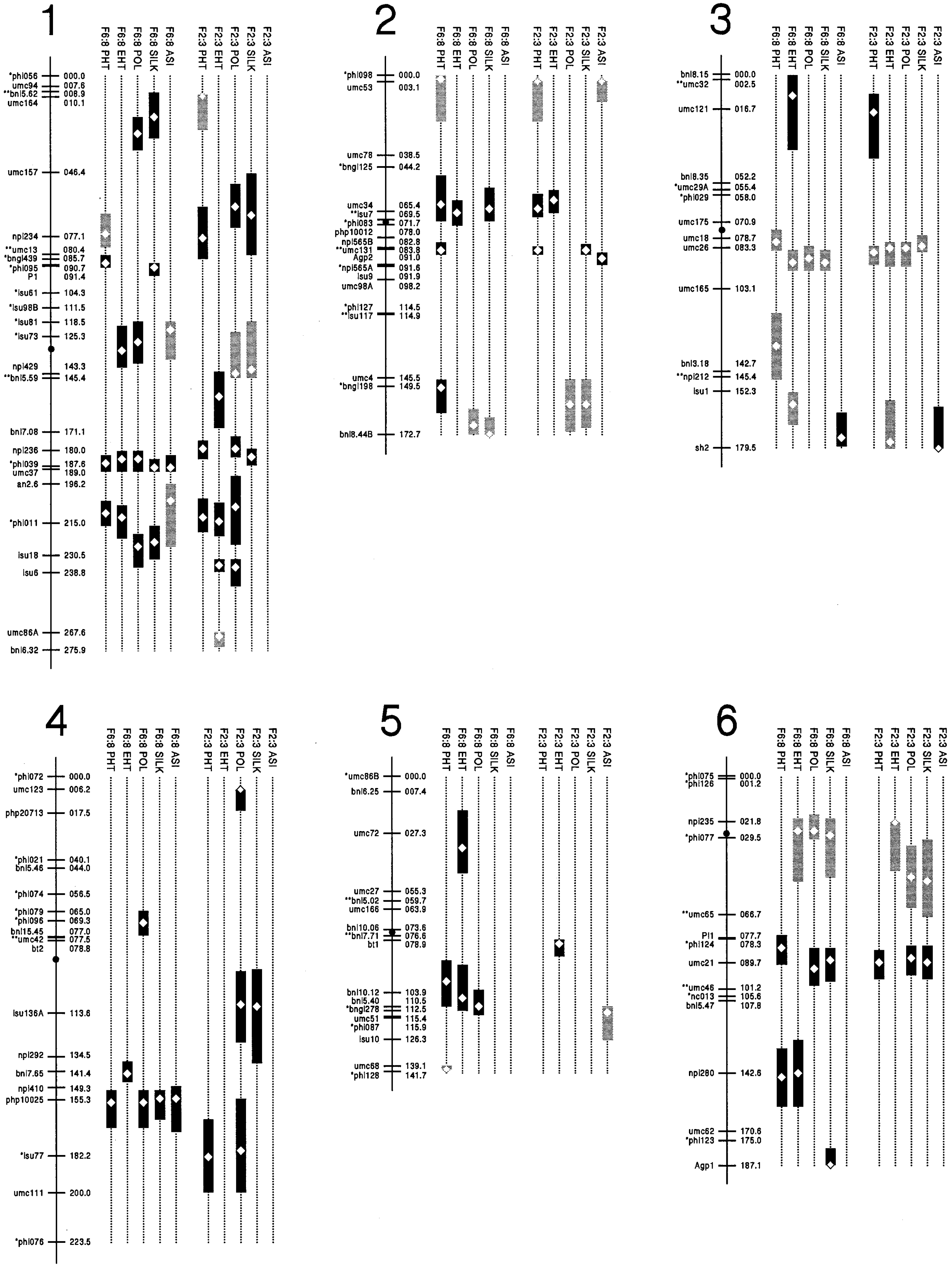
The single-cross population was developed from the adapted and widely utilized U.S. Corn Belt maize inbreds Mo17 and H99, both classified as members of the Lancaster Sure Crop (LSC) heterotic group based on pedigree and RFLP data (Melchinger et al. 1991). One hundred and ninety-four unselected $F_{2:3}$ lines were developed from the population (Veldboom 1994). Due to limited seed supplies, 150 of the $F_{2:3}$ lines were sib-mated by using ten plants and pollinating the ear shoot of one plant with the pollen from the next plant. Equal quantities of sib-mated seed were bulked from each plant within a line. From the same population, 186 unselected $F_{6:7}$ lines were produced by single-seed descent, 147 of which are descendants of the $F_{2:3}$ lines (Austin and Lee 1998). Ten plants per $F_{6:7}$ line were self-pollinated, and equal quantities of $F_{6:8}$ seed per plant were bulked. Each $F_{2:3}$ and $F_{6:7}$ line was manually mated with each tester to produce the hybrid progeny.

Development of the hybrid progeny has been previously described in detail (Austin et al. 2000). For both the $F_{2:3}$ and $F_{6:8}$ generations, crosses were made to three inbred testers (B91, A632, B73). B91 is derived from Iowa Corn Borer Synthetic #1 (BSCB1), which has some progenitor LSC lines and is considered unrelated by pedigree to Reid Yellow Dent and certainly unrelated to the two other testers. B91 was released in 1989 and has a maturity classification of AES800 (Russell 1989). B73 and A632 both represent Reid Yellow Dent inbreds (Gerdes et al. 1993). A632, released in 1964, was derived through three backcross generations with selection for earliness with B14, a stiff-stalk inbred, as the recurrent parent. A632 has a maturity classification of AES600. B73 is also a stiff-stalk inbred (released in 1972) with a maturity classification of AES800 (Russell 1972). B14 and B73 were both derived from the same synthetic; however, they are distinct and exhibit a high level of genetic dissimilarity for elite stiff-stalk germplasm (Melchinger et al. 1991). Both A632 and B73 were widely used in commercial hybrids with Mo17 and H99 (Zuber and Darrah 1980).

Field evaluations

The $F_{2:3}$ TC populations were evaluated for morphological traits at three locations in Iowa in 1992 and 1993 (Veldboom 1994). These included two northern locations (Kanawha and Nashua) and one central (Ames) location. Similar to an early generation testing breeding program, the $F_{6:8}$ hybrid populations were evaluated at the same three locations but in different years (1995 and 1996). Each tester population was treated as a separate experiment, and the same experimental design (14×14 lattice, two replications) was utilized for each tester-location year combination. At each location, the three experiments were evaluated in adjacent plots. For the $F_{2:3}$ evaluations, entries consisted of hybrid progeny of the 194 lines and single entries for the Mo17 and H99 hybrids, whereas the $F_{6:8}$ entries consisted of hybrid progeny of the 186 lines and five entries each of the parental hybrids. The entries were machine-planted in two-row plots which were 5.5 m long with 0.76 m spacing between rows. Planting densities were 76500 kernels ha^{-1} for the $F_{2:3}$ and 86100 kernels ha^{-1} for the $F_{6:8}$. For both generations, plots were thinned to 62000 plants ha^{-1} at the 6–8 leaf stage.

Fig. 1 Genetic linkage map for Mo17×H99 $K_{6.8}$ lines and QTL positions for $F_{6.8}$ and $F_{2.3}$ testcross progeny marker. Loci unique to the $F_{6:8}$ generation (*) are indicated. Loci unique to the $F_{2:3}$ generation (**) are placed based on relative position to the 87 loci common to both generations. Positions of DNA marker loci are given in cM to the right of the linkage groups relative to the first locus (*position 0.0*) in each chromosome. Morphological-trait QTL positions for $F_{6.8}$ and $F_{2.3}$ MTC are indicated to the right of the linkage groups. One-LOD support intervals are indicated by *vertical bars* with the position of the maximum LOD peak indicated by an *open diamond.* The parental allele conferring increased trait value at the QTL is also indicated (*solid*=Mo17; *stippled*=H99) ▶


1
F6:8 PHT
F6:8 EHT
F6:8 POL
F6:8 SILK
F6:8 ASI
F2:3 PHT
F2:3 EHT
F2:3 POL
F2:3 SILK
F2:3 ASI
*phi056 000.0
umc94 007.6
**bnl5.62 008.9
umc164 010.1
umc157 046.4
npi234 077.1
**umc13 080.4
*bngl439 085.7
*phi095 090.7
P1 091.4
*isu61 104.3
*isu98B 111.5
*isu81 118.5
*isu73 125.3
npi429 143.3
**bnl5.59 145.4
bnl7.08 171.1
npi236 180.0
*phi039 187.6
umc37 189.0
an2.6 196.2
*phi011 215.0
isu18 230.5
isu6 238.8
umc86A 267.6
bnl6.32 275.9
2
*phi098 000.0
umc53 003.1
umc78 038.5
*bngl125 044.2
umc34 065.4
**isu7 069.5
*phi083 071.7
php10012 078.0
npi565B 082.8
**umc131 083.8
Agp2 091.0
*npi565A 091.6
isu9 091.9
umc98A 098.2
*phi127 114.5
**isu117 114.9
umc4 145.5
*bngl198 149.5
bnl8.44B 172.7
3
bnl8.15 000.0
**umc32 002.5
umc121 016.7
bnl8.35 052.2
*umc29A 055.4
*phi029 058.0
umc175 070.9
umc18 078.7
umc26 083.3
umc165 103.1
bnl3.18 142.7
**npi212 145.4
isu1 152.3
sh2 179.5
4
*phi072 000.0
umc123 006.2
php20713 017.5
*phi021 040.1
bnl5.46 044.0
*phi074 056.5
*phi079 065.0
*phi096 069.3
bnl15.45 077.0
**umc42 077.5
bt2 078.8
isu136A 113.6
npi292 134.5
bnl7.65 141.4
npi410 149.3
php10025 155.3
*isu77 182.2
umc111 200.0
*phi076 223.5
5
*umc86B 000.0
bnl6.25 007.4
umc72 027.3
umc27 055.3
**bnl5.02 059.7
umc166 063.9
bnl10.06 073.6
**bnl7.71 076.6
bt1 078.9
bnl10.12 103.9
bnl5.40 110.5
*bngl278 112.5
umc51 115.4
*phi087 115.9
isu10 126.3
umc68 139.1
*phi128 141.7
6
*phi075 000.0
*phi126 001.2
npi235 021.8
*phi077 029.5
**umc65 066.7
Pl1 077.7
*phi124 078.3
umc21 089.7
**umc46 101.2
*nc013 105.6
bnl5.47 107.8
npi280 142.6
umc62 170.6
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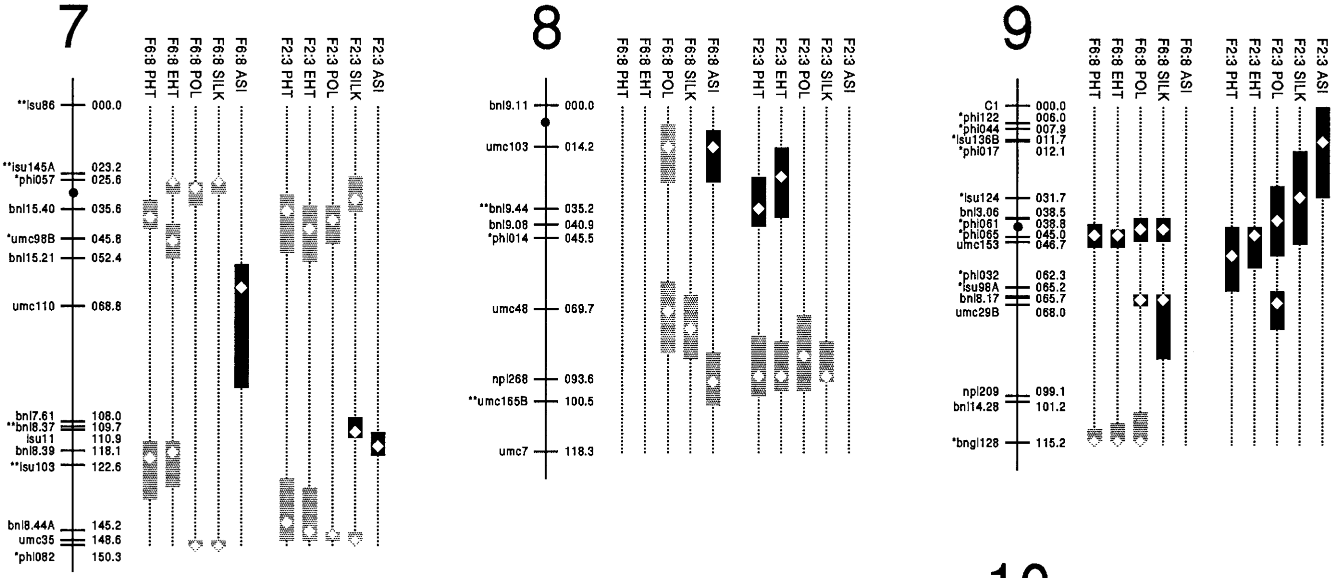
Agp1 187.1



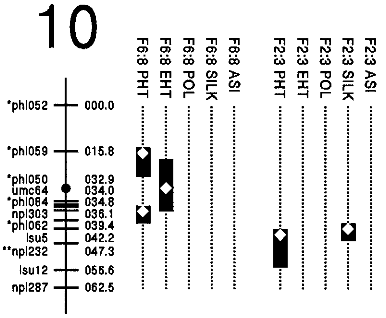


Fig. 1 continued

Three measurements of flowering, growing degree days (GDD) to 50% anthesis (POL), GDD to 50% silk emergence (SILK), and silk delay or anthesis-to-silking interval (ASI), were recorded for both generations, as described in Veldboom et al. (1994), for each plot at the Ames location only. Plant height (PHT) was measured on ten competitive plants per plot from ground level to the tip of the central tassel spike. Ear height (EHT) was measured on ten competitive plants per plot from ground level to the node of primary ear attachment. PHT and EHT were recorded at all three locations for the $F_{6:8}$ evaluations. For the $F_{2:3}$ evaluations, PHT was measured at all three locations, whereas EHT was measured at the Ames location only.

Marker assays

DNA isolation, Southern hybridization, and RFLP assay procedures have previously been described (Veldboom et al. 1994). The $F_{2:3}$ linkage map was developed using RFLP data for 303 lines including the 194 lines used for the hybrid evaluations (Veldboom 1994; Austin et al. 2000). One hundred and six RFLP loci and one morphological locus, P1, provided a linkage map spanning 1413 cM with an average interval length of 15 cM. The $F_{6:8}$ linkage map has been previously described (Austin and Lee 1998; available electronically on Maize DB website, www.agron.missouri.edu), and consists of one morphological (P1), 100 RFLP, and 41 SSR (Senior et al. 1996) loci. The $F_{6:8}$ linkage map covers 1601 cM with an average distance between adjacent loci of 12 cM (see Fig. 1). Centromeres were placed approximately based on previous maps (Coe et al. 1990; Veldboom et al. 1994; Coe et al. 1995; Matz et al. 1995). On the basis of centromere placement, chromosomal regions will be referred to herein as a number (1–10) followed by L (long arm), S (short arm), or C (region including the centromere).

Eighty six RFLP loci and one morphological marker (P1) are common between the $F_{2:3}$ and $F_{6:8}$ linkage maps. Twenty of the loci mapped in the $F_{2:3}$ were not mapped in the $F_{6:8}$. These loci are placed on the $F_{6:8}$ generation linkage map (see Fig. 1) based on relative position to the 87 common loci.

Trait data analysis

The $F_{2:3}$ and $F_{6:8}$ experiments were evaluated separately using the same procedures. Adjusted entry means for each year location-experiment combination were obtained by correcting for incomplete block effects according to Cochran and Cox (1957). A combined analysis of variance was conducted separately for each tester, and estimates of genetic (σ^2_g) and genotypic by environment (σ^2_{ge}) variance components were obtained. The experimental design allowed the experiments to be combined across testers, and variance components were estimated for genetic (σ^2_g), genotype×tester (σ^2_{gt}), genotype x environment (σ^2_{ge}), and genotype x tester x environment (σ^2_{gte}). Heritabilities were calculated on an entry mean basis (Hallauer and Miranda 1988) for each tester and across testers. Within each generation, simple phenotypic correlations were calculated among the testers for each trait. Phenotypic correlations between traits were calculated within each generation using MTC values. Simple phenotypic correlations were also calculated between the $F_{2:3}$ and $F_{6:8}$ generations using mean values for the 147 lines of common descent.

QTL detection

Previous studies in this population with $F_{2:3}$ (Veldboom and Lee 1996a, b) and $F_{6:7}$ (Austin 1997; Austin and Lee 1998) inbred progeny have shown the mean environment (i.e. the average of all environments) to be the most representative for QTLs with consistent effects across environments. Similar conclusions were made for grain yield with TC progeny of $F_{6:8}$ lines of this population (Austin 1997, Austin et al. 2000). Therefore, progeny means across environments within the $F_{2:3}$ and $F_{6:8}$ TC progeny evaluations were utilized for all QTL identification reported herein. For both the $F_{2:3}$ and $F_{6:8}$ generations, QTL determinations were made separately for each tester population. QTLs for MTC were detected by using mean performance across all testers. QTLs were identified by composite interval mapping (Jansen and Stam 1994; Zeng 1994). All computations for this method were performed with the software package PLABQTL (Utz and Melchinger 1996) which employs interval mapping by the regression approach (Haley and Knott 1992) with selected markers as cofactors. The underlying model for TC progeny has been described previously (Lübberstedt et al. 1997a; Austin et al. 2000). To enable comparisons across testers and generations, a LOD threshold of 2.0 was selected for QTL detection. Using the chi-square approximation suggested by Zeng (1994), this corresponds to a comparison-wise type-I error rate of $P<0.01$ based on the number of intervals being tested in the $F_{6:8}$ TC evaluations (Utz and Melchinger 1996). For each QTL, a one-LOD support interval was constructed as described by Lander and Botstein (1989). On a given chromosome, QTLs with non-overlapping one-LOD support intervals (SI) were considered as different. To allow comparison of QTL positions across generations, $F_{2:3}$ TC population QTL positions were adjusted to correspond to the $F_{6:8}$ linkage map (see Fig. 1) based on relative position to the 87 RFLP loci common to the linkage maps constructed in both generations.

Estimates of the percentage of phenotypic variance explained by individual QTLs were obtained by the square of the partial correlation coefficient between the respective QTLs and the phenotypic observations, keeping all other QTL effects fixed. Estimates of the single QTL effects, as well as the total phenotypic variation explained by all QTLs, were obtained by simultaneously fitting a model including all QTLs detected for the trait by tester combination (Utz and Melchinger 1996).

Results and discussion

The means for the lines are shown for each TC population and for the mean across testers (MTC) in Table 1. In the combined analyses of variance across testers for the $F_{2:3}$ and $F_{6:8}$ generations (Austin 1997), significant ($P\leq 0.01$) differences among tester population means were observed for PHT ($F_{6:8}$ only), EHT ($F_{6:8}$ and $F_{2:3}$), and SILK ($F_{6:8}$ and $F_{2:3}$). For the TC population means, the same general trend was observed across traits and generations with B73 progeny having the greatest values. The $F_{2:3}$ and $F_{6:8}$ progeny had very similar mean values

Table 1 Parental means, progeny means, and heritabilities of morphological traits for testcross progeny of 186 $F_{6:8}$ and 194 $F_{2:3}$ progeny of Mo17×H99 evaluated across environments in 1995–96 and 1992–93, respectively

Trait	Generation	Tester	Parental means		Progeny		h^2
			Mo17	H99[a]	Mean	Range	
PHT (cm)	$F_{6:8}$	B91	288	273^{d}	278	256–306	0.94
		A632	292	266^{d}	280	258–300	0.95
		B73	300	277^{d}	286	261–310	0.96
		MTC	293	272^{d}	281	261–305	0.98
	$F_{2:3}$	B91	285	269^{d}	279	262–300	0.87
		A632	285	261^{d}	273	258–292	0.89
		B73	295	272^{d}	281	263–301	0.94
		MTC	288	267^{d}	277	262–294	0.95
EHT (cm)	$F_{6:8}$	B91	117	102^{d}	110	88–129	0.96
		A632	113	96^{d}	108	84–132	0.96
		B73	123	108^{d}	115	91–144	0.97
		MTC	118	102^{d}	111	90–135	0.98
	$F_{2:3}$	B91	112	92^{d}	104	85–126	0.83
		A632	109	79^{d}	94	79–114	0.87
		B73	115	95^{d}	106	89–131	0.86
		MTC	112	91^{d}	103	88–125	0.94
POL (GDD)	$F_{6:8}$	B91	797	784^{d}	789	748–831	0.91
		A632	793	773^{d}	787	754–819	0.87
		B73	816	796^{d}	804	769–852	0.91
		MTC	802	784^{d}	793	762–832	0.95
	$F_{2:3}$	B91	793	795	797	772–840	0.66
		A632	777	782	780	752–800	0.77
		B73	817	793^{c}	800	772–834	0.78
		MTC	797	794	796	774–827	0.87
SILK (GDD)	$F_{6:8}$	B91	808	785^{d}	794	751–844	0.89
		A632	798	779^{d}	792	757–823	0.83
		B73	828	799^{d}	811	773–860	0.89
		MTC	811	788^{d}	799	765–842	0.93
	$F_{2:3}$	B91	818	809	815	784–865	0.44
		A632	796	792	797	766–824	0.60
		B73	835	800^{d}	820	783–869	0.79
		MTC	817	806^{b}	814	786–852	0.79
ASI (GDD)	$F_{6:8}$	B91	11	1^{d}	5	–6–21	0.34
		A632	5	6	5	–6–24	0.57
		B73	12	4^{c}	7	–3–36	0.55
		MTC	9	4^{c}	6	–2–24	0.62
	$F_{2:3}$	B91	23	14	18	2–47	0.21
		A632	18	11	16	1–35	0.44
		B73	17	8	20	3–59	0.61
		MTC	19	12	18	5–36	0.64

[a] Significance of difference between Mo17 and H99 values in combined analysis across environments
noted for [b]0.05, [c]0.01, and [d]0.001 probability levels

Table 2 Phenotypic correlations among testcross progeny within the $F_{6:8}$ (above diagonal) and F2:3 (below diagonal) generations of Mo17xH99. Phenotypic correlations between the $F_{6:8}$ and $F_{2:3}$ generations are given along the diagonal

Trait	Tester	MTC	B91	A632	B73
PHT	MTC	***0.55***	0.94	0.92	0.95
	B91	0.89	***0.49***	0.78	0.86
	A632	0.87	0.68	***0.45***	0.80
	B73	0.90	0.71	0.66	***0.55***
EHT	MTC	***0.57***	0.96	0.93	0.97
	B91	0.95	***0.50***	0.83	0.92
	A632	0.86	0.77	***0.48***	0.85
	B73	0.91	0.78	0.76	***0.59***
POL	MTC	***0.63***	0.93	0.86	0.93
	B91	0.91	***0.61***	0.69	0.84
	A632	0.64	0.48	***0.39***	0.67
	B73	0.86	0.63	0.45	***0.56***
SILK	MTC	***0.64***	0.92	0.84	0.94
	B91	0.85	***0.60***	0.67	0.80
	A632	0.61	0.36	***0.41***	0.68
	B73	0.83	0.51	0.41	***0.52***
ASI	MTC	***0.43***	0.71	0.73	0.80
	B91	0.73	***0.21***	0.32	0.38
	A632	0.64	0.25	***0.35***	0.34
	B73	0.76	0.22	0.49	***0.35***

All correlations significant at the 0.01 probability level

for PHT, EHT, and POL. For SILK and ASI, mean values were greater in the $F_{2:3}$ progeny for each tester and MTC. The majority (147) of the 186 $F_{6:8}$ are direct descendants of the $F_{2:3}$ lines. Assuming no forces other than natural selection during the $F_{6:8}$ line development, no change in average gene frequency would be expected in the two sets of lines (Hallauer and Lopez-Perez 1979). Previous evaluations of the RFLP data for the $F_{2:3}$ (Veldboom et al. 1994) and $F_{6:7}$ (Austin and Lee 1996a) generations revealed a distribution of marker classes within expectations and average parental allele frequencies near 50%, indicating no evidence of unintentional selection during inbreeding. Thus, differences in mean performance of the $F_{2:3}$ and $F_{6:8}$ hybrid progeny for SILK and ASI are most likely the result of environmental factors as the two experiments were conducted in different years.

For the parental checks, significant differences in PHT and EHT were observed for each tester and MTC in both the $F_{6:8}$ and $F_{2:3}$ generations (Table 1). In all instances, Mo17 had greater height than H99. For POL, Mo17 had significantly ($P \leq 0.001$) greater values than H99 for all three testers and MTC in the $F_{6:8}$ evaluations, whereas Mo17 had a significantly greater POL only for B73 in the $F_{2:3}$ generation. For SILK, Mo17 had greater values for all tester-generation combinations, with the differences significant in all instances in the $F_{6:8}$ and for B73 and MTC in the $F_{2:3}$. Mo17 had significantly greater ASI values for B91, B73, and MTC in the $F_{6:8}$ evaluations. Although non-significant, Mo17 also had greater values for ASI across all three testers in the $F_{2:3}$ evaluations. The trend of Mo17 having greater PHT and EHT and later flowering was also observed in the inbred progeny of this population (Veldboom and Lee, 1996a; Austin and Lee, 1997a).

Heritability (h^2) values were moderate for the flowering traits and high for PHT and EHT (Table 1). In general, h^2 values were greater for the $F_{6:8}$ than the $F_{2:3}$ progeny. The higher h^2 values observed for the $F_{6:8}$ generation were not surprising since the $F_{6:8}$ lines and their TC progeny should be more homogeneous with less opportunities for segregation and sampling variation. Overall, h^2 values were relatively high, which should enhance the detection of QTLs associated with larger portions of the genetic variance (Lande and Thompson 1990).

For both generations, significant genetic variation was observed within each of the three hybrid populations (Austin 1997). The genotype x environment variance components were significant for most of the tester-generation combinations; however, the estimates of genetic variance were approximately 10-times greater than the genotype×environment variance estimates indicating that environmental interactions were not large for these morphological traits. Comparison of σ^2_g estimates for MTC reveals greater values in the $F_{6:8}$ than the $F_{2:3}$ for four of the five traits. Assuming no dominance effects or a gene frequency of 0.5, variation among $F_{6:8}$ lines should be about double that among $F_{2:3}$ lines (Hallauer and Miranda 1988). In agreement with theoretical expectations, $F_{6:8}$ estimates were 1.6–2.2-times greater for all traits except ASI.

Within both generations, phenotypic correlations among tester populations were moderate for PHT, EHT, POL and SILK, and low for ASI (Table 2). The relationship of the testers did not appear to influence the correlations between pairs of tester progeny. Hybrid progeny of the two testers from the same heterotic group, B73 and A632, were not more highly correlated to each other than to the unrelated tester, B91. For all five traits in both generations, there were high correlations between a given tester and MTC. This observation is not surprising since MTC is derived from the mean values of the three tester populations, and increasing trait values for a given tester would also increase MTC.

Table 3 Phenotypic correlations between morphological traits for $F_{6:8}$ (above diagonal) and $F_{2:3}$ (below diagonal) MTC values across environments. Values along the diagonal are the phenotypic correlations between $F_{6:8}$ MTC and $F_{6:8}$ inbred per se performance

Trait	PHT	EHT	POL	SILK	ASI
PHT	***0.80***^{b}	0.82^{b}	0.68^{b}	0.66^{b}	0.05
EHT	0.76^{b}	***0.84***^{b}	0.72^{b}	0.64^{b}	–0.13
POL	0.54^{b}	0.59^{b}	***0.70***^{b}	0.94^{b}	–0.02
SILK	0.54^{b}	0.42^{b}	0.85^{b}	***0.71***^{b}	0.31^{b}
ASI	0.17^{a}	–0.13	0.04	0.56^{b}	***0.48***^{b}

[a,b] Significant at the 0.05 and 0.001 probability levels, respectively

For individual tester populations, moderate phenotypic correlations (r_p=0.39–0.61) between the $F_{2:3}$ and $F_{6:8}$ generation progeny were observed for all traits except ASI (Table 3). MTC tended to have higher correlations between the generations than individual tester values. Correlations for MTC were the greatest for POL (r_p=0.63) and SILK (r_p=0.64) and lowest for ASI (r_p=0.43). In agreement with the objectives of early generation testing, the relationship observed herein between the $F_{2:3}$ and $F_{6:8}$ generation TC progeny should be sufficient to allow the identification of lines with undesirable morphological characteristics at the early generation (Hallauer and Miranda 1988).

Phenotypic correlations among the five traits for MTC were similar within both generations (Table 3). The highest correlations were between POL and SILK and between PHT and EHT. ASI had a positive correlation with SILK in both generations, but had weak correlations with all other traits. POL and SILK had moderate correlations with EHT and PHT, which indicated a relationship between reproductive maturity and vegetative growth. These correlations among traits with TC progeny were very similar to correlations among the same traits observed with inbred progeny (Veldboom and Lee 1996b; Austin 1997).

QTL detection in $F_{2:3}$ and $F_{6:8}$ generations

QTL position and parental contribution information is presented for all trait-tester-generation combinations in Fig. 1. Detailed QTL information is presented for PHT and POL in Table 4 (see Austin 1997 for detailed summaries for all traits). Overall, more QTLs were detected in the $F_{6:8}$ than the $F_{2:3}$ generation for the three testers and the MTC effects. Summed over all five traits, QTL numbers for the $F_{2:3}$ generation were 49, 47, and 51 for testers B91, A632, and B73, respectively. In the $F_{6:8}$ the numbers of QTLs detected were 59, 83, and 68 over the five traits for B91, A632, and B73, respectively. Similarly for MTC, 69 QTLs were detected in the $F_{2:3}$, whereas 81 were detected in the $F_{6:8}$ generation. The increased number of QTLs detected in the $F_{6:8}$ corresponds with larger portions of the phenotypic variance associated with the QTLs. The $F_{6:8}$ generation should be more efficient and powerful for QTL detection because of increased homozygosity, homogeneity, and increased recombination for the separation of linked QTLs (see Austin and Lee 1996a for a review); however, a portion of the increase in $F_{6:8}$ QTL detection may be due to the use of more markers, better map coverage, and greater trait h^2 values (Austin et al. 2000). As discussed previously, the majority of the $F_{6:8}$ lines are direct descendants of the $F_{2:3}$ lines, and no evidence is present to suggest any unintentional selection during inbreeding. Thus, any differences in QTL detection are most likely due to the greater precision of RI lines, environmental effects (generations grown at same locations but in different years), or sampling variation (Beavis 1994).

For PHT, three (B91) to eight (B73) QTLs for tester effects were detected in both generations representing 27 to 51% of the $F_{2:3}$ QTLs (Table 4). B73 had the highest correlation between generations for PHT (r_p=0.55) and also had the greatest number of common QTLs. For all three testers, the QTLs which were common across generations usually included those with the largest effects within the $F_{2:3}$ and $F_{6:8}$ generations. MTC displayed a greater number of common QTLs than any individual tester. Twelve MTC QTLs were common across generations representing 71% of the $F_{2:3}$ QTLs detected. The QTLs with the largest effects for MTC were detected on 1L (an2.6-phi011) explaining 30% of the $F_{6:8}$ and 36% of the $F_{2:3}$ phenotypic variation. The common MTC QTLs included seven ($F_{6:8}$) and eight ($F_{2:3}$) of the ten QTLs with the largest effects within each generation. In all instances of common PHT QTLs across generations, the parental contributions were the same.

For EHT, the number of TC QTLs common across the $F_{2:3}$ and $F_{6:8}$ generations ranged from 6 (B91) to 12 (A632) representing 46 to 92% of the $F_{2:3}$ QTLs, respectively. A632 had the most common QTLs despite having the lowest correlation between $F_{2:3}$ and $F_{6:8}$ performance; however, this is most likely due to the high number (23) of $F_{6:8}$ QTLs, which was the greatest number of QTLs for a generation-trait-tester combination in the study. The QTL on 1L (an2.6-phi011-isu18) had the largest effect for all three testers in both generations explaining from 21 to 43% of the phenotypic variation. Ten QTLs were common across generations for MTC representing 76% of the $F_{2:3}$ QTLs. The QTLs with the largest effects for MTC in both generations were also detected on 1L (an2.6-phi011-isu18) and explained 30% ($F_{6:8}$) and 36% ($F_{2:3}$) of the phenotypic variation. The common MTC QTLs included seven of the ten QTLs with the largest effects within each generation. For both tester and MTC QTLs common across generations, consistent parental allele contributions were observed.

The number of POL QTLs detected in both generations ranged from five (A632) to eight (B73) representing 29 to 53% of the $F_{2:3}$ QTLs for their respective testers (Table 4). In all instances of common tester QTLs, the same parental contributions were observed in both generations. Contrary to the results of PHT and EHT, the QTLs with the largest effects were not as con-

Table 4 PHT and POL QTL substitution effects in the mean environment for testcross progeny of $F_{6:8}$ and $F_{2:3}$ lines of Mo17×H99

Trait	Region	Nearest locus[a]					
		(a-b-c-d)	Gen.	B91[b]	A632	B73	MTC
PHT (cm)	1S	umc164	$F_{6:8}$	–	–	–	–
			$F_{2:3}$	2.7H	–	2.7H	1.9H
	1S	npi234	$F_{6:8}$	–	–	–	4.4H
			$F_{2:3}$	–	–	–	1.2M
	1S	phi095	$F_{6:8}$	–	–	–	2.9M
			$F_{2:3}$	–	–	–	–
	1L	npi236-phi039	$F_{6:8}$	–	4.6M,b	5.5M,b	4.1M,b
			$F_{2:3}$	–	–	3.4M,a	3.1M,a
	1L	an2.6-phi011	$F_{6:8}$	10.0M,b	5.6M,b	7.2M,b	7.5M,b
			$F_{2:3}$	12.2M,a	10.0M,a	11.7M,a	10.1M,a
	2S	umc53	$F_{6:8}$	–	–	–	2.2H
			$F_{2:3}$	4.5H	–	1.6H	2.2H
	2S	umc34	$F_{6:8}$	3.5M	–	–	2.4M
			$F_{2:3}$	6.2M	–	4.2M	3.4M
	2L	npi565B-umc131-Agp2	$F_{6:8}$	6.1M,a	5.0M,c	3.5M,a	4.4M,a
			$F_{2:3}$	–	5.8M.b	2.6M,b	2.7M,b
	2L	bngl198-bnl8.44B	$F_{6:8}$	–	2.6M,a	4.0M,a	2.8M,a
			$F_{2:3}$	–	4.6H,b	–	–
	3S	umc121	$F_{6:8}$	–	–	–	–
			$F_{2:3}$	–	5.0M	–	2.0M
	3S	umc29A	$F_{6:8}$	3.5M	–	–	–
			$F_{2:3}$	–	–	–	–
	3L	umc18-umc26	$F_{6:8}$	6.9H,b	–	8.8H,b	4.5H,a
			$F_{2:3}$	–	–	6.5H,b	1.9H,b
	3L	bnl3.18	$F_{6:8}$	–	–	3.8H	3.5H
			$F_{2:3}$	–	–	–	–
	3L	sh2	$F_{6:8}$	–	–	–	–
			$F_{2:3}$	–	–	1.6M	–
	4S	bnl15.45	$F_{6:8}$	–	–	–	–
			$F_{2:3}$	–	–	2.3H	–
	4L	php10025-umc111	$F_{6:8}$	–	4.0M,a	6.6M,a	3.0M,a
			$F_{2:3}$	3.4M,b	–	–	3.1M,b
	5S	bnl6.25	$F_{6:8}$	–	–	–	–
			$F_{2:3}$	2.7M	–	–	–
	5L	bnl10.12-umc51	$F_{6:8}$	4.0M,a	5.4M,a	–	3.8M,a
			$F_{2:3}$	1.8M,b	–	–	–
	5L	umc68-phi128	$F_{6:8}$	3.1H,a	3.9H,b	–	3.3H,a
			$F_{2:3}$	–	–	–	–
	6L	phi124-umc21	$F_{6:8}$	–	3.0M,b	2.5M,a	2.1M,a
			$F_{2:3}$	2.8M,b	–	–	3.3M,b
	6L	nc013	$F_{6:8}$	–	2.5H	–	–
			$F_{2:3}$	–	–	–	–
	6L	npi280	$F_{6:8}$	–	2.1M	–	2.4M
			$F_{2:3}$	–	–	–	–
	7S	isu86	$F_{6:8}$	–	–	–	–
			$F_{2:3}$	–	–	3.9H	–
	7C	phi057-bnl15.40	$F_{6:8}$	4.9H,a	3.7H,b	2.9H,b	3.8H,b
			$F_{2:3}$	–	5.6H,b	–	4.0H,b
	7L	bnl8.39	$F_{6:8}$	–	6.6H	3.7H	4.0H
			$F_{2:3}$	3.2H	–	–	–
	7L	bnl8.44A-umc35-phi082	$F_{6:8}$	2.7H,b	–	3.2H,c	–
			$F_{2:3}$	–	–	2.7H,a	3.7H,a
	8L	umc103-bnl9.44	$F_{6:8}$	–	–	3.5H,a	–
			$F_{2:3}$	2.3M,b	2.8M,b	0.8M,b	2.6M,b
	8L	phi014	$F_{6:8}$	–	3.3M	4.0M	–
			$F_{2:3}$	–	–	–	–
	8L	umc48-umc165B-	$F_{6:8}$	–	2.9H,a	4.0H,a	–

Table 4 (continued)

Trait	Region	Nearest locus[a]					
		(a-b-c-d)	Gen.	B91[b]	A632	B73	MTC
PHT (cm)	8L	npi268	$F_{2:3}$	3.8H,b	–	4.5H,c	3.3H,c
	9L	phi065-umc153	$F_{6:8}$	–	4.1M,a	5.6M,a	3.8M,a
			$F_{2:3}$	–	3.5M,b	6.9M,b	4.1M,b
	9L	bngl128	$F_{6:8}$	3.0H	3.3H	3.2H	3.1H
			$F_{2:3}$	–	–	–	–
	10S	phi059	$F_{6:8}$	–	4.6M	3.4M	2.0M
			$F_{2:3}$	–	–	–	–
	10	npi303-phi062-isu5	$F_{6:8}$	5.2M,b	–	–	2.3M,a
			$F_{2:3}$	–	2.8M,a	–	3.0M,c
POL (GDD)	1S	umc164-umc157-npi234	$F_{6:8}$	–	6.8M,b	8.0M,a	8.8M,a
			$F_{2:3}$	–	4.7M,b	13.1M,a	8.6M,c
	1S	phi095	$F_{6:8}$	3.9M	–	–	–
			$F_{2:3}$	–	–	–	–
	1C	isu81-isu73-npi429	$F_{6:8}$	2.6M,b	4.2M,a	5.6M,b	4.8M,a
			$F_{2:3}$	–	–	–	4.5H,c
	1L	bnl7.08	$F_{6:8}$	6.9M	7.4M	–	–
			$F_{2:3}$	–	10.9H	–	–
	1L	npi236-phi039	$F_{6:8}$	–	–	4.7M,b	4.7M,b
			$F_{2:3}$	9.7M,a	13.0M,a	–	8.3M,a
	1L	an2.6-isu18	$F_{6:8}$	13.5M,b	6.9M,b	7.0M,b	6.9M,b
			$F_{2:3}$	–	6.2M,b	16.1M,b	6.1M,a
	1L	isu6	$F_{6:8}$	–	–	–	–
			$F_{2:3}$	10.3M	–	–	5.2M
	2S	umc34	$F_{6:8}$	4.9M	–	–	–
			$F_{2:3}$	–	–	–	–
	2L	npi565B-umc131	$F_{6:8}$	–	–	4.8M,a	–
			$F_{2:3}$	6.2M,b	–	–	–
	2L	umc4	$F_{6:8}$	1.9H	–	5.8H	–
			$F_{2:3}$	11.8H	–	6.6H	8.7H
	2L	bnl8.44B	$F_{6:8}$	8.7H	6.6H	–	6.7H
			$F_{2:3}$	–	13.2H	–	–
	3S	umc121	$F_{6:8}$	–	–	–	–
			$F_{2:3}$	–	3.8M	–	–
	3L	umc18-umc26	$F_{6:8}$	9.9H,b	–	13.5H,b	7.8H,b
			$F_{2:3}$	8.0H,a	–	13.1H,b	8.7H,b
	4S	umc123	$F_{6:8}$	–		–	–
			$F_{2:3}$	–	–	–	3.8M
	4S	bnl5.46	$F_{6:8}$	–	4.6H	–	–
			$F_{2:3}$	–	–	–	–
	4S	phi074-phi096	$F_{6:8}$	4.4M,b	6.3M,a	–	3.0M,b
			$F_{2:3}$	–	–	–	–
	4L	isu136A	$F_{6:8}$	–	–	–	–
			$F_{2:3}$	–	8.5M	–	4.9M
	4L	php10025-umc111	$F_{6:8}$	–	6.1M,a	9.5M,a	6.7M,a
			$F_{2:3}$	8.0M,a	–	–	5.7M,b
	4L	phi076	$F_{6:8}$	–	5.9M	–	–
			$F_{2:3}$	–	–	–	–
	5S	bnl6.25	$F_{6:8}$	–	–	–	–
			$F_{2:3}$	–	3.8M	–	–
	5S	bnl5.02	$F_{6:8}$	–	–	–	–
			$F_{2:3}$	–	5.3H	–	–
	5L	bnl10.12-bnl5.40	$F_{6:8}$	–	5.6M,a	–	3.6M,b
			$F_{2:3}$	–	–	–	–
	5L	umc68	$F_{6:8}$	5.4M	3.6M	–	–
			$F_{2:3}$	–	–	–	–
	6C	npi235-phi077-umc65	$F_{6:8}$	3.3H,b	7.2H,b	7.5H,a	5.6H,b

Table 4 (continued)

Trait	Region	Nearest locus[a] (a-b-c-d)	Gen.	B91[b]	A632	B73	MTC
POL (GDD)		npi235-phi077-umc65	$F_{2:3}$	9.4H,c	–	7.3H,a	9.8H,c
	6L	umc21	$F_{6:8}$	–	–	7.2M	5.5M
			$F_{2:3}$	8.7M	–	10.1M	8.1M
	6L	npi280	$F_{6:8}$	–	5.3M	–	–
			$F_{2:3}$	–	–	–	–
	7C	isu86-isu145A-phi057-bnl15.40	$F_{6:8}$	8.5H,d	9.1H,d	6.2H,c	7.5H,c
			$F_{2:3}$	8.2H,d	12.8H,a	7.6H,b	7.8H,d
	7L	umc35-bnl8.44A	$F_{6:8}$	–	–	–	2.8H,a
			$F_{2:3}$	–	–	–	4.2H,b
	8L	umc103	$F_{6:8}$	–	–	3.5H	2.7H
			$F_{2:3}$	–	–	–	–
	8L	umc48-npi268	$F_{6:8}$	7.8H,a	–	–	3.8H,a
			$F_{2:3}$	7.1H,a	–	5.4H,b	6.1H,b
	8L	npi268	$F_{6:8}$	3.5M	–	–	–
			$F_{2:3}$	–	–	–	–
	9C	bnl3.06-phi065-umc153	$F_{6:8}$	5.5M,b	–	9.1M,b	6.2M,b
			$F_{2:3}$	–	8.2M,c	6.7M,a	4.0M,a
	9L	phi032-bnl8.17-umc29B	$F_{6:8}$	5.0M,a	8.3M,a	–	5.2M,b
			$F_{2:3}$	8.2M,c	–	5.1M,c	5.9M,c
	9L	bngl128	$F_{6:8}$	–	2.7H	–	3.2H
			$F_{2:3}$	–	–	–	–
	10S	phi059	$F_{6:8}$	–	5.6M	–	–
			$F_{2:3}$	–	–	–	–

[a] Loci which are nearest QTL LOD peaks in region are listed in map order.

[b] Upper case letter indicates the parental allele that increased the trait value (M = Mo17, H = H99). The lower case letter indicates the locus nearest the LOD peak with loci in a region referred to in alphabetical order. Within each region, QTL one-LOD support intervals overlap across testers and generations

sistent in rank across generations for POL. For B91, the QTL with the largest effect in the $F_{6:8}$ (1L, isu18) was not detected in the $F_{2:3}$, whereas the QTL with the largest effect in the $F_{2:3}$ (2L, umc4) was detected in the $F_{6:8}$ but had the smallest effect. For A632 and B73, the QTLs with the largest effects in one generation were always detected in the other generation; however, the relative rankings of their effects were not the same. Of the five traits, POL had the greatest number of common QTLs for MTC with 13 representing 76% of the $F_{2:3}$ QTLs for MTC. The $F_{2:3}$ MTC QTL with the largest effect on 6 C (phi077-umc65) was detected in the $F_{6:8}$ with the eighth largest effect. Likewise, the $F_{6:8}$ MTC QTL with the largest effect (1 S, umc164-npi234) was detected in the $F_{2:3}$ with the fourth largest effect. Despite the differences in rank, the common MTC QTLs included nine of the ten QTLs with the largest effects within each generation. One common MTC region (1C, isu81-npi429) had QTLs with opposite parental contributions, which could represent a cross-over type QTL×environment interaction. However, the QTL effects in this region were small with the eleventh and fourteenth largest effects in the $F_{6:8}$ and $F_{2:3}$, respectively. The other 12 common MTC QTL regions had the same parental contributions.

The number of SILK QTLs common to both generations ranged from three (A632) to eight (B73) representing 30 to 89% of the $F_{2:3}$ QTLs. Similar to POL, the regions with QTLs having the largest effects for SILK in one generation were nearly always detected in the other generation, but the relative magnitude of the effects differed. For MTC, the $F_{6:8}$ QTL with the largest effect (3L, umc26) was detected in the $F_{2:3}$ with the ninth largest effect, whereas the QTL with the largest effect in the $F_{2:3}$ (1L, npi236-phi039) had the eighth largest effect in the $F_{6:8}$. The common MTC QTLs included six ($F_{6:8}$) and seven ($F_{2:3}$) of the ten QTLs with the largest effects in each generation. In all instances of common tester and MTC QTLs for SILK, no evidence of crossover-type parental allele interaction was observed.

ASI, which displayed the lowest h^2 of the five traits, also had the fewest QTLs detected within each generation. In addition to the low QTL numbers for ASI, little consistency of QTL detection was observed across generations. Few QTLs were common between generations for B91 (0), A632 (1), and B73 (2). For B73, the two common QTLs (3L and 9S) had the same parental contributions across generations. For A632, the common region (5S, umc27-bnl5.02) had QTLs with opposite parental contributions in the two generations indicating a possible cross-over-type environmental interaction. The common MTC region on 3L (sh2) had the third largest effect in the $F_{6:8}$ and the largest in the $F_{2:3}$; however, the

QTL explained only 6% and 12% of the phenotypic variation in the $F_{6:8}$ and $F_{2:3}$ generations, respectively. ASI also displayed a low h^2 and a poor correspondence of QTL locations between the $F_{2:3}$ and $F_{6:7}$ generation inbred-progeny evaluations (Austin 1997).

Comparison of MTC and individual tester QTLs and their effects

QTLs for tester and/or MTC effects for PHT, EHT, POL, SILK and ASI were detected in 33, 31, 35, 33 and 27 genomic regions, respectively (Fig. 1). Over all five traits, 81% and 62% of the QTLs were represented in the $F_{6:8}$ and $F_{2:3}$ generations, respectively. Previous evaluations in this population reported that 58% of the QTLs for grain yield and 47% of the QTLs for grain moisture were associated with a single tester (Austin et al. 2000). Herein, the flowering traits displayed a similar trend, whereas PHT and EHT had a lower frequency of regions associated with a single tester. For the flowering traits, the number of QTLs with effects for a single tester ranged from 15 (POL) to 16 (SILK and ASI) representing 43 to 59% of the QTLs for each trait. Nine (27%) such regions were detected for PHT, and ten (32%) were detected for EHT. The population alleles at QTLs associated with effects for a single tester presumably have specific dominance interactions with the respective testers that do not occur with other tester loci. As previously reported by Ajmone-Marson et al. (1995), trait data averaged over multiple testers may decrease the significance of the LOD score when the QTL is detectable with only one of the testers. Thus, QTLs associated with a single tester would need to have a large effect to be of great significance for MTC variation. Herein, fewer than one-third (19 of 66) of QTLs associated with a single tester were also detected for MTC. In contrast, 83% (40 of 48) of QTLs associated with two testers were detected for MTC, and 100% (38 of 38) of QTLs associated with all three testers were detected for MTC. Single-tester QTLs also appear to be more environment specific. Nearly all (62 of 66) of the regions associated with a single tester were detected in one generation only. However, 43 of the single-tester QTL regions were unique to the $F_{6:8}$ generation, which had more QTL overall. Rather than environmental interaction, some of these could represent QTLs detected because of the increased precision and better map coverage of the $F_{6:8}$ generation.

For each trait, QTLs were identified with effects (either generation) for all three testers (Table 4; Austin 1997). PHT (9) and EHT (11) had the most QTLs associated with all three testers, whereas ASI had the fewest (2). These results are consistent with the phenotypic correlations among the hybrid progeny of the three testers which were greatest for EHT and lowest for ASI (Table 2). The regions controlling TC performance for the morphological traits appear to be much more consistent across testers in this population than for grain yield which had only one QTL associated with effects for all three testers and had poor correlation among testers (Austin et al. 2000). Similarly, Lübberstedt et al. (1997a) reported more consistent QTL detection across testers for PHT than for dry matter yield (50% of which is contributed by grain yield). Other hybrid progeny studies have also reported consistent QTL detection across tester populations for PHT (Schön et al. 1994; Ajmone-Marsan et al. 1995).

The relationship among testers did not appear to influence the consistency of QTL locations for the tester pairs. Although B73 and A632 are both stiff-stalk testers, ASI was the only trait that displayed more common QTLs for A632 and B73 (6) than for the other two pairs of unrelated testers (B91-A632, 5; B91-B73, 3). Summed over all five traits, A632 and B73 shared 45 QTLs, whereas more QTLs were common for pairs B91-A632 (52) and B91-B73 (47). However, QTLs were observed for PHT (9L, phi065-umc53), EHT (5S, umc72), and POL (1S, umc164-umc157-npi234) which had major QTL effects for A632 and B73 in both generations that were not associated with effects for B91. These QTLs could indicate an interaction of the population alleles with the stiff-stalk alleles of B73 and A632 that is consistent across environments (generations).

Regions associated with QTL effects for all three testers and MTC in both generations indicate stable QTL effects across testers and environments. For both PHT and EHT, the QTL on 1L (an2.6-phi011-isu18) had the largest effects for MTC in both generations. This QTL also had the largest effects for all EHT and four of six PHT generation-tester combinations. EHT had three additional regions (3L, bnl3.18-isu1-sh2; 7L, isu11-bnl8.39-isu103-bnl8.44A; 9C, bnl3.06-phi065-umc153) which contained QTLs for all three testers and MTC in both generations. One QTL for POL (7C, isu86-isu145A-phi057-bnl15.40) and two QTLs for SILK (1L, npi236-phi039-an2.6; 2L, umc4-bnl8.44B) were consistently detected across testers and generations; however, the relative rankings of effects were not as consistent as observed for PHT and EHT. As discussed previously, QTLs that were identified for a single tester were usually also detected in only one generation indicating possible environmental interactions as the $F_{2:3}$ and $F_{6:8}$ generations were evaluated in different years. Although rare, some QTLs with effects across testers also seemed to be unique to the environments of one generation. QTLs detected for all three testers and MTC in the $F_{6:8}$ generation were observed for EHT on 1L (npi236-phi039) and 9L (bngl128). These could be regions detected only in the $F_{6:8}$ generation because of the increased power of RI progeny; however, regions associated with effects for all three testers and MTC in the $F_{2:3}$ generation only were detected for EHT (8L, umc103-bnl9.44) and SILK (2L, umc131). More frequently, regions seemed to have consistent effects across generations for MTC, but detection of QTLs for individual tester effects varied across generations. For example, QTLs for PHT MTC effects were detected on 4L (php10025-umc111) and 6L (phi124-umc21) in both generations; however, effects at both QTLs were detected for B91 only in the $F_{2:3}$ and for A632 and B73 only in the $F_{6:8}$. Similar patterns were observed for other traits (Austin 1997) and for grain yield and moisture (Austin et al. 2000) in agreement with the observation of more consistent QTL detection across generations for MTC than individual tester effects.

Comparison of QTL locations across traits

PHT and EHT, which were highly correlated for MTC in both the $F_{2:3}$ (r_p=0.76) and $F_{6:8}$ (r_p=0.82) generations, had many common features. In the $F_{6:8}$ generation, 10 of the 18 regions with EHT QTLs for MTC also contained PHT QTLs for MTC effects (based on overlapping SI, Fig. 1). Similarly, 6 of 14 $F_{2:3}$ EHT QTL regions for MTC also contained QTLs for PHT. In all instances, the parental contributions were the same for both traits. Five regions (1L, 2S, 3L, 7L, 9C) contained QTLs for both traits in both generations. The QTL on 1L (an2.6-phi011-isu18) had the largest effect on MTC for both traits and generations. In this region, the QTL effect for PHT appears to be almost completely due to changes in EHT. The MTC substitution effects for PHT (from Mo17) were 7.5 cm ($F_{6:8}$) and 10.1 cm ($F_{2:3}$), whereas the substitution effects for EHT (from Mo17) were 7.1 cm ($F_{6:8}$) and 10.1 cm ($F_{2:3}$). This observation is in agreement with evaluations of $F_{6:7}$ inbred progeny from this population that showed some QTLs have an effect on EHT and PHT with no effect on height above the ear (Austin and Lee 1996a, Austin 1997). Other researchers have also observed corresponding regions for PHT and EHT (Beavis et al. 1991; Stuber et al. 1992).

POL and SILK, both measures of maturity, displayed the highest correlation for MTC effects in both the $F_{2:3}$ (r_p=0.85) and $F_{6:8}$ (r_p=0.94) generations. In the $F_{6:8}$ generation, 13 of 16 regions with MTC QTLs for SILK also contained QTLs for POL (based on overlapping SI, Fig. 1). Similarly in the $F_{2:3}$, 12 of 15 SILK MTC QTL regions also had QTLs for POL. Nine regions including 1L, 2L, 3L, 6C, 6L, 7C, 7L, 8L and 9C contained QTL for both traits and generations. Similar consistency of QTLs for these two traits was observed in inbred progeny evaluations of this population (Veldboom and Lee 1996b; Austin 1997).

QTL Detection in Inbred and Hybrid Progeny

Inbred progeny from this population were evaluated at the Ames location for plant height and flowering traits during the 1989 ($F_{2:3}$), 1990 ($F_{2:3}$), 1993 ($F_{6:7}$), and 1994 ($F_{6:7}$) growing seasons. All 185 of the $F_{6:8}$ lines and 150 of the $F_{2:3}$ lines evaluated herein for hybrid progeny were also evaluated in the inbred per se studies. For the $F_{6:8}$ generation, phenotypic correlations between mean inbred per se performance and MTC were highest for PHT and EHT, slightly lower for POL and SILK, and moderate for ASI (Table 3). Similar correlations were also observed for the $F_{2:3}$ generation (Veldboom 1994). The correlations for the morphological traits were greater than those observed for grain yield in the $F_{6:8}$ (r_p=0.19) and $F_{2:3}$ (r_p=0.20) generations (Austin et al. 2000). Loci commonly detected in inbreds and hybrid progeny may explain the higher correlation between the two progeny types observed for high-h^2 traits such as flowering compared to low-h^2 traits such as grain yield (Hallauer and Miranda 1988). QTLs detected in the mean environments of both the $F_{6:8}$ and $F_{2:3}$ inbred per se evaluations for PHT (5), EHT (6), POL (5), SILK (6) and ASI (4) were identified as regions conferring consistent, stable performance across diverse environmental conditions (Austin 1997). QTL detection methods and thresholds were consistent for the inbred and hybrid progeny evaluations. Over all five traits, 20 of the 26 (77%) consistent inbred-progeny QTL regions were also associated with MTC in at least one generation. In all instances of common inbred and hybrid QTL regions, parental contributions were consistent, with the same allele increasing trait values for both progeny types.

PHT had five regions including 1L (2 QTLs), 2L, 6L, and 7 C with consistent inbred per se QTL effects. The QTL on 1L (phi039-umc37) had the largest effect in both inbred progeny evaluations, explaining 23 ($F_{6:7}$) and 35 ($F_{2:3}$) percent of the phenotypic variation. This region was also detected for MTC in both generations, explaining 13 ($F_{6:8}$) and 7($F_{2:3}$) percent of the phenotypic variation. Approximately 25 cM distal of umc37, a second inbred per se QTL region was identified on 1L (phi011-isu6), explaining 16 ($F_{6:7}$) and 14 ($F_{2:3}$) percent of the phenotypic variation representing the second and third largest effects, respectively. This region had the largest MTC effects in both generations, explaining 30 ($F_{6:8}$) and 36 ($F_{2:3}$) percent of the phenotypic variation. Region 1L appears to have a major effect on PHT in several maize populations and progeny types (Beavis et al. 1991; Edwards et al. 1992; Stuber et al. 1992; Koester et al. 1993; Beavis et al. 1994; Schön et al. 1994; Ragot et al. 1995; Lübberstedt et al. 1997a). In two sorghum studies, QTLs with the largest effect on PHT have been identified in a region orthologous to maize 1L (Ahnert 1995; Periera and Lee 1995). Region 7 C was also detected in both generations for inbred per se and MTC performance, whereas the QTL detected with inbred progeny on 2L appears not to be associated with hybrid performance. Region 6L was detected for MTC only in the $F_{6:8}$ generation. EHT, which had the highest correlations between per se and MTC performance, had four regions (3L, 6C, 7C, 7L) which were consistent in the per se evaluations and were detected for MTC in both generations. Similar to PHT, the same two regions on 1L were associated with EHT variation. The proximal region (phi039-an2.6) had the largest ($F_{6:7}$) and second largest ($F_{2:3}$) inbred per se QTL effects. This region was only associated with MTC effects in the $F_{6:7}$ generation and had the thirteenth largest effect. The distal region on 1L (phi011-isu18) contained QTLs with the largest MTC effects. This region was detected in the $F_{6:7}$ per se evaluation with the third largest effect but was not detected in the $F_{2:3}$ generation. Region 1S was detected in both inbred progeny evaluations but was not associated with MTC effects.

Similar to the height traits, several of the flowering trait QTL regions with consistent inbred progeny effects were also associated with MTC effects. POL had the best agreement for QTLs controlling traits for the two progeny types with all five regions (1L, 4L, 6 C, 7 C, 9 C) with consistent inbred per se effects also being detected for MTC effects in both generations. QTLs on 6 C (npi235-phi077-umc65) had the most consistent relative rankings with the largest effects for $F_{6:7}$ inbred per se and $F_{2:3}$ MTC, the second largest effect for $F_{2:3}$ inbred per se, and the eighth largest effect for $F_{6:8}$ MTC. SILK had six QTLs (1L, 5 S, 5 S, 6 C, 6L, 7 C) with a consistent inbred progeny performance, and three regions (5 S, 5 S, 6L) appear to be unique to inbred per se performance. The QTL on 1L (npi236-phi039-umc37) had the most consistent relative rankings with the largest effects for $F_{2:3}$ per se and $F_{2:3}$ MTC, the ninth largest effect for $F_{6:7}$ per se, and the eighth largest effect for $F_{6:8}$ MTC. QTLs on 6 C and 7 C were also detected for MTC in both generations. Four regions (1L, 3L, 6L, 9 S) had consistent inbred per se QTL effects for ASI. Similar to SILK, region 6L appears to be unique to per se performance. Region 3L had the most consistent effects across progeny types with the largest effect for $F_{2:3}$ MTC, the second largest effect for $F_{6:7}$ per se, the third largest effect for $F_{6:8}$ MTC, and the sixth largest effect for $F_{2:3}$ per se. Regions 1L and 9 S, which had consistent inbred per se effects for ASI, were each detected in one generation for MTC.

The results reported herein indicate that regions with consistent QTL effects on morphological traits for inbred progeny per se are often also associated with consistent MTC effects; however, some regions appear to be unique to per se performance. Evaluations in this population found only partial agreement for grain yield (Austin et al. 2000) in accordance with observations for various traits from other studies (Guffey et al. 1988, 1989; Beavis et al., 1994; Schön et al. 1994; Groh et al. 1998; Kerns et al. 1999) that indicate only partial agreement between regions controlling inbred per se and hybrid performance. Herein, only those regions with consistent effects across two inbred progeny evaluations were compared to QTLs controlling MTC. The inbred per se QTL evaluations were conducted under diverse environmental conditions, which may explain the higher correspondence reported herein. The QTLs that were common to inbred per se and MTC effects were also frequently associated with effects for multiple testers. Of the 20 regions common for inbred per se and MTC effects, 14 were associated with effects for all three testers. These regions appear to have consistent effects across diverse environmental and genetic (tester alleles) environments.

Conclusions

Herein, QTLs controlling morphological traits were detected for three tester populations and for mean performance across testers (MTC). Choice of the appropriate tester remains a difficult issue among maize breeders (Hallauer 1990), and it may also be a difficult choice in mapping QTLs in hybrid populations. A previous evaluation of this population for grain yield revealed 58% of QTLs were associated with effects for a single tester. The flowering traits displayed similar frequency of single tester QTL, whereas PHT and EHT displayed lower frequencies. Regions containing QTL effects for a single tester appear to be less stable across environments (generations) and less likely to be detected for MTC than those associated with two to three testers. MTC effects, however, appear to be less sensitive to environmental factors with the majority of QTLs with the largest MTC effects being consistently detected across generations. Herein, QTLs for MTC were usually also detected for two to three testers. Based on the results reported herein, it would seem that the regions with major, consistent effects for individual testers are represented by the MTC QTL regions. Thus, selecting QTLs identified for MTC should improve a trait across diverse genetic (multiple testers) and environmental conditions.

Flowering and plant-stature traits generally have higher heritabilities and higher correlations between inbred and hybrid progeny than do traits such as grain yield (Hallauer and Miranda 1988). Regions with consistent morphological trait QTL effects for inbred progeny were often associated with consistent MTC effects as well. Parental contributions were also consistent across progeny types. The morphological traits which had higher heritabilities and higher correlations between progeny types than grain yield, had more QTLs consistently detected across generations, testers, and progeny type (inbred and hybrid). Based on the results for the traits in this study, a marker-assisted selection program could utilize regions with consistent effects across progeny types to simultaneously improve per se and hybrid performance for morphological traits.

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