Molecular studies for determination of quantitative trait loci for acid soil tolerance in maize

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Acid soils include approximately four billion hectares of the earth's surface. Soils with pH < 5.6, deficiency of calcium, magnesium, phosphorous, molybdenum, iron, and aluminum saturation > 35% with phosphorous level < 16 parts per billion are considered acidic for maize growth and production. Because of acid soils, fewer and smaller roots are produced, which reduces the maize plant's capacity to uptake water and nutrients from the soil. Objectives of the study were to develop a marker linkage map for a segregating F2 population derived from a cross of acid tolerant and acid susceptible lines to dissect the quantitative trait loci (QTLs) for several traits, and to determine if the QTLs could be used in a marker assisted selection program for acid tolerance in maize. Based on previous evaluation of 783 S4 yellow lines and 755 S_6 white lines, representing two heterotic groups, in normal-fertile and acid soils, six acid tolerant and six acid susceptible lines from the heterotic groups were selected. The 12 lines were evaluated as lines themselves in one normal-fertile and two acid soil environments. Based on the performance of the 12 lines, one acid tolerant line and one acid susceptible line were selected as the parental lines for this study. An F2 population of 221 individuals was genotyped for 118 simple sequence repeats (SSRs) and 214 S1 progenies were evaluated in an alpha lattice design (22 x 10) at five environments (three acidic and two normal fertile) in Colombia, SA. Data were collected for dates of male and female flowering, anthesis-silking interval, grain yield, ears per plant, and plant and ear heights. The genomic DNA isolation protocol was based on the method of Saghai-Maroof et al. (PNAS 81:8014-8018, 1984), and the details of SSR protocol were given by Hoisington et al. (2nd ed., CIMMYT, 1994). The linkage map was constructed using the computer program MapMaker/EXP 3.0. QTL detection was performed with complete interval mapping, a software program developed by Jiang (CIMMYT, 1998).

Average grain yield of 214 S1 progenies was 0.7 t ha^{-1} for the three acid soil locations, which was an 84.3% lower yield than the best normal-fertile soil location (4.5 t ha^{-1}). Acid soil environments tended to reduce the genetic variability among S1 progenies for all traits (Table 1). The average heritability estimate of grain yield, for example, was 2.2 times greater for the normal-fertile soil environments compared with the acid-soil environments; the differences in heritability estimates were similar for all traits. Phenotypic correlations between the seven traits were similar in magnitude and sign for both the acid soil and normal-fertile environments (Table 2). Correlations between days to pollen shed and silk emergence, between grain yield and ears per plant, and between plant and ear height had the largest positive correlations.

Table 1. Average broad-sense heritabilities (h^2) for 214 S1 progenies evaluated at three acid-soil and two normal-fertile soil environments evaluated in Colombia, SA.

Trait	Acid soils	Normal-fertile soils
	h^2*	h^2*
Date of male flowering, no.	0.22	0.68
Date of female flowering, no.	0.23	0.73
Anthesis-silking interval, no.	0.17	0.37
Grain yield, t ha^{-1}	0.32	0.71
Ears per plant, no.	0.31	0.52
Plant height, cm	0.18	0.68
Ear height, cm	0.10	0.48

*Broad-sense heritabilities calculated as $\sigma^2_g/(\sigma^2/re + \sigma^2_{ge}/e + \sigma^2_g)$, where σ^2_g is genetic variation among S1 progenies, σ^2_{ge} is interaction of S1 progenies with environments, σ^2 is experimental error, r is number of replications, and e is number of environments.

Table 2. Average phenotypic correlations between seven maize traits for 214 S1 progenies evaluated in three acid soils (below diagonal) and two normal-fertile (above diagonal) environments in Colombia, SA.

	Traits						
Traits[1]	Male	Female	ASI	Yield	Ears	Plant	EAR
Male	-----	0.78**	-0.38**	-0.31**	-0.17*	0.14	0.03
Female	0.80**	-----	0.28**	-0.28**	-0.20**	0.14	0.02
ASI	-0.18*	0.43**	-----	0.10	0.07	-0.03	-0.03
Yield	-0.33**	-0.47**	-0.29**	-----	0.49**	0.19**	0.12
Ears	-0.36**	-0.42**	-0.31**	0.67**	-----	0.24**	0.26**
Plant	-0.18*	-0.27**	-0.19**	0.36**	0.30**	-----	0.57**
Ear	-0.08	-0.17*	-0.17*	0.29**	0.24**	0.72**	-----

[1]Traits included days to pollen shed (Male) and silk emergence (Female), pollen-silk-interval (ASI), grain yield (Yield), ears per plant (Ears), and plant (Plant) and ear (Ear) heights.

There were 66 QTLs identified across each environment, based on the composite interval mapping analyses (CIM-model 4) with LOD = 2.5. Thirteen QTLs were detected for acid soils, 33 QTLs for normal-fertile soils and 40 QTLs for the combined across environments. No QTLs with major effects were identified. QTLs had low single and total R^2 values for individual environments and combined across the five environments. QTLs were estimated across the five environments (three acid and two normal) and the total phenotypic variance (R^2) explained across five environments was 10% and 7%, respectively, for days to male and female flowering, 1% for ASI, 3% for grain yield, 4% for ears per plant, and 4% and 15%, respectively, for plant and ear height. There were few QTLs common for single environments and combined across environments.

Ten QTLs were detected in all single environments for grain yield (Table 3). Single R^2 values ranged from 0.3% to 11% and the largest total R^2 was 19%. The main goal of the study was acid soils and grain yield, but 10% was the highest total R^2 value at acid environment 3 with a QTL on chromosomes 1 and 5. The complex acid soil environment showed that Al toxicity is important but Al toxicity is not the only factor affecting grain yields. Acid soils had significantly lower grain yields, greater genotype by environment interactions, and decreased genetic variability which affected QTL detection. No QTLs with major effects were identified.

Table 3. QTLs associated with grain yield expression at five environments.

Environment	Chromosome	QTL (cm)	SSR locus	LR score[1]	Additive[2] t ha^{-1}	Dominance[3] t ha^{-1}	R^2 %
Acid soils[4]							
1	1	103	*bmc1273*	13.3	0.05	-0.18	8
	2	96	*bnlg1887*	12.2	-0.15	0.00	0
2	1	181	*mmc0011*	16.4	-0.45	-0.30	2
3	1	137	*dup12*	13.0	0.03	0.10	5
	5	100	*bnlg2323*	12.4	-0.06	0.10	5
Combined	1	116	*bmc1273*	19.4	0.04	0.02	7
Normal soils							
1	2	2	*bmc1017*	11.9	-0.39	0.10	5
	5	79	*dup10*	13.3	-0.57	0.01	6
	6	19	*bngl1371*	15.8	-0.57	0.01	11
2	4	118	*umc1031*	12.6	0.27	0.10	5
	8	25	*bmc1067*	15.0	0.33	0.20	5
Combined	4	118	*umc1031*	18.9	0.23	0.17	2
	8	28	*bmc1067*	18.8	0.29	0.27	3

[1]LR scores > LR critical values at LOD = 2.5 by CIM-model 4. LR critical values were 11.5, 18.7, and 15.3 for single environments and combined across acid and normal-fertile environments.

[2]Substitution effect of "A" allele from tolerant parent for "B" allele of susceptible parent to either reduce (-) or increase (+) grain yield at this locus.

[3]Effect that mean of heterozygote is either less (-) or more (+) than the mean of homozygous parents at this locus.

[4]All saturation was 55% at environment 1 and 65% at environments 2 and 3.