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Additive, dominant, and epistatic effects for maize grain yield in acid and non-acid soils

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Abstract Acid soils severely reduce maize (*Zea mays* L.) yield in the tropics. Breeding for tolerance to soil acidity provides a permanent, environmentally friendly, and inexpensive solution to the problem. This study was carried out to determine the relative importance of additive, dominant, and epistatic effects on maize grain-yields in different tropical genotypes. Divergent selection in three populations (SA4, SA5, and SA7) provided inbred lines tolerant or sensitive to acid soils. The tolerant and sensitive lines from each population were used to obtain the F₁, F₂, F₃, back-crosses, second back-crosses, and selfed back-cross generations. In addition, the tolerant lines from SA4 and SA5 were crossed with a sensitive line from the Tuxpeño Sequía population, from which the same generations were also derived. All generations from each of the five sets of crosses were evaluated in three acid-soil environments and one non-acid-soil environment. A generation-mean analysis was performed on each set for yield. The sequential sum of squares associated with additive, dominance, and digenic epistatic effects were used to estimate the relative importance of each genetic effect. Epistasis was not important in any set in the non-acid-soil environment, with dominance accounting for 80.76% of the total variation among generation means across sets. In acid-soil environments, epistasis was more important. The relative importance of digenic epistasis was greater in those evaluations with large experimental errors. The tolerant line from population

SA5 was prone to severe root lodging, suggesting a very poor root system. Apparently, the tolerance to soil acidity in this line is not associated with a large root system.

Key words Acid soils · Tropical maize · *Zea mays* L. · Genetic components · Tolerance

Introduction

Acid soils (pH < 5.6) adversely affect maize yields mainly because of Al and Mn toxicities and Ca, Mg, and P deficiencies (Sanchez and Salinas 1981). Although maize is not tolerant to acid-soil conditions (Sanchez and Salinas 1981), more than 8 × 10³ ha of acid soils are planted with maize in the tropics (Duque-Vargas et al. 1994). Many of the problems associated with soil acidity can be corrected by using amendments such as lime. Liming, however, is not always economically feasible for farmers in developing countries (Pandey et al. 1994). Breeding for acid-soil tolerance is desirable because it is a permanent, environmentally friendly, and inexpensive solution to the problem (Foy 1976).

There is considerable genetic variability for tolerance to acid soils in maize which has allowed for considerable gains through recurrent selection (Lima et al. 1992; Granados et al. 1993; Ceballos et al. 1995). Rhue et al. (1978) and Miranda et al. (1984) reported qualitative inheritance of tolerance. More recent studies, on the other hand, suggested that tolerance is quantitatively inherited (Magnavaca et al. 1987; Sawasaki and Furlani 1987; Duque-Vargas et al. 1994; Pandey et al. 1994; Borrero et al. 1995; Salazar et al. 1997). Both additive and dominance variances play an important role in the expression of tolerance (Duque-Vargas et al. 1994; Magnavaca et al. 1987), and the additive × environment interaction also has a substantial effect (Duque-Vargas

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et al. 1994; Pandey et al. 1994). Reciprocal effects may also contribute to the inheritance of tolerance to acid soils. Campbell et al. (1994) found significant reciprocal effects for dry weight in a diallel study evaluating alfalfa cultivars in nutrient solutions. A cytoplasmic effect on different traits has been observed in maize, mainly associated with male sterility (Duvick 1965; Garwood et al. 1970). However, Salazar et al. (1997) found no evidence of significant maternal effects for the expression of several traits under acid soils.

Little information is available on the relative importance of epistatic effects in the expression of maize yield. Wolf and Hallauer (1977) found that epistatic effects on grain yield were more important in extreme environments (either higher- or lower-yield environments). The present study was carried out to provide information about the relative importance of additive, dominance, and epistatic effects on grain yield under acid- and non-acid-soil conditions.

Materials and methods

In 1990, a divergent selection scheme was initiated on three acid-soil-tolerant populations from CIMMYT (International Maize and Wheat Improvement Center): SA4, SA5, and SA7. These populations are adapted to the tropics and had been improved through full-sib, multi-location, recurrent selection (Pandey et al. 1995). The first two populations have yellow flint to semi-dent kernels, whereas the latter has white flint kernels. The highest- and lowest-yielding families, based on acid-soil evaluations, carried out in Carimagua, Villavicencio and/or Quilichao (see Table 1), were selected and selfed in a non-acid soils location at Palmira. By the end of 1993, a set of S_5 inbred lines, tolerant or sensitive to acid-soils, were available from each of the three populations. In the first semester of 1994, selected tolerant (P_T) and sensitive (P_S) lines from each population were crossed to obtain the three respective F_1 hybrids. In addition, the tolerant lines from populations SA4 and SA5 were also crossed with a sensitive S_6 line from the Tuxpeño Sequía (TXP) population, also from CIMMYT (Pandey et al. 1994). Thus, five F_1 hybrids were produced: SA4-T \times TXP (set 1); SA4-T \times SA4-S (set 2); SA5-T \times TXP (set 3); SA5-T \times SA5-S (set 4); and SA7-T \times SA7-S (set 5).

During the subsequent two semesters, the parental lines and the F_1 crosses from each of the five sets were planted, and pollinations made to obtain the following generations: back-cross to the tolerant ($F_1 \times P_T = B_T$) or sensitive parent ($F_1 \times P_S = B_S$); F_2 (F_1 selfed); F_3 (F_2 selfed); second back-cross to the tolerant ($B_T \times P_T = B_{TT}$) or sensitive parent ($B_S \times P_S = B_{SS}$); and selfed progeny of the back-cross to the tolerant ($B_{T\otimes}$) or sensitive parent ($B_{S\otimes}$). As many plants as possible were included to adequately sample the segregating populations. A balanced bulk of a mean number of 51 ears was used across the five sets to obtain the F_3 generation. The mean number of ears bulked to represent B_{TT} was 39 and for B_{SS} was 40. The selfed generations of the back-crosses ($B_{T\otimes}$ and $B_{S\otimes}$), in turn, were represented by a bulk of an average of 41 and 48 ears, respectively. When reciprocal crosses were available, they were bulked together. Because of a lack of an adequate number of ears, the second back-cross generations from sets 3 and 4 were not included in this study.

The 11 generations from sets 1, 2, and 5 and the nine generations from sets 3 and 4 were evaluated during 1996 in three acidic soils and one non-acidic, fertile, soil-environment (Table 1). A randomized complete block design with three (Villavicencio-1, Villavicencio-2, and Palmira), or two replications (Quilichao) in each environment was used. Trials were planted using a 5-m rows, spaced 75 cm apart.

Plots were overplanted and thinned to two plants per hill, to give a final plant density of approximately 53 000 plants ha^{-1} . Experimental units had a varying number of rows, depending on the genetic uniformity of each generation. For non-segregating generations (P_T , P_S , and F_1) the experimental unit contained only one row. Those for the F_2 or F_3 generations included four rows. First back-crosses (B_T and B_S) were represented by three rows per experimental unit, whereas the remaining generations (B_{TT} , B_{SS} , $B_{T\otimes}$, and $B_{S\otimes}$) had two rows. Border rows were planted on both sides of the parental genotypes.

Data were recorded for plant height (from soil surface to the tip of highest tassel branch), grain yield ($t ha^{-1}$), ears per plant (total number of ears harvested/total number of plants harvested), number of days from planting to 50% of plants with receptive silks, and percent root lodging (number of lodged plants/total number of plants harvested). Plots were hand-harvested and grain yield, adjusted to 15.5% moisture, was calculated. A grain:ear ratio of 80% was assumed. The arcsin $\sqrt{(\% \text{ root lodging})}$ transformation was used for statistical analyses of this trait.

Analysis of variance was first performed combined across locations and then, based on the significances of the genotype-by-environment interactions, individually on the Quilichao and Palmira data and combined across the two environments at Villavicencio. A quantitative generation-mean analysis for yield was also performed for each of the five sets. Mean yield for each generation, across replications within each location, was obtained and then fitted by weighted regression to the genetic model proposed by Hayman and Mather (1955) and further described by Mather and Jinks (1977).

The importance of additive, dominance, and epistatic effects was determined by analyzing the sequential sums of squares derived from the addition of each genetic effect in the model, including digenic epistatic effects. The relative importance of the gene-effect estimates was determined based on the ratio between the sequential sum of squares and the total sum of squares, after sequentially entering the different effects into the model (Allen and Cady 1982; Cukadar-Olmedo and Miller 1997).

Phenotypic and genetic correlation coefficients between traits were estimated by dividing the covariance components by the square root of the product of appropriate variance components (Falconer 1981). Variance and statistical significance of the genetic correlation coefficients were determined as suggested by Vencovsky and BARRIGA (1992).

Results

Locations, sets, and generations within sets differed for most of the variables evaluated (data not presented). A large difference was observed between the location with non-acidic soils (Palmira) and the remaining locations with acid soils. As reported earlier (Borrero et al. 1995; Ceballos et al. 1995; Salazar et al. 1997), plant height, yield, and the number of ears per plant are significantly reduced by soil acidity, whereas the number of days to 50% silking is increased (Table 1). No significant genotype-by-environment interaction was found for the two environments at Villavicencio. Therefore, statistical and genetic analyses were performed by pooling the data from these two environments.

The mean yield at Palmira (across sets and generations within sets) was 3.59 $t ha^{-1}$, whereas in acid-soil locations it was only 0.51 $t ha^{-1}$ (Table 1). High parent-heterosis in acid-soil locations ranged from 183 to 2960% for sets 1 and 5, respectively, and the mean was

Table 1 Mean response of 9 or 11 generations from the five sets evaluated at four different edaphic environments, during 1995. All environments are located in Colombia and, except for Palmira, have acid soils

| Environment | pH | Al sat. % | P ppm | Days-to-silk n | Plant height m | Yield t ha ⁻¹ | Ears/plant n | Root lodging % |
|-----------------|-----|-----------|-------|----------------|----------------|--------------------------|--------------|----------------|
| Villavicencio-1 | 4.6 | 50 | 10 | 71.8 | 1.05 | 0.50 | 0.51 | 15.8 |
| Villavicencio-2 | 4.6 | 65 | 10 | 68.9 | 1.08 | 0.51 | 0.45 | 11.8 |
| S. Quilichao | 4.9 | 65 | 10 | – | – | 0.52 | 0.48 | 17.6 |
| Palmira | 6.6 | < 1 | > 60 | 63.4 | 2.06 | 3.59 | 1.18 | 17.5 |

Table 2 Mean yield (t ha⁻¹) of different generations derived from five sets of crosses between maize inbred lines evaluated at three acid-soil locations (Villavicencio 1, Villavicencio 2, and Quilichao) and in one non-acid-soil location (Palmira), during 1995

| Generation | Across acid-soil locations | | | | | Palmira | | | | |
|---------------------|----------------------------|-------|-------|-------|-------|---------|-------|-------|-------|-------|
| | Set 1 | Set 2 | Set 3 | Set 4 | Set 5 | Set 1 | Set 2 | Set 3 | Set 4 | Set 5 |
| P _T | 0.41 | 0.59 | 0.39 | 0.22 | 0.05 | 2.98 | 3.41 | 2.23 | 1.74 | 1.90 |
| P _S | 0.14 | 0.10 | 0.21 | 0.15 | 0.02 | 2.21 | 0.65 | 2.01 | 0.91 | 1.62 |
| F ₁ | 1.16 | 1.87 | 1.37 | 0.91 | 1.53 | 8.68 | 7.73 | 7.27 | 4.24 | 9.35 |
| F ₂ | 0.86 | 0.61 | 0.44 | 0.36 | 0.72 | 4.66 | 3.88 | 3.54 | 2.29 | 4.62 |
| F ₃ | 0.36 | 0.38 | 0.27 | 0.28 | 0.41 | 3.79 | 2.64 | 2.61 | 1.98 | 3.21 |
| B _T | 0.90 | 0.85 | 0.69 | 0.31 | 0.98 | 5.32 | 5.51 | 4.30 | 3.41 | 4.71 |
| B _{TT} | 0.58 | 0.82 | – | – | 0.34 | 5.01 | 4.90 | – | – | 3.59 |
| B _T ⊗ | 0.59 | 0.46 | 0.28 | 0.40 | 0.48 | 3.78 | 3.50 | 3.02 | 1.59 | 2.98 |
| B _S | 0.67 | 0.45 | 0.38 | 0.17 | 0.60 | 4.84 | 3.31 | 4.59 | 2.38 | 5.16 |
| B _{SS} | 0.46 | 0.24 | – | – | 0.24 | 3.52 | 1.69 | – | – | 3.37 |
| B _S ⊗ | 0.34 | 0.27 | 0.27 | 0.15 | 0.35 | 3.49 | 2.06 | 2.59 | 1.49 | 2.88 |
| Mean | 0.63 | 0.60 | 0.48 | 0.31 | 0.49 | 4.39 | 3.57 | 3.57 | 2.23 | 3.94 |
| LSD _{0.05} | 0.20 | 0.35 | 0.22 | 0.21 | 0.22 | 0.78 | 0.68 | 0.82 | 0.66 | 1.14 |
| Heterosis (%) | 183 | 217 | 251 | 314 | 2960 | 191 | 127 | 226 | 144 | 392 |

785%. In Palmira, high parent-heterosis ranged from 127 (set 2) to 392% (set 5), with an average of 216% (Table 2). Set 5 always showed the highest heterosis, both because of the excellent performance of its F₁ generation and the very low yields of the two parents (particularly in acid-soil environments). The F₁ from this set yielded the highest at Palmira, and was the second highest-yielding across acid-soil locations (after the F₁ cross from set 2). Heterosis was higher in crosses between lines from the same population (sets 2 and 4) than in crosses between lines from different populations (sets 1 and 3) in acid-soil locations (266 vs 217%), but was lower at Palmira (136 vs 209%). As expected, the tolerant line from each set yielded more in acid-soil locations than the respective sensitive line (0.33 vs 0.12 t ha⁻¹). The same was true at Palmira, but relative differences were not as large (2.45 vs 1.50 t ha⁻¹).

The genetic analysis across the two Villavicencio environments, Quilichao and Palmira, indicated that a large proportion of the total sum of squares for yield was accounted for by the additive and dominance genetic effects (Table 3). In the case of the two Villavicencio environments, these values ranged from 60 to 97%, with a mean of 83%. In Quilichao, which presented a higher soil variability and a relatively larger experimental error, additivity and dominance accounted for

an average (across sets) of 57% of the total sum of squares, ranging from 16 to 93%. In Palmira, 91% of the total sum of squares for yield was due to additive and dominance effects alone across the five sets, ranging from 78 (Set 4) to 97% (set 1). The model adjusted very well for sets 1 and 5 (except for set 1 at Quilichao, which was planted in an extremely variable sector of the field), and moderately for the remaining sets. The significance of the different effects was evaluated by the lack-of-fit test (Allen and Cady 1982), which, in many instances, failed to reach statistical significance mainly because of the few degrees of freedom involved in each test.

Dominance played a very important role in every case, failing to reach statistical significance in several sets in the less-uniform location of Quilichao, which was also where only two replications were used. In the combined analysis for data from Villavicencio 1 and 2, additive, dominance, and epistatic effects, averaged across sets, accounted for 20, 63 and 15% of the total sum of squares, respectively. In Palmira the relative importance of dominance increased to account for 81% of the total sum of squares, whereas epistasis explained only 3%. The contrary was evident in the more variable location of Quilichao where dominance and epistasis explained 35 and 27% of the total variability for yield, respectively.

Table 3 Relative importance of additive, dominance, and digenic (additive \times additive, additive \times dominance, and dominance \times dominance) epistatic effects, measured as percent of total sum of squares accounted for by the respective genetic coefficients for grain yield. The coefficient of determination (R^2) corresponds to the model that includes only additive and dominance effects (excluding epistasis)

| Item | df | Set 1 | Set 2 | Set 3 | Set 4 | Set 5 | Mean |
|-----------------------------------|----|---------|---------|---------|---------|---------|-------|
| Villavicencio-1 + Villavicencio-2 | | | | | | | |
| Additive | 1 | 15.23* | 40.67* | 2.99 | 26.39* | 15.23 | 20.10 |
| Dominance | 1 | 78.97** | 39.84** | 80.15** | 33.94* | 81.49** | 62.88 |
| Epistasis | 3 | 5.02 | 16.70* | 16.21* | 32.82 | 1.87 | 14.52 |
| R ² | | 0.94 | 0.81 | 0.83 | 0.60 | 0.97 | |
| Quilichao | | | | | | | |
| Additive | 1 | 13.52 | 78.73** | 1.24 | 12.28 | 3.30* | 21.81 |
| Dominance | 1 | 3.05 | 7.70 | 38.36 | 36.89 | 89.43** | 35.09 |
| Epistasis | 3 | 50.56 | 3.34 | 39.74 | 39.39 | 4.17 | 27.44 |
| R ² | | 0.16 | 0.86 | 0.40 | 0.49 | 0.93 | |
| Palmira | | | | | | | |
| Additive | 1 | 1.96* | 43.85** | 0.60 | 4.09 | 1.38 | 10.38 |
| Dominance | 1 | 95.26** | 46.12** | 94.16** | 74.39** | 93.85** | 80.76 |
| Epistasis | 3 | 2.11 | 4.26 | 4.08 | 3.42 | 2.06 | 3.19 |
| R ² | | 0.97 | 0.90 | 0.95 | 0.78 | 0.95 | |
| Mean across locations | | | | | | | |
| Additive | 1 | 10.23 | 54.42 | 1.61 | 14.25 | 6.63 | 17.43 |
| Dominance | 1 | 59.09 | 31.22 | 70.89 | 48.41 | 88.26 | 59.58 |
| Epistasis | 3 | 19.23 | 8.10 | 20.01 | 25.21 | 2.70 | 15.05 |

*** Significant at the $P \leq 0.05$ or $P \leq 0.01$ probability level, respectively

It was observed that, the lower the experimental error of the trials, the higher the proportion of the total sum of squares accounted for by additive and dominance effects, and the lower the relative importance of epistasis. The correlation between the coefficient of variation of each trial and the magnitude of epistatic effects was 0.74 and highly significant ($P \leq 0.01$).

It was interesting to observe that the tolerant line from population SA5 (used as the tolerant parent in sets 3 and 4) was susceptible to root lodging (Table 4). Even in acid-soil environments, where plant height was severely reduced, this line showed a mean of 34.9 (set 3) or 41.6 (set 4) degrees (after using the arc-sin transformation) for root lodging. At Palmira the equivalent means were 43.2 (set 3) and 40.9 (set 4) degrees. The analysis of variance for this trait (data not shown) detected significant differences among the generation means for sets 2, 3 and 4.

Table 5 shows the phenotypic and genotypic correlations among different traits evaluated in the two soil environments at Villavicencio and Palmira. The only significant genetic correlations (based on entry means across sets) were between days-to-silk and plant height (-0.80) and prolificacy and yield (0.85), at the two Villavicencio locations, and grain yield and days-to-silk (-0.70) at Palmira. Significant phenotypic correlations were found at Villavicencio and Palmira between days-to-silk and plant height (-0.70 and -0.52); days-to-silk and yield (-0.55 and -0.68); plant height and yield (0.34 and 0.50); yield and prolificacy (0.83 and 0.39); and between yield and root lodging (-0.50 and -0.40). The phenotypic correlation between days-to-silk and lodging was significant only at Palmira

(0.37). Finally, a significant phenotypic correlation between prolificacy and root lodging was found at the two Villavicencio locations (-0.62) but not at Palmira.

Discussion

Our results suggest that yield in acid soils is not independent of that in non-acid soils. Phenotypic correlations between Palmira and acid-soil locations (based on the mean yield of the 51 genotypes involved in this study) were 0.653, 0.883, and 0.892 for Quilichao, Villavicencio-1, and Villavicencio-2, respectively (all significant at $P \leq 0.01$). These results agree with previous reports of positive correlations between yield at acid- and non-acid locations (Duque-Vargas et al. 1994; Borrero et al. 1995; Ceballos et al. 1995). During the divergent selection process, selected sensitive lines not only had a poor performance in acid soils but also gave a relatively high yield potential in non-acid-soil conditions. Similarly, tolerant lines were selected not only because of their outstanding performance in acid-soil environments but also because they were not particularly high yielding at non-acid locations. In spite of this selection criterion, tolerant lines yielded more than sensitive lines at Palmira, suggesting an association between high-yield performance in acid- and non-acid-soil locations, which the selection process was unable to break.

The inheritance of yield at Palmira showed a very high dependence on dominance effects which accounted for 81% of the total variability, with

Table 4 Percent root lodging (after arc-sin transformation) across acid-soil locations or at the non-acid-soil location of Palmira for different generations derived from the five crosses between maize inbred lines

| Generation | Across acid-soil locations | | | | | Palmira | | | | |
|---------------------|----------------------------|-------|-------|-------|-------|---------|-------|-------|-------|-------|
| | Set 1 | Set 2 | Set 3 | Set 4 | Set 5 | Set 1 | Set 2 | Set 3 | Set 4 | Set 5 |
| P _T | 15.3 | 19.0 | 34.9 | 41.6 | 22.7 | 6.0 | 15.8 | 43.2 | 40.9 | 4.4 |
| P _S | 18.6 | 24.2 | 21.0 | 33.6 | 13.0 | 14.3 | 36.1 | 25.5 | 20.8 | 7.8 |
| F ₁ | 7.0 | 8.0 | 13.8 | 32.7 | 5.7 | 13.4 | 10.0 | 21.8 | 44.8 | 7.6 |
| F ₂ | 14.3 | 17.4 | 18.7 | 30.1 | 16.8 | 15.1 | 21.7 | 33.6 | 42.1 | 9.5 |
| F ₃ | 19.7 | 21.4 | 23.2 | 34.8 | 16.5 | 14.2 | 18.0 | 24.2 | 40.0 | 11.8 |
| B _T | 10.7 | 14.1 | 24.7 | 34.9 | 14.5 | 14.2 | 12.9 | 38.3 | 42.3 | 9.6 |
| B _{TT} | 16.0 | 16.3 | – | – | 17.9 | 12.1 | 11.1 | – | – | 5.9 |
| B _T ⊗ | 15.1 | 21.0 | 26.4 | 41.4 | 20.7 | 7.5 | 15.6 | 31.1 | 44.6 | 4.3 |
| B _S | 12.3 | 10.4 | 14.3 | 28.7 | 17.6 | 23.7 | 20.6 | 26.0 | 35.5 | 15.9 |
| B _{SS} | 15.8 | 14.6 | – | – | 18.5 | 23.0 | 36.4 | – | – | 17.2 |
| B _S ⊗ | 10.9 | 16.2 | 19.1 | 33.1 | 22.3 | 21.9 | 25.1 | 20.3 | 32.8 | 21.1 |
| Mean | 14.2 | 16.6 | 17.8 | 34.5 | 16.9 | 15.0 | 20.3 | 24.0 | 31.3 | 10.5 |
| LSD _{0.05} | 7.5 | 7.1 | 7.5 | 10.0 | 7.1 | 14.1 | 13.1 | 10.2 | 12.4 | 13.3 |

Table 5 Phenotypic (above diagonal) and genotypic (below diagonal) correlation coefficients between maize traits evaluated at two acid-soil locations (Villavicencio) or in the non-acid-soil location of Palmira. Estimations based on entry mean at each location

| Variable | Days-to-silk | Plant height | Yield | Ears/plant | Root lodging |
|---------------|--------------|--------------|----------|------------|--------------|
| Days-to-silk | | | | | |
| Villavicencio | – | – 0.70** | – 0.55** | – 0.29* | – 0.07 |
| Palmira | – | – 0.52** | – 0.68** | – 0.12 | 0.37** |
| Plant height | | | | | |
| Villavicencio | – 0.80** | – | 0.34* | 0.12 | 0.06 |
| Palmira | – 0.55 | – | 0.50** | 0.06 | 0.16 |
| Yield | | | | | |
| Villavicencio | – 0.58 | 0.37 | – | 0.83** | – 0.50** |
| Palmira | – 0.70** | 0.54 | – | 0.39** | – 0.40** |
| Ears/plant | | | | | |
| Villavicencio | – 0.30 | 0.13 | 0.85** | – | – 0.62** |
| Palmira | – 0.14 | 0.06 | 0.39 | – | 0.06 |
| Root Lodg. | | | | | |
| Villavicencio | 0.10 | 0.06 | – 0.54 | – 0.67 | – |
| Palmira | 0.36 | 0.23 | – 0.43 | – 0.01 | – |

***Significant at the $P \leq 0.05$ or $P \leq 0.01$ probability level, respectively

epistasis having a small and non-significant influence on the final performance of different generations. These results agree with those from other studies for yield under highly productive environments as summarized by Hallauer and Miranda Fo (1988). On the other hand, Lamkey et al. (1995) found that unlinked additive-by-additive epistasis accounted for at least 21% of the variation among the testcross generation means derived from elite maize inbred lines. These authors suggested, however, that their results are evidence that breeding for high-yielding hybrids has resulted in the accumulation of favorable epistatic gene combinations in the B73 and B84 elite parental lines.

In acid-soil locations, dominance was not as important. Epistasis, on the other hand, could account for a higher proportion of the total variability (15 and 27% of the total sum of squares for Villavicencio and

Quilichao, respectively). Epistatic effects were significant ($P \leq 0.05$) for sets 3 and 4 in Villavicencio. The greater importance of epistasis in acid-soil locations may be due to genetic and/or physiological effects or because of the higher environmental variability found in acid-soils, which made the fitting on any theoretical model to the actual data more difficult.

The correlation between the coefficient of variation at each location and the proportion of the total sum of squares accounted for by epistatic effects was 0.74 and highly significant. The higher the relative importance of the experimental error, the higher the proportion of the total sum of squares accounted for by epistatic effects. In other words, large experimental errors seem to imply that additive and dominance effects will fail to explain a large proportion of the total variability observed, which can consequently be explained by the epistatic

effects. In Palmira, on the other hand, means were more precisely estimated. The fitting to the actual data by the simple additive/dominance model can be accomplished readily (91.14% of the total sum of squares), leaving a very small proportion of the total sum of squares to be explained by epistasis.

Mean yields at each acid-soil location were similar (Table 1), suggesting that the degree of stress caused by soil acidity was also similar at the three acid-soil environments. Therefore, the severity of stress does not seem to influence the relative importance of epistasis, which was twice as large in Quilichao compared with the two environments at Villavicencio.

The analysis of the genetic results from each individual set (Table 3) suggests that the relative importance of epistasis may also be genotype-dependent, in addition to its apparent relationship with the experimental error. For instance, epistasis in acid-soil environments in set 4 was consistently higher (32.82 and 39.39% for Villavicencio and Quilichao, respectively) than in set 5 (1.87 and 4.17% for the same locations, respectively).

As in many other studies (Hallauer and Miranda Fo 1988) the results from the present study about the relative importance of epistasis are not conclusive. In general, epistasis was found to have little influence on yield, particularly in non-acid-soil environments. But in certain genotype-environment combinations (such as sets 3 and 4 at both, Villavicencio and Quilichao, locations) epistasis played a more important role in determining final yield.

Tolerance to soil acidity can be explained by the capacity of genotypes to produce a large root system in spite of the edaphic constraints, such as the Al and Mn toxicity, commonly found in these soils (Magnavaca et al. 1987; Lima et al. 1992; Urrea-Gomez et al. 1996). It was, therefore, surprising to observe the strong susceptibility to root lodging of the tolerant line from sets 3 and 4 (Table 4), which would indicate that it does not develop a large root system in the environments tested. It is suggested, therefore, that tolerance to soil acidity, in the case of this line, does not depend on a large root system.

Pellet et al. (1995), found that citrate release was triggered by exposure to Al in nutrient solutions and was related to the tolerance in CIMMYT's maize population SA3. However, tolerant population SA3 also has a large root system compared with that of the sensitive Tuxpeño population (Urrea-Gomez et al. 1996). In other words, the chemical tolerance attained from the release of organic acids is pleiotropic or linked to the development of a large root system.

The line used as the tolerant parent in sets 3 and 4 has a tolerance to soil acidity which seems to be associated with a smaller root system (at least at harvest time). Therefore, this line should provide interesting material for studies on the physiological basis of tolerance to soil acidity in maize.

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