# RELATIVE IMPORTANCE OF GENERAL COMBINING ABILITY AND SPECIFIC COMBINING ABILITY AMONG TROPICAL MAIZE (*ZEA MAYS* L.) INBREDS UNDER CONTRASTING NITROGEN ENVIRONMENTS

**M. Worku[1], M. Bänziger[2], D. Friesen[3], G. Schulte auf'm Erley[4], W.J. Horst[4], B.S. Vivek[5],***

[1] *Bako Agricultural Research Center, P.O. Box 03, Bako, West Shoa, Oromia, Ethiopia*
[2] *CIMMYT-Kenya, P.O. Box 25171, Nairobi, Kenya*
[3] *CIMMYT-Ethiopia, P.O. Box 5689, Addis Ababa, Ethiopia*
[4] *Institute of Plant Nutrition, University of Hannover, Herrenhaeuser Str. 2, D 30419 Hannover, Germany*
[5] *CIMMYT-Zimbabwe, P.O. Box 163, Mount Pleasant, Harare, Zimbabwe*

**ABSTRACT** - Low-N stress is among the major abiotic stresses causing yield reductions in maize grown in the mid-altitude tropical environments of Africa. This study estimates the relative importance of general combining ability (GCA) and specific combining ability (SCA) in CIMMYT's tropical mid-altitude inbred lines under contrasting N environments. Six hundred and thirty five lines ($S_2$-$S_7$) were evaluated in different crossing designs (Diallels, North Carolina Design II and Line x Tester crosses). Results of experiments conducted under low and high N at the same site in adjacent fields with the same soil type within the same year and season from 1999-2003 were compared. The contribution of GCA to total genetic variation was higher than SCA for anthesis date, ear height and plant height under both high and low N levels. However, contribution of GCA was higher for grain yield only under high-N conditions. The average relative contribution of SCA, indicative of non-additive gene effects, to total genetic variation for grain yield under low-N accounted for 51% (average across all trials) but only for 36% under high-N. Pair-wise t-test for diallels and Design IIs showed significant difference (P<0.05) between the proportion of SCA sum of squares for grain yield under high and low N conditions. This implies that breeding strategies that increase grain yield under optimal (high N) conditions will not address the needs of a resource poor farmer producing maize under low N conditions, especially in sub-Saharan Africa. Targeted strategies that increase yield under low N conditions are thus required.

KEY WORDS: Diallel cross; GCA - general combining ability; Inbred lines; Maize; Nitrogen environments; N-stress; SCA - specific combining ability; *Zea mays* L.

## INTRODUCTION

Crop performance is a function of the genotype and the nature of the production environment (COOPER and BYTH, 1996). Genotypic differences for grain yield observed in the absence of stress are largely unrelated to differences observed in the presence of severe stress (BÄNZIGER *et al*., 1997; CECCARELLI, 1989; CECCARELLI and GRANDO, 1991; CECCARELLI *et al*., 1992; MOSISA, 2005). This may indicate that different physiological mechanisms are associated with high yield in favourable conditions and high yield in unfavourable conditions (BLUM, 1997; CECCARELLI, 1996). Variation for quantitative characters is under the control of many genes and the contribution of the genes can differ among environments (BASFORD and COOPER, 1998; DELACY *et al*., 1996; MESEKA *et al*., 2006). This conditional contribution of genes is the basis of genotype-by-environment (G x E) interactions.

Low-N stress is among the major abiotic stresses causing yield reductions in maize grown in the tropics (LAFITTE and EDMEADES, 1994; BECK *et al*., 1996; BÄNZIGER *et al*., 2000; BÄNZIGER and MEYER, 2002). Understanding the genetic basis of hybrid performance under this stress is crucial to the design of appropriate breeding strategies (HALLAUER and MIRANDA, 1988; BETRÁN *et al*., 2003a,b). Although improved N efficiency has been a desirable goal of maize breeders, the information available regarding the relative contribution of general combining ability (GCA) effects and specific combining ability (SCA) effects for different traits related to grain yield under low-N is limited (BELOW *et al*., 1997; DASS *et al*., 1997).

BELOW *et al*. (1997) evaluated hybrids from a diallel mating design under high and low N availabili-

---
* For correspondence (fax: +263-4-301327; e.mail: bvivek@cgiar.org).

ty (where low-N stress results in approximately 35% yield reduction) in a temperate environment and reported that the mean squares for general combining ability (GCA) and specific combining ability (SCA) were significant for all traits measured at both levels of N. They concluded that, based on the magnitude of the difference between GCA and SCA mean squares, the majority of the genetic effects were associated with GCA, indicative of additive genetic effects. KLING et al. (1997) conducted a diallel experiment in the tropical lowlands of West Africa for one season under high and low N conditions and reported that GCA for grain yield was significant under both N treatments while SCA was only significant under high-N. For ears per plant, GCA was significant only under low-N while SCA was significant under high-N.

However, non-additive gene effects under low-N were common in other studies. BETRAN et al. (2003a) evaluated diallel crosses under high-N and low-N for one season and reported that under low-N, non-additive genetic effects were more important for grain yield than the additive genetic effects. A significant crossover interaction was observed between the GCA of lines under low and high N conditions. Similar results were reported by LAFITTE and ED-MEADES (1995). BÄNZIGER et al. (1997) found that N stress severity influenced genotype-by-N stress inter-

actions. In addition to other environmental effects and type of families used, the contradictory results of different researchers may, therefore, be due to differences in the N stress level (testing environment) under which the genotypes were evaluated and/or genotypic difference among sets of genotypes included in the studies.

A detailed study of the relative importance of GCA effects and SCA effects under contrasting N environments is crucial to generate precise information and design breeding strategies that serve the interests of resource-poor farmers in the tropics, particularly in sub-Saharan Africa (BÄNZIGER et al., 2000). This study estimates the relative importance of GCA and SCA in several sets of CIMMYT tropical mid-altitude inbred lines under contrasting N environments.

## MATERIALS AND METHODS

### Germplasm, experimental site and trial management

Four different diallel (Griffing Method IV) trials (GRIFFING, 1956), two different North Carolina Design II (L x T) trials and eight different Line x Tester (L x T) trials (DHILLON and POLLMER, 1978; SINGH and CHAUDHARY, 1985; HALLAUER and MIRANDA, 1988) were conducted at CIMMYT-Zimbabwe between 1999 and 2003 and used for this study (Table 1). Experiments were conducted in Harare, Zimbabwe (17°49'S, 31°1'E and 1478 m above sea lev-

TABLE 1 - *Trials, mating designs and testing sites of the crosses used for the study (1999-2003).*

| Mating Design | No. of parents | Trial No. | Trial code | No. of entries | No. of reps | Field design | Year | Testing site | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | HHN | HLN | RAHN | RALN |
| Diallel | 7 | 1 | 99ELITESC | 144 | 2 | Alpha lattice | 1999 | x | x | | |
| | 9 | 2 | 01ELISC | 84 | 2 | Alpha lattice | 2001 | x | x | | |
| | 8 | 3 | VESB01 | 60 | 2 | Alpha lattice | 2001 | x | x | | |
| | 11 | 4 | VESA03 | 196 | 2 | Alpha lattice | 2003 | x | x | | |
| Design II | 7 x 7 | 5 | 99ELITESC | 144 | 2 | Alpha lattice | 1999 | x | x | | |
| | 15 x11 | 6 | 00ELISC | 192 | 2 | Alpha lattice | 2000 | x | x | | |
| | 15 x11 | 7 | 00ELISC | 192 | 2 | Alpha lattice | 2000 | | | x | x |
| Line x Tester | 103x3 | 8 | VETA01 | 316 | 1 | Augmented | 2001 | x | x | | |
| | 96x3 | 9 | VETB01 | 292 | 1 | Augmented | 2001 | x | x | | |
| | 26x3 | 10 | VETB02 | 180 | 2 | Alpha lattice | 2002 | x | x | | |
| | 83x2 | 11 | VETC02 | 170 | 2 | Alpha lattice | 2002 | x | x | | |
| | 69x2 | 12 | VETD02 | 165 | 2 | Alpha lattice | 2002 | x | x | | |
| | 68x2 | 13 | VETE02 | 156 | 2 | Alpha lattice | 2002 | x | x | | |
| | 52x2 | 14 | VETD03 | 108 | 2 | Alpha lattice | 2003 | x | x | | |
| | 67x2 | 15 | VETH03 | 140 | 2 | Alpha lattice | 2003 | x | x | | |

Note: CIMMYT-Zimbabwe. Harare high-N (HHN), Harare low-N (HLN), Rattray Arnold high-N (RAHN) and Rattray Arnold low-N (RALN).

el) at high-N (HHN) and low-N (HLN), and in Rattray Arnold, Zimbabwe (17°40'S, 31°1'E and 1308 m above sea level) at high-N (RAHN) and low-N (RALN) (Table 1). Alpha (0,1) lattice experimental designs with two replications (PATTERSON and WILLIAMS, 1976) were used for most of the trials while two trials in 2001 were evaluated using augmented designs (FEDERER, 1977).

All parental lines were CIMMYT experimental inbred lines of tropical mid-altitude adaptation which had been selected for agronomic performance including resistance to streak virus, turcicum leaf blight (*Exserohilum turcicum*), common rust (*Puccinia sorghi*) and grey leaf spot (*Cercospora zeae-maydis*) and other agronomic traits at CIMMYT-Zimbabwe. In total, 1707 crosses of 635 different inbred lines were used for the study (Table 1). All the lines included in the diallels and North Carolina Design II trials were fixed. The lines included in the different trials of Line x Tester were at $S_2$-$S_7$ stage and all the testers were genetically narrow based.

Experiments were conducted under low and high N conditions at the same site in adjacent fields with the same soil type within the same year and season. All management practices, including planting date, were applied uniformly under both N levels except nitrogen levels. Experiments under low-N conditions were planted in fields that had been depleted of N by growing unfertilized, non-leguminous crops for several seasons and removing the crop biomass after each season. No additional N fertilizer was applied for low-N experiments. Under high-N conditions, the recommended dosage of nitrogen (168 kg N ha$^{-1}$) was applied in splits at planting (28 kg N ha$^{-1}$), 30 and 50 days after planting (70 kg N ha$^{-1}$ each).

Plot size was 4 x 0.75 m with one row for each entry. Plant spacing was 0.25 m between plants, corresponding to 53,333 plants per hectare. To avoid border effects, the first and last plant of each row were not harvested. Phosphorus (142 kg $P_2O_5$ ha$^{-1}$) and potassium (32 kg K ha$^{-1}$) fertilizers were applied uniformly prior to planting. The experiments were conducted under rainfed conditions and were kept clean of weeds using herbicides (Atrazine, 4.5 litres ha$^{-1}$, and Dual, 1.8 litres ha$^{-1}$, 96% Metalchlor) and hand weeding.

### Measurements

Anthesis (AD) and silking (SD) dates were calculated as number of days from planting when 50% of the plants in the plot shed pollen and extruded silks, respectively. Anthesis-silking interval (ASI) was calculated as: ASI = SD - AD. Plant height (PH) was recorded from ground level to the insertion of the first tassel branch of the same plant. Ear height was measured from ground level to the insertion of the top ear of the same plant. The number of ears per plant (EPP) was equal to the number of ears with at least one fully developed grain divided by the number of harvested plants. An EPP of below 1.0 indicates partial barrenness (some plants within the plot had no ear) while an EPP of above 1.0 indicates partial prolificacy (some plants within the plot had more than one ear). Leaf senescence was rated on a scale of 1 (10% dead leaf area) to 10 (100% dead leaf area) during several stages of grain-filling. Grey leaf spot (*Cercospora zeae-maydis)* was assessed on a scale of 1 (clean, no infection) to 5 (severly diseased). The percentage of rotten ears was also recorded. The trials under high and low N conditions were harvested at the same time. All ears from the harvestable area were shelled, and grain weight recorded. Grain moisture percentage was recorded using DICKEY-john multi-grain moisture tester (Dickey-John Corporation, USA). Grain yield was adjusted to 12.5% grain moisture.

### Statistical analyses

Lattice-adjusted genotype means were calculated for each experiment using PROC MIXED procedures of SAS (2001) with genotypes considered as fixed effects and replicate and incomplete blocks within replicates considered as random factors. Adjusted means were used to estimate general combining ability (GCA) effects and specific combining ability (SCA) effects. The checks were excluded for genetic analysis. GRIFFING's (1956) Method 4 (exclusion of parents and reciprocal F1s), model I (fixed model for parental effects) for diallel analysis was used to estimate GCA and SCA effects of the lines and crosses, respectively in each environment (high and low N) for each diallel (BAKER, 1978; GRIFFING, 1956). For the diallels, the significance of GCA and SCA sources of variation in each N environment was determined using the error mean square (BETRÁN et al., 2003b). In the factorial crosses, the significance of line GCA mean squares (GCA (L)) and that of tester (GCA (T)) in each N environment was determined using the L x T interaction as the error term (SINGH and CHAUDHARY, 1985) The significance of the L x T interaction (SCA) was determined using the error mean square (DHILLON and POLLMER, 1978; SINGH and CHAUDHARY, 1985). Analyses of GCA and SCA effects in each environment (high and low N) in factorial crosses (Design II and L x T) were conducted using the procedures described in DHILLON and POLLMER (1978) and SINGH and CHAUDHARY (1985). Genetic analyses were computed using the SAS program (SAS, 2001).

The relative contribution of GCA vs. SCA to total genetic variation in the diallels was calculated as the ratio between sum of squares due to GCA or SCA and entry sums of squares (GCA + SCA sum of squares) (BAKER, 1978; BETRÁN et al., 2003a). Similarly, proportional contribution of lines (GCA (L)), testers (GCA (T)) and their interactions (SCA (L x T)) to entry sum of squares among the crosses, GCA (L) + GCA (T) + SCA (L x T) in the factorial crosses (Design II and Line x Tester) were calculated as the ratio between sum of squares of each component and entry sum of squares among the crosses (SINGH and CHAUDHARY, 1985). Pairwise t-test (for diallels and Design IIs) for the proportion of SCA sum of squares for grain yield under high and low N conditions was conducted.

## RESULTS

### Mean grain yield and low-N stress intensity

Mean trial yields under high-N (HN) varied from 5.40 Mg ha$^{-1}$ (Trial 10) to 8.9 Mg ha$^{-1}$ (Trial 4) at Harare in 2002 and 2003, respectively (Table 2). Under low-N, mean grain yields of the trials varied from 1.4 Mg ha$^{-1}$ (Trial 11) to 5.2 Mg ha$^{-1}$ (Trial 15), both at Harare (Table 2). Low-N stress reduced grain yield by 64% as compared to high-N conditions across all trials. The highest grain yield reduction was recorded in Trial 11 in 2002 and the lowest reduction was recorded in Trial 15 in 2003, both at Harare. The level of yield loss between low and high N varied depending on the degree of N depletion in different fields. Simple linear correlation coefficients (*r*) between grain yields under high and

TABLE 2 - *Mean trial grain yields under high-N (HN) and low-N (LN), percentage of low-N yield (LNGY) as compared to high-N yield (HNGY) and simple correlations (r) between HN and LN grain yields.*

| Trial No. | Mean grain yield, Mg ha$^{-1}$ | | LNGY as % of HNGY | r |
|---|---|---|---|---|
| | HN | LN | | |
| 1 | 6.3 | 3.4 | 54 | 0.29* |
| 2 | 7.6 | 2.2 | 29 | 0.12 |
| 3 | 6.6 | 2.1 | 31 | 0.45* |
| 4 | 8.9 | 3.3 | 37 | 0.31* |
| 5 | 6.3 | 3.4 | 54 | 0.29* |
| 6 | 7.0 | 2.5 | 35 | 0.24 |
| 7 | 8.1 | 2.1 | 26 | 0.22 |
| 8 | 6.8 | 2.1 | 31 | 0.09 |
| 9 | 7.2 | 2.1 | 30 | -0.01 |
| 10 | 5.4 | 1.7 | 31 | 0.04 |
| 11 | 8.1 | 1.4 | 17 | -0.03 |
| 12 | 5.8 | 1.7 | 29 | 0.19 |
| 13 | 8.5 | 2.9 | 34 | 0.08 |
| 14 | 8.7 | 2.5 | 29 | 0.23 |
| 15 | 7.3 | 5.2 | 71 | 0.07 |
| Mean | 7.2 | 2.6 | 36 | 0.17 |

*Significant at P < 0.05.

low N conditions at each site were not significant in most of the trials (mean *r* = 0.17) (Table 2) indicating that ranking and/or response of the genotypes were different under low and high N conditions. However, significant genotypic differences were observed under both N fertility environments at both sites in all trials included in this study (data not shown).

### GCA vs. SCA effects for grain yield

In all diallels, the GCA mean squares were significant under both high and low N conditions (Table 3) for grain yield. SCA mean squre was significant under high-N conditions in two out of four diallels. GCA mean squares for males (testers, T) in the three Design II experiments also showed significant differences under both N environments. GCA mean squares for the females (lines, L) were significant under both N levels except for Trial 6 in Harare at low-N in 2000 (Table 3). The mean square for L x T (SCA variation) was significant under high-N in all Design II experiments but it was significant under low-N only for Trial 7 at Rattray Arnold in 2000.

Line x Tester (L x T) crosses differed significantly for GCA mean squares of lines for four experiments

TABLE 3 - *Mean square for general combining ability (GCA) and specific combining ability (SCA) and percent sum of squares of GCA and SCA under high-N (HN) and low-N (LN) for grain yields for different diallel (Trials 1 to 4) and Design II (Trials 5 to 7) trials.*

| Trial No. | Source of variation | Mean square | | % Sum of squares | |
|---|---|---|---|---|---|
| | | HN | LN | HN | LN |
| 1 | GCA | 6.2** | 0.9$^+$ | 79 | 35 |
| | SCA | 0.7* | 0.7 | 21 | 65 |
| 2 | GCA | 12.4** | 0.5* | 80 | 33 |
| | SCA | 0.9 | 0.3* | 20 | 67 |
| 3 | GCA | 7.2** | 1.4** | 58 | 76 |
| | SCA | 1.8** | 0.2 | 42 | 24 |
| 4 | GCA | 3.3* | 0.6$^+$ | 42 | 27 |
| | SCA | 1.0 | 0.4 | 58 | 73 |
| Mean | GCA | | | 65 | 43 |
| | SCA | | | 35 | 57 |
| 5 | Line (L) | 5.8** | 2.3** | 39 | 30 |
| | Tester (T) | 3.9** | 2.0** | 26 | 27 |
| | L x T | 0.9** | 0.5 | 35 | 43 |
| 6 | Line (L) | 8.3** | 0.7 | 35 | 8 |
| | Tester (T) | 11.2** | 3.4** | 34 | 31 |
| | L x T | 0.7* | 0.5 | 31 | 61 |
| 7 | Line (L) | 14.7** | 1.1** | 30 | 24 |
| | Tester (T) | 30.1** | 1.2** | 44 | 18 |
| | L x T | 1.3** | 0.3** | 26 | 58 |
| Mean | Line (L) | | | 35 | 21 |
| | Tester (T) | | | 34 | 25 |
| | L x T | | | 31 | 54 |

$^+$, *, ** Significant at P < 0.1, 0.05 and 0.01, respectively.

under high-N (Trials 8 to 15) and five experiments under low-N conditions (Table 4). GCA mean squares for testers were significant for six experiments under high-N and seven experiments under low-N. The L x T (SCA effects) interactions were significant for five experiments under low-N conditions and two experiments under high-N conditions.

In addition, comparison of GCA sum of squares to SCA sum of squares under high and low N conditions revealed that GCA was more important than SCA for grain yield under high-N conditions. But the proportion of SCA sum of squares increased dramatically under low-N conditions in all diallels except in Trial 3 at Harare 2001 (Table 3). On average, GCA sum of squares explained 65% of varia-
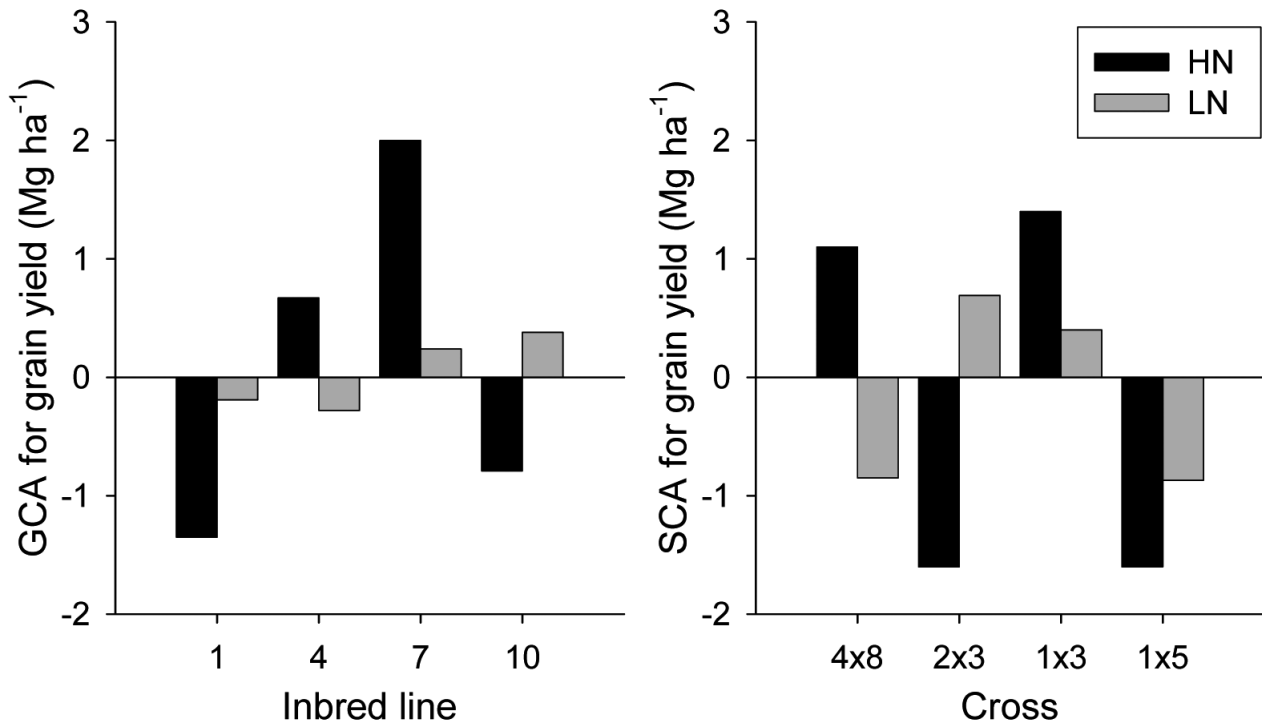
FIGURE 1 - (Left) GCA (Mg ha$^{-1}$) of selected inbred lines in Trial 6 and, (Right) SCA (Mg ha$^{-1}$) of selected crosses in Trial 2 under high and low N.

tion among crosses (GCA and SCA) under high-N conditions whereas it explained only 43% under low N conditions.

Similarly, the proportion of GCA sum of squares of females (L) and males (T) for grain yield was higher under high-N conditions than under low-N conditions in all Design II trials (Table 3). On average, SCA (L x T interaction) explained 54% of the total sum of squares among crosses (GCA (L) + GCA (T) + SCA (L x T)) under low-N conditions but

only 31% under high-N conditions. Similar trends were observed in all Line x Tester (L x T) crosses except in all L x T crosses of 2002 (Table 4). A pairwise t-test for diallels and Design II's showed a significant difference (P<0.05) between the proportion of SCA sum of squares for grain yield under high and low N conditions.

Some inbred lines had consistent GCA effects for grain yield under both N levels while others had opposing GCA effects under low and high-N (Fig-

TABLE 4 - *Mean squares and percent of general combining ability (GCA) and specific combining ability (SCA) sum of squares for grain yields for different Line x Tester (L x T) trials.*

| Source of variation | Trial | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 8 | | 9 | | 10 | | 11 | | 12 | | 13 | | 14 | | 15 | | Mean | |
| | HN | LN | HN | LN | HN | LN | HN | LN | HN | LN | HN | LN | HN | LN | HN | LN | HN | LN |
| Line (L) | 0.7* | 0.6** | 0.6* | 0.4 | 1.3 | 0.3* | - | 0.3** | 1.8 | 0.3** | 1.7 | 0.6 | 2.1$^{+}$ | 0.2 | 2.3** | 0.9$^{+}$ | - | - |
| Tester (T) | 33.4** | 3.7** | 28.3** | 2.6** | 3.3* | 2.6** | - | 1.1* | 5.7* | 0.6$^{+}$ | 0.3 | 0.9 | 16.8** | 2.6** | 4.6* | 8.3** | - | - |
| L x T | 0.5 | 0.4* | 0.4 | 0.4** | 1.0** | 0.2 | - | 0.2** | 1.4* | 0.2 | 1.5 | 0.5* | 1.4 | 0.2$^{+}$ | 1.1 | 0.6 | - | - |
| %GCA SS (L) | 30 | 43 | 29 | 35 | 37 | 37 | - | 61 | 55 | 63 | 54 | 57 | 55 | 48 | 67 | 54 | 47 | 50 |
| %GCA SS (T) | 29 | 5 | 29 | 5 | 7 | 22 | - | 3 | 3 | 2 | 0 | 1 | 9 | 10 | 2 | 8 | 11 | 7 |
| %SCA SS (L x T) | 41 | 52 | 42 | 60 | 56 | 41 | - | 36 | 42 | 35 | 46 | 42 | 36 | 42 | 31 | 38 | 42 | 43 |

$^{+}$, *, ** Significant at P < 0.1, 0.05 and 0.01, respectively.

TABLE 5 - *Simple correlation (r) between GCA of inbred lines under high-N (HN) vs. low-N (LN) at the same site (first three Diallels, 1, 2 and 3, and Design IIs, 5 and 6 at Harare; Design II, 7 at Rattray Arnold) and HN vs. HN and LN vs. LN at different sites (Harare vs. Rattray Arnold, 6 vs. 7).*

| Trial | GCA | r |
|-------|-----|---|
| 1 | HN vs. LN | 0.48 |
| 2 | HN vs. LN | -0.50 |
| 3 | HN vs. LN | 0.59 |
| 5 | GCA (Line) HN vs. LN | -0.24 |
| 6 | GCA (Line) HHN vs. HLN | 0.26 |
| 7 | GCA (Line) RHN vs. RLN | 0.00 |
| | Mean | 0.10 |
| 6 vs. 7 | GCA (Line) HHN vs. RHN | 0.82** |
| | GCA (Line) HLN vs. RLN | 0.61* |
| | Mean | 0.72 |

*, **, Significant at P < 0.05 and 0.01, respectively.

ure 1 Left). Similarly, some combinations had consistent SCA effects under both N levels while the SCA of others changed between low and high-N (Figure 1 Right). Simple linear correlation coefficients ($r$) indicated that there was a very low correlation (mean $r$ = 0.10) between GCA of inbred lines under high and low N conditions (diallels and Design II's). However, the correlation between GCA effects of lines at Rattray Arnold high N versus Harare high N and that of Rattray Arnold low N versus Harare low N were significant (mean $r$ = 0.72) (Trial 6 and 7, Design II, Table 5).

### GCA vs. SCA effects for secondary traits

Estimates of GCA mean squares for anthesis date (AD), ear height (EH), plant height (PH) and ear rot (ER) were significant in both N environments for all diallels (Table 6). SCA effects were only significant under both N conditions for plant height in Trial 1 and for AD in Trial 2. GCA and SCA effects were significant for grey leaf spot (GLS) under high-N in three diallels (where it was recorded) and GCA effect was significant for leaf senescence (LS) in all diallels under low-N (where it was recorded). Both GCA and SCA effects were significant for anthesis-silking interval (ASI) under both N levels in all diallels. GCA and SCA effects were also significant for ear per plant (EPP) in all diallels under high-N. Un-

der low-N, GCA for EPP was generally non-significant whereas SCA for EPP was significant only for Trial 2 (Table 6).

In Design II crosses GCA mean squares for females (L) and males (T) were significant for PH, EH, ER and AD under both N levels. GCA effects for GLS and LS were also significant (Table 6). The SCA effect for ASI was significant under low-N in Trial 6 at Harare and for EPP in the same Trial (Trial 7) at Rattray Arnold under low-N conditions.

For most of the secondary traits (AD, EH, PH, ER) the proportion of GCA sum of squares accounted for a higher percentage of the total sum of squares among crosses than SCA sum of squares in all diallels under both N environments implying that GCA effects were more important than SCA effects for these traits under both N environments (Table 7). Similar results were observed in all Design II trials. The relative importance of GCA was greater than SCA for AD, EH and PH under both N environments. The proportion of GCA was also higher than SCA for GLS under high-N and LS under low-N (where it was recorded) in all trials. However, SCA sums of squares explained the greater portion for ER than GCA sum of squares under low-N conditions in all design II trials (Table 7).

Comparison of GCA sum of squares with SCA sum of squares revealed that SCA was more important than GCA for EPP under low-N in all diallels and Design II trials. The percentages of SCA sum of squares were also higher than GCA sum of squares for ASI under low-N condition than under high-N condition in all diallels and Design II trials (Table 7).

### DISCUSSION

In this study, 635 CIMMYT tropical mid-altitude inbred lines developed over the years, including experimental inbred lines ($S_2$-$S_7$) and well tested CIMMYT Maize Lines (CMLs), were used in different groups of crosses. The inbred lines were developed from different CIMMYT populations and pools. Although intensive selection was practiced during the development of these inbred lines, a large sample of tropical maize germplasm was included in the study.

COOPER and BYTH (1996) argued that the association between quantitative characters measured in two separate environments is a function of the degree to which the same genes influence genetic variation in both environments. They further ex-

TABLE 6 - *Mean square for general combining ability (GCA) effects and specific combining ability (SCA) effects for anthesis-silking interval (ASI), ear per plant (EPP), leaf senescence (LS), anthesis date (AD), ear (EH) and plant (PH) heights, ear rot (ER) and grey leaf spot (GLS) in different diallel (1-4) and Design II (5-7) trials under high-N (HN) and low-N (LN).*

| Trial | Source of variation | ASI | | EPP | | LS | AD | | EH | | PH | | ER | | GLS |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | HN | LN | HN | LN | LN | HN | LN | HN | LN | HN | LN | HN | LN | HN |
| 1 | GCA | - | - | - | - | 7.8** | 38.2** | 43.8** | 934** | 204** | 1208** | 155+ | 473** | 70** | 1.7** |
| | SCA | - | - | - | - | 0.10 | 1.2 | 3.3* | 117* | 56 | 146* | 122+ | 15 | 20 | 0.5** |
| 2 | GCA | 3.1** | 11.1** | 0.04** | 0.01 | 0.3** | 28.6** | 59.3** | 1210** | 977** | 1945** | 1308** | 57** | 762** | 1.5** |
| | SCA | 0.7** | 3.9+ | 0.01** | 0.01** | 0.2* | 1.0** | 2.3** | 55 | 49 | 73** | 87+ | 13+ | 196 | 0.6** |
| 3 | GCA | 1.6** | 9.2** | - | - | 0.7** | 17.7** | 23.7** | 510** | 269** | 995** | 445** | 72** | 1102** | 1.6** |
| | SCA | 0.6** | 3.3* | - | - | 0.2* | 2.2** | 4.7** | 120** | 90** | 160** | 97 | 23 | 188+ | 0.1* |
| 4 | GCA | 2.2** | 10.1** | 0.04** | 0.01 | 1.0** | 15** | 32** | 591** | 462** | - | - | 46** | 35 | - |
| | SCA | 0.7 | 5.5** | 0.02* | 0.00 | 0.2* | 1.6 | 4.1** | 97** | 80+ | - | - | 15** | 30 | - |
| 5 | Line (L) | 1.7* | 1.3 | 0.02* | - | 0.5** | 44.4** | 92.2** | 1497** | 210** | 2231** | 448** | 372** | 45 | 1.3* |
| | Tester (T) | 3.3** | 5.61* | 0.04** | - | 0.9** | 26.7** | 57.6** | 764** | 255** | 663** | 349** | 112 | 23 | 1.0* |
| | L x T | 0.6 | 2.3 | 0.01 | - | 0.1 | 3.1** | 2.6* | 74 | 40 | 87 | 73 | 61** | 25** | 0.4** |
| 6 | Line (L) | 4.1** | 9.3 | 0.05** | 0.04** | 1.5** | 30.4** | 48.1** | 1809** | 644** | 1868** | 971** | 2022** | 202** | 4.9** |
| | Tester (T) | 10.2** | 24.1** | 0.05** | 0.04** | 1.4** | 68.8** | 76.8** | 2327** | 941** | 1793** | 684** | 918** | 157** | 3.9** |
| | L x T | 0.7** | 6.0** | 0.01** | 0.01 | 0.2 | 1.3** | 5.7 | 89* | 54* | 124 | 98** | 80** | 43 | 0.3** |
| 7 | Line (L) | - | 2.6* | 0.04** | 0.08** | - | - | 22.2** | 1628** | 416** | 1264** | 740** | 897** | 667** | - |
| | Tester (T) | - | 6.6** | 0.07** | 0.02 | - | - | 47.3** | 3543** | 570** | 2014** | 681** | 389** | 623** | - |
| | L x T | - | 1.5 | 0.01** | 0.02** | - | - | 2.1+ | 96** | 115** | 87** | 142 | 70** | 163* | - |

+, *, ** Significant at $P < 0.1$, 0.05 and 0.01, respectively.

plained that the greater the degree of genotype-by-environment interaction, the more dissimilar the genetic systems control the physiological processes confering adaptation to both environments. The ranking of maize genotypes also differed between low and high N conditions in this study, as reflected in low relationship ($r$) between grain yields of high-N and low-N (Table 2), implying that alleles controlling high grain yield under low-N conditions are at least partially different from those controlling high grain yield under high-N conditions. This confirms results reported by CECCARELLI *et al.* (1992) for barley and BÄNZIGER *et al.* (1997) for tropical maize. GALLAIS and HIREL (2004) also found that genetic variability in maize is expressed differently under high and low N conditions. They detected different Quantitative Trait Loci (QTL) for grain yield under high and low N conditions.

When an organism is subjected to environmental stress, its performance may depend on those genes that are stress responsive and stress adaptive (BLUM, 1997). DIALLO *et al.* (2003) reported a greater importance of SCA effects for maize grain yield under low-N conditions as compared to high-N conditions.

Our results confirm that, although GCA effects, indicative of additive gene effects, constitutively contributed to grain yield across high and low N conditions, the relative contribution of SCA effects, indicative of non-additive gene effects, was more important than GCA effects under low-N conditions. The contributions of GCA sum of squares were higher than SCA sum of squares only in the 2002 Line x Tester crosses. Severe drought occurred in southern Africa in 2002 and this might have influenced the results. In agreement with the present result, BETRAN *et al.* (2003a) reported that GCA effects are more important than SCA effects under drought conditions while SCA effects are more important than GCA effects under low N conditions.

The association (correlations) between GCA effects of inbred lines for grain yield under high-N at different sites (Harare, Trial 6 and Rattray Arnold, Trial 7) was stronger than the association between GCA effects of inbred lines under high and low N conditions at the same site. This may indicate genotype-by-N level interaction for GCA effects. This is in agreement with the results of BETRAN *et al.* (2003a) who reported a genotype-by-environment

TABLE 7 - *Proportion (%) of sum of squares for general combining ability (GCA) effects and specific combining ability (SCA) effects for anthesis-silking interval (ASI), ear per plant (EPP), leaf senescence (LS), anthesis date (AD), ear (EH) and plant (PH) heights, ear rot (ER) and grey leaf spot (GLS) in different diallel (1-4) and Design II (5-7) trials under high N (HN) and low N (LN).*

| Trial | Source of variation | ASI | | EPP | | LS | AD | | EH | | PH | | ER | | GLS |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | HN | LN | HN | LN | LN | HN | LN | HN | LN | HN | LN | HN | LN | HN |
| 1 | GCA | - | - | - | - | 69 | 93 | 85 | 77 | 61 | 78 | 35 | 93 | 60 | 58 |
| | SCA | - | - | - | - | 31 | 7 | 15 | 23 | 39 | 22 | 65 | 7 | 40 | 42 |
| 2 | GCA | 56 | 45 | 49 | 15 | 34 | 89 | 88 | 87 | 85 | 89 | 82 | 56 | 54 | 43 |
| | SCA | 44 | 55 | 51 | 85 | 66 | 11 | 12 | 13 | 15 | 11 | 18 | 44 | 46 | 57 |
| 3 | GCA | 49 | 49 | - | - | 57 | 74 | 64 | 60 | 51 | 69 | 62 | 53 | 67 | 84 |
| | SCA | 51 | 51 | - | - | 43 | 26 | 36 | 40 | 49 | 31 | 38 | 47 | 33 | 16 |
| 4 | GCA | 41 | 29 | 29 | 30 | 58 | 69 | 64 | 58 | 57 | - | - | 40 | 21 | - |
| | SCA | 59 | 71 | 71 | 70 | 42 | 31 | 36 | 42 | 43 | - | - | 60 | 79 | - |
| Mean | GCA | 49 | 41 | 39 | 23 | 55 | 81 | 75 | 71 | 64 | 79 | 60 | 61 | 51 | 62 |
| | SCA | 51 | 59 | 61 | 77 | 45 | 19 | 25 | 29 | 36 | 21 | 40 | 39 | 49 | 38 |
| 5 | GCA (L) | 20 | 6 | 18 | - | 28 | 50 | 55 | 56 | 30 | 65 | 37 | 44 | 21 | 27 |
| | GCA (T) | 37 | 27 | 44 | - | 52 | 29 | 35 | 28 | 36 | 20 | 28 | 13 | 10 | 22 |
| | SCA (LxT) | 44 | 67 | 38 | - | 20 | 21 | 10 | 16 | 34 | 15 | 35 | 43 | 69 | 51 |
| 6 | GCA (L) | 22 | 11 | 27 | 25 | 38 | 33 | 30 | 42 | 35 | 43 | 40 | 58 | 28 | 44 |
| | GCA (T) | 39 | 20 | 19 | 17 | 25 | 53 | 34 | 38 | 36 | 29 | 20 | 19 | 15 | 25 |
| | SCA (LxT) | 39 | 69 | 54 | 59 | 37 | 14 | 36 | 20 | 29 | 28 | 40 | 23 | 57 | 31 |
| 7 | GCA (L) | - | 12 | 21 | 28 | - | - | 29 | 32 | 21 | 36 | 28 | 48 | 24 | - |
| | GCA (T) | - | 21 | 26 | 5 | - | - | 44 | 49 | 21 | 40 | 18 | 15 | 16 | - |
| | SCA (LxT) | - | 68 | 53 | 67 | - | - | 27 | 19 | 58 | 24 | 54 | 37 | 59 | - |
| Mean | GCA (L) | 21 | 10 | 22 | 26 | 33 | 42 | 38 | 44 | 29 | 48 | 35 | 50 | 24 | 35 |
| | GCA (T) | 38 | 22 | 30 | 11 | 39 | 41 | 38 | 38 | 31 | 30 | 22 | 16 | 14 | 24 |
| | SCA (LxT) | 42 | 68 | 48 | 63 | 28 | 18 | 24 | 18 | 40 | 22 | 43 | 34 | 62 | 41 |

interaction for GCA effects of CIMMYT inbred lines. Crossover interactions were also observed for GCA effects of the inbred lines and SCA effects of the crosses. However, there were also some inbred lines and some specific hybrid combinations with consistent GCA and SCA effects across the N levels (Fig. 1) indicating that varieties / genotypes stable under low N conditions can be identified provided evaluations are done under the target stress. The evaluation of genotypes under optimum and stress conditions will enable the identification of genotypes with consistent performance across the environments (DASS *et al.*, 1997; MENKIR *et al.*, 2003).

The contribution of GCA effects was higher than SCA effects for most of the secondary traits under both high and low N conditions (Table 7) suggesting that selection for secondary traits could be carried out at an early stage of inbred line develop-

ment. This is in agreement with the results of Lafitte and Edmeades (1995) and BETRAN *et al*. (2003b) who indicated that inbred line performance *per se* for secondary traits could be predictive of hybrid performance for secondary traits across N fertility gradients. However, SCA effects were more important than GCA effects for EPP and ASI under low-N conditions, which is not consistent with the earlier report from BETRAN *et al*. (2003b). This may show the importance of evaluation of hybrid combinations under both high and low N conditions to identify hybrids with short ASI and higher EPP under low N conditions.

Genetic variability in N-uptake efficiency and N-utilization efficiency was reported in maize by different researchers (SATTELMACHER *et al.*, 1994; PRESTERL *et al.*, 2002). GALLAIS and HIREL (2004) also detected QTLs for these traits in maize genotypes

which explain the genetic variation in N efficiency. In this study genetic differences in N-uptake efficiency and N-utilization efficiency were not studied. This may indicate the importance of genetic study in tropical maize for these important traits in the future.

The results of different experiments in this study indicate that GCA effects for grain yield were more important than SCA effects under high-N conditions. LAMKEY and EDWARDS (1999) also reported that under temperate environments additive genetic variance for grain yield is usually two to four times larger than dominance variance for maize populations. However, in this study, under low-N conditions, the relative contribution of GCA effects to genetic variation observed among the progeny performance was less as compared to the SCA effects as found by MESEKA *et al*. (2006). As highlighted by LAFITTE and EDMEADES (1995), BÄNZIGER *et al*. (2000), and PRESTERL *et al*. (2003), the need to use sites with both managed low-N stress and optimum-N conditions to develop varieties targetted to resource-poor farmers in the tropical mid-altitude ecology who produce maize mainly under low-N conditions is further strengthened by this study. Integration of plant molecular biology with conventional maize breeding may also assist in developing N-efficient cultivars.

## REFERENCES

BAKER R.J., 1978  Issues in diallel analysis. Crop Sci. **18:** 533-536.

BÄNZIGER M., F.J. BETRÁN, H.R. LAFITTE, 1997  Efficiency of high-nitrogen selection environments for improving maize for low-nitrogen target environments. Crop Sci. **37:** 1103-1109.

BÄNZIGER M., G.O. EDMEADES, D. BECK, M. BELLON, 2000  Breeding for Drought and N Stress Tolerance in Maize: From Theory to Practice. CIMMYT, Mexico, D.F.

BÄNZIGER M., J.D. MEYER, 2002  Collaborative maize variety development for stress prone environments in Southern Africa Farmers, Scientists and Plant Breeding. pp. 269-296. CAB International, London.

BASFORD K.E., M. COOPER, 1998  Genotype-by-environment interactions and some considerations of their implications for wheat breeding in Australia. Aust. J. Agric. Res. **49:** 153-174.

BECK D.L., J. BETRAN, M. BÄNZIGER, G.O. EDMEADES, J.M. RIBAUT, M. WILLCOX, S.K. VASAL, A. ORTEGA, 1996  Progress in developing drought and low soil N tolerance in maize. pp. 85-111. *In:* D. Wilkinson (Ed.), Proc. 51st Annual Corn and Sorghum Research Conf., Chicago, 10-11 Dec. 1996. ASTA, Washington, DC.

BELOW F.E., P.S. BRANDAU, R.J. LAMBERT, R.H. TEYKER, 1997  Combining ability for nitrogen use in maize. pp. 316-319. *In:* G.O. Edmeades, M. Bänziger, H.R. Mickelson, C.B. Pena-Valdiva (Eds.), Developing Drought and Low N-Tolerant Maize. Proc. Symposium, March 25-29, 1996. CIMMYT, El Batan, Mexico. Mexico, D.F.: CIMMYT.

BETRÁN F.J., D. BECK, M. BÄNZIGER, G.O. EDMEADES, 2003a  Genetic analysis of inbred and hybrid grain yield under stress and non-stress environments in tropical maize. Crop Sci. **43:** 807-817.

BETRÁN F.J., D. BECK, M. BÄNZIGER, G.O. EDMEADES, 2003b  Secondary traits in parental inbreds and hybrids under stress and non-stress environments in tropical maize. Field Crops Res. **83:** 51-65.

BLUM A., 1997  Constitutive traits affecting plant performance under stress. pp. 131-135. *In:* G.O. Edmeades, M. Bänziger, H.R. Mickelson, C.B. Pena-Valdivia (Eds.), Developing Drought and Low-N Tolerant Maize. Proc. Symposium, 25-29 March 1996. Elbatan, Mexico, CIMMYT, Mexico, D.F.

CECCARELLI S., 1989  Wide adaptation: How wide? Euphytica **40:** 197-205.

CECCARELLI S., 1996  Adaptation to low /high input cultivation. Euphytica **92:** 203-214.

CECCARELLI S., S. GRANDO, 1991  Environment of selection and type of germplasm in barley breeding for low- yielding conditions. Euphytica **57:** 207-219.

CECCARELLI S., S. GRANDO, J. HAMBLIN, 1992  Relationship between barley grain yield measured in low and high yielding environments. Euphytica **64:** 49-58.

COOPER M., D.E. BYTH, 1996  Understanding plant adaptation to achieve systematic applied crop improvement: A fundamental challenge. pp. 5-23. CAB International and IRRI, UK.

DASS S., Y.P. DANG, A.K. DHAWAN, N.N. SINGH, S. KUMAR, 1997  Morho-physiological basis for breeding drought and low-N tolerant maize genotypes in India. pp. 106-111. *In:* G.O. Edmeades, M. Bänziger, H.R. Mickelson, C.B. Pena-Valdiva (Eds.), Developing Drought and Low N-Tolerant Maize. Proc. Symposium, March 25-29, 1996. CIMMYT, El Batan, Mexico. Mexico, D.F.

DeLACY I.H., K. BASFORD, M. COOPER, M. BULL, J.K. MacLAREN, 1996  Analysis of multienvironment trials-An historical perspective. pp. 39-124. *In:* M. Cooper, G.L. Hammer (Eds.), Plant adaptation and crop improvement, CAB International.

DHILLON B.S., W.G. POLLMER, 1978  Combining ability analysis of an experiment conducted in two contrasting environments. Medzin und Biologie **9:** 109-111.

DIALLO A.O., W. MUASYA, H.D. GROOTE, 2003  Combining ability of early maize inbred lines and yield responses of their single cross hybrids tested under drought, low N and optimum conditions. pp. 36-37. *In:* J. Conrad, D. Fox, K. Harrington, M. Listman (Eds.), Book of Abstracts: Arnel R. Hallauer Intl. Symposium on Plant Breeding, 17-22 August 2003. CIMMYT, Mexico City. Mexico, D.F.

FEDERER W.T., 1977  Experimental Design, Theory and Application. McMillan, New York.

GALLAIS A., B. HIREL, 2004  An approach to the genetics of nitrogen use efficiency in maize. J. Exp. Botany **55:** 295-306.

GRIFFING B., 1956 Concept of general and specific combining abilitiy in relation to diallel crossing system. Aust. J. Biol. Sci. **9:** 463-493.

HALLAUER A.R., J.B. MIRANDA, 1988 Quantitative genetics in maize breeding. 2nd ed. Iowa State University Press, Ames, USA.

KLING J.G., S.O. OIKEH, H.A. AKINTOYE, H.T. HEUBERGER, W.J. HORST, 1997 Potential for developing N use-efficient maize for low input agricultural systems inthe moist savannas of Africa. pp. 490-501. *In:* G.O. Edmeades, M. Bänziger, H.R. Mickelson, C.B. Peña-Valdivia (Eds.), Developing Drought and Low-N Tolerant Maize. CIMMYT, Mexico, D.F., El Batan, Mexico 25-29 March 1996.

LAFITTE H.R., G.O. EDMEADES, 1994 Improvement for tolerance to low soil nitrogen in tropical maize. III. Variation in yield across environments. Field Crops Res. **39:** 27-38.

LAFITTE H.R., G.O. EDMEADES, 1995 Association between traits in tropical maize inbred lines and their hybrids under high and low soil nitrogen. Maydica **40:** 259-267.

LAMKEY K.R., J.W. EDWARDS, 1999 Quantitative genetics of heterosis. pp. 31-48. *In:* J.G. Coors, S. Pandey (Eds.), The Genetics and Exploitation of Heterosis in crops. ASA, CSS, and SSSA, Madison, Wisconsin, USA.

MENKIR A., B. BADU-APRAKU, C. THE, A. ADEPOJU, 2003 Evaluation of heterotic patterns of IITA's lowland white maize inbre lines. Maydica **48:** 161-170.

MESEKA S.K., A. MENKIR, A.E.S. IBRAHIM, S.O. AJALA, 2006 Genetic analysis of performance of maize inbred lines selected for tolerance to drought under low nitrogen. Maydica **51:** 487-495.

MOSISA W., 2005 Genetic and Crop-Physiological basis of Nitrogen Efficiency in Tropical Maize: Field Studies-University of Hannover.

PATTERSON H.D., E.R. WILLIAMS, 1976 A new class of resolvable incomplete block designs. Biometrika **63:** 83-89.

PRESTERL T., S. GROH, M. LANDBECK, G. SEITZ, W.SCHMIDT, H.H. GEIGER, 2002 Nitrogen uptake and utilization efficiency of European maize hybrids developed under conditions of low and high nitrogen input. Plant Breed. Rev. **121:** 480-486.

PRESTERL T., G. SEITZ, M. LANDBECK, E.M. THIEMT, W. SCHMIDT, H.H. GEIGER, 2003 Improving nitrogen-use efficiency in European maize: Estimation of quantitative genetic parameters. Crop Sci. **43:** 1259-1265.

SAS, 2001 The SAS System for Windows, Release 8.02. SAS Institute, Inc., Cary, NC.

SATTELMACHER B., W.J. HORST, H.C. BECKER, 1994 Factors that contribute to genetic variation for nutrient efficiency of crop plants. Z. Pflanzenernahr. Bodenk. **157:** 215-224.

SINGH R.K., B.D. CHAUDHARY, 1985 Biometrical Methods in Quantitative Genetics Analysis. 2nd ed. Kalyani Publishers, New Delhi, India.