

## HETEROSIS AND COMBINING ABILITY AMONG CIMMYT'S MID-ALTITUDE EARLY TO INTERMEDIATE MATURING MAIZE (*ZEA MAYS* L.) POPULATIONS

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**ABSTRACT** - Maize is an important food crop in sub-Saharan Africa. There is an increasing demand for early maturing maize cultivars even though long-season maize cultivars yield more than early maturing cultivars under favourable conditions. This is because vast areas of maize are routinely affected by drought and low N fertility and early maturing maize cultivars offer more flexibility than full season cultivars for a farmer with respect to cultivation and food security. CIMMYT's early maturing maize program, which aims to supply seed to approximately 3 million hectares of maize area in east and southern Africa lacks adequate information on heterotic relationships of its germplasm. 190 crosses (generated from a diallel of eighteen populations and two within heterotic group single crosses) and their 20 parentals were evaluated for heterotic relationships at six locations in Zimbabwe (four optimal conditions of rainfall and fertilizers (but different agro-ecological regions / mega-environments), one managed low nitrogen environment and one managed drought environment). Three heterotic patterns were seen under stress while six heterotic patterns were seen under optimal conditions. P9 (CML312/CML442) expressed a consistent heterotic pattern across stress and non-stress environments thus justifying its continued use as a tester. Moving towards the use of multiple heterotic groups in the CIMMYT-Zimbabwe program may be worthwhile provided that the budgetary scenario still supports its core mandate of germplasm development, germplasm exchange and strengthening of national research systems.

**KEY WORDS:** Combining ability; Heterosis; Diallel; Open-pollinated variety; Maize.

### INTRODUCTION

Maize is an important food crop in sub-Saharan Africa providing 50% of the calories in diets in southern Africa, 30% in eastern Africa and 15% in

West and Central Africa. Many African countries frequently experience maize shortages and approximately a 100 million people are malnourished in this region. Average maize yield is 1.3 t ha<sup>-1</sup> (FAO statistics: [www.fao.org](http://www.fao.org)). CIMMYT (International Maize and Wheat Improvement Center) is involved in strengthening and augmenting plant-breeding efforts of various private sector and national programs in the fight for food security in the region. Some of CIMMYT's efforts are directed towards developing early-maturing maize germplasm (varieties that flower between 55 to 60 days, and reach physiological maturity at 120 days, after emergence, at Harare, Zimbabwe (1500 meters above sea level, latitude 17.48° South and longitude 31.05° East), in the main season) (CIMMYT-ZIMBABWE, 2000). In Eastern and Southern Africa, early maturing varieties are planted to an estimated total area of about 3.5 million ha which translates to a little over 3.5 million tons of grain annually capable of feeding 40.2 million people per year (average consumption -87 kg/person) (PINGALI, 2001). Farmers grow early maturing maize varieties because such varieties: (i) are ideal for off-season plantings in drying riverbeds; (ii) provide an early harvest to bridge the "hungry-season" before harvest of a full-season crop which is especially important in areas where there are two growing seasons; (iii) can be used to produce a crop during the secondary, short rains, which enables the plating of a full season maize crop or other crops in the following main season; (iv) are ideal for intercropping as they provide less competition for moisture, light, and nutrients than later maturing varieties (CIMMYT, 2000); (v) offer flexibility in planting dates (i.e. enables multiple plantings in a season to spread risk of losing a single crop to drought and enables late plantings during delayed onset of rainfall), and (vi) avoidance of terminal droughts at the end of a cropping season.

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Due to an increasing interest in hybrid maize seed production among national agricultural research programs and private seed companies in sub-Saharan Africa, CIMMYT-Zimbabwe has been conducting various activities related to hybrid development. To initiate hybrid development, information on the heterotic relationships among germplasm is essential to maximize their use for hybrid development. Several studies describing heterotic relationships in CIMMYT's Mexican early to intermediate maturing sub-tropical maize pools and populations have been reported (BECK *et al.*, 1991; VASAL *et al.*, 1992). The heterosis amongst this germplasm, identified through these studies, is being effectively exploited in CIMMYT's Mexico maize breeding programs and has led to the identification and release of several hybrids in Central and Latin America. However, the direct use of sub-tropical and tropical Mexican germplasm in Africa is hindered by one important consideration, lack of resistance to maize streak virus (MSV), an important disease in Africa not present in the Americas. Lack of resistance to MSV can cause a 100% loss of crop. Hence, a study of heterosis among early maturing southern African germplasm is necessary.

Initial germplasm development at CIMMYT-Zimbabwe centered around the conversion of elite Mexican germplasm to MSV resistance. The "A" heterotic group germplasm developed at CIMMYT-Zimbabwe is essentially conversions of the Mexican Tuxpeño germplasm to MSV resistance using N3 (a major heterotic pattern of sub-Saharan Africa thought to be heterotically similar to Tuxpeño) as the donor for MSV resistance. The "B" heterotic group germplasm developed at CIMMYT-Zimbabwe is essentially conversion of the Mexican ETO Blanco germplasm to MSV using SC (a major heterotic pattern of sub-Saharan Africa thought to be heterotically similar to ETO) as the donor for MSV resistance. Further development of the early maturing germplasm at CIMMYT-Zimbabwe has come through the introgression of popular open-pollinated varieties (OPVs) in eastern and southern Africa (e.g. Katumani) and the use of lowland tropical maize germplasm from CIMMYT in West Africa and IITA (International Institute of Tropical Agriculture). As a result of these efforts there has been a lot of germplasm introgression into CIMMYT germplasm from outside and within Africa. This necessitated a study of heterotic relationships among CIMMYT's Zimbabwe germplasm especially early to intermediate maturing maize germplasm, as the history of de-

velopment of early to intermediate maturing maize is relatively short compared to improvement of late maturing germplasm. Thus, the objectives of this study were to (i) determine the combining ability and heterotic patterns for grain yield and agronomic traits among early to intermediate maize populations in Zimbabwe and (ii) identify appropriate germplasm for hybrid development by CIMMYT and interested national programs.

## MATERIALS AND METHODS

Eighteen populations and two within-heterotic group single crosses (Table 1) were crossed in a diallel to give 190 crosses excluding reciprocals. The populations were early to intermediate in maturity with the Zimbabwean and IITA populations having resistance to MSV. The diallel crosses were made in the winter of 2003 at Muzarabani, Zimbabwe. Each cross was made using paired plots of 7 rows each and 4 m length ensuring that pollen from at least 100 plants were used to pollinate at least 100 plants in the female and vice versa. All possible 190 crosses were made in both directions, using bulk pollen. Seed of each cross and its reciprocal were bulked for use in the trials. Seed increase of the parents was done simultaneously in the same season using a minimum of 200 plants.

The 190 crosses and 20 parents were evaluated in the same trial in six environments during the summer of 2004 (optimal and managed low N) and winter of 2004 (managed drought). Site information (latitude, longitude, altitude, soil types and rainfall data) for the sites is given in Table 2. ART Farm, Kadoma, Matopos and Rattray-Arnold were under optimal conditions of fertilizers and moisture. The Chiredzi trial was planted during the dry season (winter) of 2004 while ART Farm, Harare CIMMYT station and Kadoma trials were planted during the summer of 2004. At the CIMMYT Station (Harare) the trial was grown under nitrogen stress while that at Chiredzi Research Station the trial was grown under drought stress. The Harare site with managed low nitrogen was a block depleted of nitrogen by growing summer maize and irrigated winter wheat continuously for six years. There was no nitrogen applied to the crop. The stress level achieved a mean average of 2.4 t ha<sup>-1</sup>. To see crossover effects, target yields for sites severely stressed for nitrogen should be between 2 and 3 tons ha<sup>-1</sup> (BOLAÑOS and EDMEADES, 1996). Drought was managed through controlled irrigation. A total of only 250 mm irrigation was applied to the crop in the first 50 days of planting. This regime caused severe drought stress at flowering and grain filling time. The average yield achieved at the site was 1.4 t ha<sup>-1</sup>. Target yields for sites severely drought stressed should be 1 to 2 t ha<sup>-1</sup> (BOLAÑOS and EDMEADES, 1996) to be able to detect cross-over effects due to the stress.

The experimental design used was an Alpha (0, 1) lattice with 2 replicates for each environment. The experimental unit was two 4-m rows spaced 75 cm apart. Two seeds were planted per station spaced 25 cm between and thinned to one plant for each planting station to give a final planting density of 53333 plants ha<sup>-1</sup>. Data was recorded for grain yield (GY) (shelled grain weight per plot adjusted to 12.5% grain moisture and converted to tons per hectare), anthesis date (AD) (number of days after planting when 50% of the plants shed pollen), silking date (SD)

TABLE 1 - *Germplasm description of 20 populations and open pollinated varieties from CIMMYT and IITA used in this study.*

| Parent | Pedigree               | Description  | Putative Heterotic Pattern |
|--------|------------------------|--|----------------------------|
| P1     | ZEWAc1F2               | Population formed by evaluating publically available early maturing lines from Eastern and Southern Africa. MSV resistant. Improved through reciprocal recurrent selection with its heterotic partner of ZEWBc1F2. | N3, Kitale, A, Tuxpeño     |
| P2     | ZEWBc1F2               | Population formed by evaluating publically available early maturing lines from Eastern and Southern Africa. MSV resistant. Improved through reciprocal recurrent selection with its heterotic partner of ZEWAc1F2. | SC, Ecuador, B, ETO        |
| P3     | P401c2                 | Sub-tropical early maturing streak susceptible population from CIMMYT-Mexico. Improved through reciprocal recurrent selection with its heterotic partner of P401.  | N3, Kitale, A, Tuxpeño     |
| P4     | P402c2                 | Sub-tropical early maturing streak susceptible population from CIMMYT-Mexico. Improved through reciprocal recurrent selection with its heterotic partner of P401.  | SC, Ecuador, B, ETO        |
| P5     | 99SADVEA-F2            | Population formed using abiotic (drought and low N) tolerant early to intermediate maturing lines from CIMMYT-Zimbabwe. Heterotic partner of 99SADVEB.   | N3, Kitale, A, Tuxpeño     |
| P6     | 99SADVEB-F2            | Population formed using abiotic (drought and low N) tolerant early to intermediate maturing lines from CIMMYT-Zimbabwe. Heterotic partner of 99SADVEA.   | SC, Ecuador, B, ETO        |
| P7     | ZM421FA                | Population formed using abiotic (drought and low N) tolerant early to intermediate maturing lines from CIMMYT-Zimbabwe. Heterotic partner of ZM421FB.  | N3, Kitale, A, Tuxpeño     |
| P8     | ZM421FB                | Population formed using abiotic (drought and low N) tolerant early to intermediate maturing lines from CIMMYT-Zimbabwe. Heterotic partner of ZM421FA.  | SC, Ecuador, B, ETO        |
| P9     | CML312/CML442          | Within heterotic group single cross of elite inbred lines being used as a tester in the CIMMYT-Zimbabwe breeding program.  | N3, Kitale, A, Tuxpeño     |
| P10    | CML395/CML444          | Within heterotic group single cross of elite inbred lines being used as a tester in the CIMMYT-Zimbabwe breeding program.  | SC, Ecuador, B, ETO        |
| P11    | ZM301c1F2              | An early maturing population from CIMMYT-Zimbabwe improved through intra-population selection.   | Unknown                    |
| P12    | ZM303c1                | An early maturing population from CIMMYT-Zimbabwe improved through intra-population selection.   | Unknown                    |
| P13    | Syn01E3                | Synthetic formed from tropical materials from Western Africa.  | Unknown                    |
| P14    | EEComposite            | Extra early streak susceptible composite from southern Africa  | Unknown                    |
| P15    | ECAEE16                | Extra early streak tolerant population from eastern Africa   | Unknown                    |
| P16    | CompNIP25              | Composite from the east African adapted population NIP25; streak tolerant  | Unknown                    |
| P17    | TZECComp3c3            | Population from IITA; streak resistant and tropical adaptation   | Unknown                    |
| P18    | AK95DMR-ESRW           | Population from IITA; streak resistant and tropical adaptation   | Unknown                    |
| P19    | Ac99TZECComp4DMRSR-BC2 | Population from IITA; streak resistant and tropical adaptation   | Unknown                    |
| P20    | ZM401                  | Synthetic formed from tropical Mexican lines and mid-altitude southern African lines; streak resistant.  | Unknown                    |

(number of days after planting when 50% of the plants extrude silk), anthesis silking interval (ASI) (SD - AD), ears per plant (EPP) (number of ears with at least one fully developed grain divided by the number of harvested plants), plant height (PH) (height between the base of a plant to the insertion of the first tassel branch of the same plant), ear height (EH) (height between the base of a plant to the insertion of the top ear of the

same plant), senescence (SEN) (leaf senescence score reported on scale from 1 to 10 taken during grain-filling by estimating the percentage of dead leaf area and dividing it by 10), husk cover (HC) (percentage of plants with ears that are not completely covered by the husks), grain texture (TEX) (rated on a scale from 1 (= flint) to 5 (= dent)), root lodging (RL) (percentage of plants that show root lodging, i.e. those stems that are inclining by

TABLE 2 - Locations in Zimbabwe used for evaluations.

| Location         | Altitude  | Latitude     | Longitude   | Rainfall (annual) | Management   |
|------------------|-----------|--------------|-------------|-------------------|--------------|
| ART-Farm, Harare | 1468 masl | 17°48' South | 31°05' East | 890 mm            | Optimal      |
| Kadoma           | 1155 masl | 18°32' South | 30°90' East | 727 mm            | Optimal      |
| Matopos          | 1370 masl | 20°24' South | 28°28' East | 604 mm            | Optimal      |
| Ratray-Arnold    | 1308 masl | 17°40' South | 31°05' East | 820 mm            | Optimal      |
| CIMMYT-Harare    | 1480 masl | 17°43' South | 31°05' East | 820 mm            | Low nitrogen |
| Chiredzi         | 433 masl  | 21°02' South | 31°58' East | 300 mm            | Drought      |

more than 45°), stem lodging (SL) (percentage of plants that show stem lodging, i.e. those stems that are broken below the ear) and moisture percentage in grain (MOI). Disease data was recorded for *Puccinia sorghii* (PS), *Exserohilum turcicum* (ET) and maize streak virus (MSV) measured as a score for the severity of common rust symptoms rated on a scale from 1 (= clean, no infection) to 5 (severely diseased). Number of ears rotten was recorded at harvest and ear rot (ER) was expressed as the percentage of rotten ears.

#### Statistical analysis

Analyses of variance were conducted for GY, AD, ASI, PH, EH, ear position (EPO) (ratio of ear height to plant height), RL, SL, EPP, HC, TEX, MOI, PS, ET, ER, MSV, SEN for each site and then averaged across significant sites (data not shown). Environments, reps and genotypes were considered random. Using plot data, Analysis III of GARDNER and EBERHART (1966) was done for GY. GARDNER and EBERHART (1966) model for the combining ability analysis is as follows:

$$X_{ijk} = \mu + g_i + g_j + s_{ij} + e_{ijk}$$

where  $x_{ijk}$  is the performance of the cross between the  $i^{\text{th}}$  and  $j^{\text{th}}$  genotypes in the  $k^{\text{th}}$  replication;  $\mu$  is the overall mean;  $g_i$  and  $g_j$  are GCA effects for the  $i^{\text{th}}$  and  $j^{\text{th}}$  parents, respectively;  $s_{ij}$  is the SCA effect for the cross between the  $i^{\text{th}}$  and  $j^{\text{th}}$  genotypes; and  $e_{ijk}$  is the error effect associated to the  $ijk^{\text{th}}$  observation. This model is similar to the one adopted by LONNQUIST and GARDNER (1961) to calculate combining ability estimates in intervarietal crosses in maize. GARDNER and EBERHART'S analysis III is considered superior to GRIFFING'S (1956) Model I, Method 2 analysis, especially when the parents are open-pollinated varieties or populations (GARDNER and EBERHART, 1966; SINGH, 1978). Orthogonal partitioning of the total entry variance by the least squares method was used to estimate the single degree of freedom comparison of parents vs. crosses, which is a test of average heterosis. Variation among crosses was further subdivided into that due to GCA and SCA.

The F-tests for the ANOVA were calculated as follows. Main effects, such as entries and its partitions, were tested against their respective interactions with environments, and the interaction with environment terms were tested against the pooled error. For example, mean squares for GCA was tested against the mean squares for GCA x environments and that for SCA against SCA x environments. Where the interaction with environment was non-significant, the main effects were tested using the residual. Heterosis (%) for grain yield was calculated over the high-parent values. High parent heterosis was calculated using the following formula (FEHR, 1987):

$$\text{High parent heterosis (\%)} = 100 * (F_1 - \text{HP})/\text{HP};$$

where  $F_1$  = performance of hybrid;  
HP = performance of best parent.

A biplot, based on a weighted SREG, was generated by weighting by the standard error of the site mean. Since some sites have more variance than others, a biplot generated by weighting by the standard error of the site mean adjusts for this variance and is hence a better estimate than an unweighted biplot. As this biplot revealed two groups of sites: Group 1 (Harare, Matopos and Chiredzi) and Group 2 (ART, Ratray and Kadoma) more biplots were constructed for Group 1 and Group 2 sites separately, using the mean grain yield across each of these groups to visualize relationships among parental OPVs in hybrid combinations and determine heterotic groupings. Two way data in rows and columns normally represent values for the trait in question for different sources of experimental variation (e.g. genotypes in row x environment in columns, or entry x tester). Rows and columns in diallel data are represented by parental entries which are both an entry and tester. Principal component scores (PC1 and PC2) were derived as described in YAN and HUNT (2002) using PROC PRINCOMP (SAS, 2001). PC1 and PC2 were used to construct the biplot. A polygon, connecting entries located farthest from the origin, was drawn. The polygon was divided into sectors by drawing perpendicular lines from the origin to each side of the polygon. All entries and testers included in the same sector represent potential heterotic patterns and hence the cross between a tester with its corresponding vertex entry is a potentially good hybrid. The best of such hybrids in a sector is defined by the cross of the tester located furthest from the origin with the vertex entry. The projection of the entry onto the vector of the tester or its extension is its SCA effect.

## RESULTS AND DISCUSSION

The biplot of weighted SREG, generated by weighting by the standard error of the site mean (Fig. 1) revealed two clusters of sites: Group 1 (G1) (where sites Chiredzi, CIMMYT-Harare and Matopos grouped together as they had positive PC1 and PC2) and Group 2 (where sites Kadoma, ART and Ratray grouped together as they had positive PC1 but slightly negative PC2). The grouping corresponds to the fact that Chiredzi, CIMMYT-Harare and Matopos were under stress (Chiredzi and CIMMYT-Harare

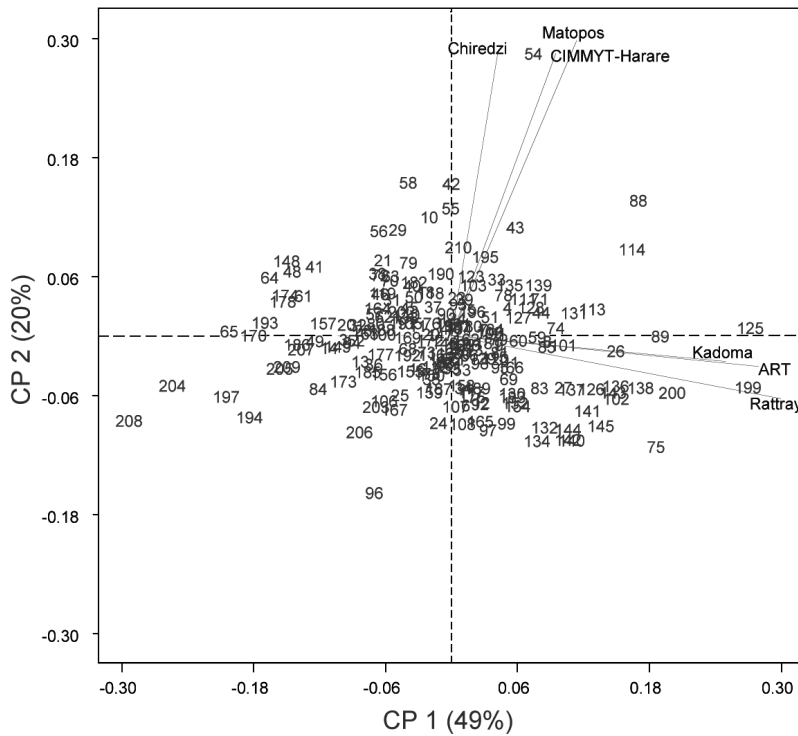


FIGURE 1 - Biplot for grain yield for 190 OPV crosses based on a weighted SREG, for six Zimbabwean environments. CP1: Principal component 1 (accounts for 49% of the variation), CP2: Principal Component 2 (accounts for 20% of the variation), numbers on the biplot are entry numbers of the hybrids.

were under managed stress and Matopos was under random drought stress). Trials at CIMMYT-Harare were grown in a block depleted of N, by continuously growing maize with no added N, while Chiredzi was under optimal fertilizer management but under managed drought, induced by stopping irrigation 6 weeks before flowering. Although Matopos was optimally managed with fertilizer, the rainfall in 2004 was scarce thus inducing a drought stress. Matopos falls within agro-ecological region IV of Zimbabwe where average annual rain fall is between 400 and 600 mm. Therefore the grouping of Matopos with the other managed stress sites was not surprising. The other sites (ART farm, Rattray and Kadoma) which were clustered in Group 2 (G2) were optimally managed, had adequate rainfall and were not under stress. ART Farm and Rattray fall within agro-ecological region II (with an average annual rainfall of 800-1000 mm) and Kadoma is in agro-ecological region III (with an average annual rainfall of 600-800 mm). These two major groups of environments do not seem to be related since the environment vectors of G1 sites were at a 90° angle to the environment vectors of G2 sites. Thus, the groups are reflective of trial management and conform to the existing agro-ecological classification. The repeatability of this grouping is consistent with other CIMMYT studies (WORKU *et al.*, 2008). Further,

a lack of site correlations implied that there was no correlation of genotype performance between these sites, an indication of cross-over effect of genotypes. Cross over performance of entries are seen only when the stress levels are around 30% of optimal (BÄNZIGER *et al.*, 2000). This implies that cultivars that performed well under optimal conditions are not necessarily the best performers under stress. Stress induced by drought and low N fertilizer use is widespread in southern Africa. Therefore selection under drought and low N is absolutely essential to ensure genetic gain and breeding progress under these widely experienced farmer constraints. However, to ensure stability of genotype performance across years and environments, evaluation under optimal conditions is also essential as there are farmers that do grow maize under optimal N conditions and there are years where rainfall is optimal. Therefore, at CIMMYT-Zimbabwe selection for stable genotypes is done by selecting across stress and optimal conditions using standardized measures like average rank, relative grain yield and selection indices.

Entry 54 (P3/P20 yielding 2.7 t ha<sup>-1</sup>) was very close to the tips of the environment vector joining the stress environments (G1) and had the highest SCA effect of 2.06 t ha<sup>-1</sup>. Entries 125 (P9/P10 - yielding 8.9 t ha<sup>-1</sup>) and 199 (P9 yielding 9.9 t ha<sup>-1</sup>) were

close to the tips of the environment vectors for G2 (ART, Rattray and Kadoma), therefore these entries were suitable for the optimal environments. Also entries 75, 89, 200 performed well in optimal environments with yields of 8.2, 7.9 and 8.7 t ha<sup>-1</sup>, respectively. Furthermore, entry 125 was close to being the ideal genotype, that is, its first principal component (which accounts for non cross-over interaction) was large and the second principal component (which accounts for cross-over interaction) was near 0. The parents for entry 125 are P9 and P10. P9 is a cross of CML312 with CML442 and P10 is a cross of CML395 and CML444. P9 and P10 are within heterotic group single cross testers representing heterotic groups A and B, respectively, being used in the program. The CIMMYT-Zimbabwe program handles two heterotic groups, A and B, which are aligned, respectively, similar to N3 and SC of southern Africa, Tuxpeño and ETO of Mexico, Kitale and Ecuador of Eastern Africa and B73 and Mo17 of the US Corn Belt. Any tester in a breeding program ought to be an “ideal” genotype in that it should have wide adaptation (i.e. stability across environments), possess good GCA and be able to discriminate among genotypes. The use of within heterotic group single-crosses as testers for early generation testing, as is being practiced in the CIMMYT-Zimbabwe program, has speeded up the process of hybrid identification. Since most of the hybrids in the region are 3-way crosses, single cross testers used in early generation testing help evaluate new inbred lines for combining abilities and simultaneously enable the identification of the final three-way hybrid. This study is in conformation with the worth of these single crosses as testers.

Entries 88 (P6/P9) and 114 (P8/P10) are equidistant from the stress and optimal sites are potentially stable across both stress and optimal sites. The ranks for entry 88 (with average rank 24 for grain yield is the best performer) and entry 114 (rank 45 for grain yield) also confirm this. P6 (99SADVEB-F2) (a parent of entry 88) is a drought tolerant OPV heterotic to P7 (99SADVEA-F2). The inter-population cross of 99SADVEA-F2 and 99SADVEB-F2 has performed very well in the region. P10 (CML395/CML444) (a parent of entry 114) is a B type single cross tester. Furthermore all the entries (208, 204, 197, 194, 206, 96, 84, etc.) on the lower-left quadrants do not perform well in any of the 6 environments used in this study as confirmed by their poor yield performance (not shown).

Due to the site similarity obtained by this biplot,

further analysis and interpretation of data was done for Group1 and Group 2 sites separately. This is because, small differences in grain yields under stress are masked by big differences of grain yield under optimal conditions as illustrated by the conceptual example in Table 3. Thus, grain yields should never be averaged across such diverse environments, such as in this study, but may be averaged only across similar environments. However to derive a measure of stable genotype performance across diverse environments one may use across site averages of standardized measures such as the rank of a genotype based on grain yield at each site (Table 3), entry grain yield relative to the mean of the trial (relative grain yield) at each site or an index appropriately weighted for each site and summed across sites.

TABLE 3 - Conceptual table explaining the utility of rank as a standard measure across stress and optimal sites.

| Variety  | Optimal                     |      | Stress                      |      | Average                     |      |
|----------|-----------------------------|------|-----------------------------|------|-----------------------------|------|
|          | Yield<br>t ha <sup>-1</sup> | Rank | Yield<br>t ha <sup>-1</sup> | Rank | Yield<br>t ha <sup>-1</sup> | Rank |
| <b>A</b> | 5                           | 1    | 1                           | 3    | 3                           | 2    |
| <b>B</b> | 3                           | 2    | 2                           | 1    | 2.5                         | 1.5  |
| <b>C</b> | 2                           | 3    | 1.5                         | 2    | 1.75                        | 2.5  |

TABLE 4 - Analysis of variance for yield of a 20-parent population diallel evaluated across 6 locations in Zimbabwe.

| Source                | G1=Stress Sites |          | G2=Optimal Sites |          |
|-----------------------|-----------------|----------|------------------|----------|
|                       | DF              | MS       | DF               | MS       |
| Env                   | 2               | 614.3 ** | 2                | 397.5 ** |
| Rep(Env)              | 3               | 2.4      | 3                | 33.0 **  |
| Entry                 | 209             | 2.8 **   | 209              | 6.6 **   |
| Parents               | 19              | 3.0 **   | 19               | 16.1 **  |
| Parents vs Crosses    | 1               | 14.2 *   | 1                | 71.6 **  |
| Crosses               | 189             | 2.7 **   | 189              | 5.2 **   |
| GCA                   | 19              | 5.2 **   | 19               | 36.1 **  |
| SCA                   | 170             | 2.4 **   | 170              | 1.8 *    |
| Env*Entry             | 418             | 1.5 *    | 418              | 1.5      |
| Parents * Env         | 38              | 0.9      | 38               | 2.1 *    |
| Parents-Crosses * Env | 2               | 0.7      | 2                | 1.8      |
| Crosses * Env         | 378             | 1.6 **   | 378              | 1.4      |
| GCA * Env             | 38              | 1.8 *    | 38               | 2.0      |
| SCA * Env             | 340             | 1.6 *    | 340              | 1.4      |
| Residual              | 611             | 1.3      | 620              | 1.5      |

Env: environment; rep: replications; \* P≤0.01, \*\* P≤0.05.

### **Group 1 (stress) sites**

Mean squares for yield were significant ( $p < 0.05$ ) for all sources of variation except for Reps(Env), Parents x Env, and Parents vs Crosses x Env which were non-significant (Table 4). The percent contribution of GCA and SCA sums of squares, respectively, to crosses sums of squares was 19.4% and 80.6%. This indicated that SCA (non-additive effects) was more important in determining the variation due to grain yield compared to GCA (additive effects) under stress. The test of average heterosis (Parents vs Crosses) was significant ( $p < 0.05$ ) and the contribution of heterosis sums of squares to the entry sums of squares to the entry sums of squares was only 2.4%. High parent heterosis ranged from -72.8 to 104.6% (Table 5). Entry 110 (P7/P18) had the highest heterosis of 104.6%. P7 (ZM421FA) is a southern African OPV of mid-altitude (sub-tropical) adaption and P18 (AK95DMR-ESRW) is of lowland tropical adaptation. Tropical x sub-tropical crosses have been known to give excellent heterosis and this is a case in point. P3 (P401c2) had the highest GCA effect ( $0.49 \text{ t ha}^{-1}$ ) followed by P8 (ZM421FB) ( $0.28 \text{ t ha}^{-1}$ ) and then by P5 (99SADVEA-F2) ( $0.27 \text{ t ha}^{-1}$ ). Entry 54 (P3/P20) had the highest SCA effect ( $4.6 \text{ t ha}^{-1}$ ). P6 and P9 (SCA  $1.03 \text{ t ha}^{-1}$ ) combine especially well under stress. This is the most stable combination with lowest average rank of 24. P8 had a GCA effect of  $0.28 \text{ t ha}^{-1}$ .

### **Group 2 (optimal) sites**

Mean squares for yield were significant ( $p < 0.05$ ) for all sources of variation except for Entry x Env which was non-significant (Table 3). The percent contribution of GCA and SCA sums of squares, respectively, to crosses sums of squares was 69.1% and 30.8%. This indicated that GCA (additive effects) was more important in determining the variation due to grain yield compared to SCA (non-additive effects) under optimal conditions. The test of average heterosis (Parents vs Crosses) was significant ( $p < 0.05$ ) and the contribution of heterosis sums of squares to the entry sums of squares to the entry sums of squares was 5.5%. Further, high parent heterosis ranged from -34.5% to 43.7%, which is quite low compared to other diallels with inbred lines (PSWARAYI and VIVEK, 2008). The parents in this diallel were broad-based open pollinated varieties (except for two within heterotic group single crosses) and heterosis amongst the OPVs would be expected to be lower compared to that of heterosis amongst inbred lines. Entry 111 (P7/P19) had the highest

heterosis of 43.7%. P7 (ZM421FA) is a southern African OPV of mid-altitude (sub-tropical) adaption and P19 (Ac99TZECComp4DMRSR-BC2) is of lowland tropical adaptation. This is another example where the highest heterosis seen is between a tropical x sub-tropical cross. Therefore such crosses should continue to be exploited in the program. It is interesting to note that P7 contributed to good heterosis both under stress and optimal conditions.

P10 (CML395/CML444) had the highest GCA effect ( $1.6 \text{ t ha}^{-1}$ ) followed by P9 (CML 312/CML442) ( $1.2 \text{ t ha}^{-1}$ ) and then by P16 (CompNIP25) ( $0.3 \text{ t ha}^{-1}$ ). The fact that P9 and P10 are within heterotic group single crosses may have given an upward bias to the GCA effects reported here. Entry 189 (P18/P20) had the highest SCA effect ( $4.3 \text{ t ha}^{-1}$ ). P6 had a GCA effect of  $0.2 \text{ t ha}^{-1}$  and SCA of  $0.4 \text{ t ha}^{-1}$ . The performance of a genotype depends on genes that are stress responsive and stress adaptive (BLUM, 1997) and hence the additive effects for yield are known to increase under drought stress compared to optimal environments (BETRÁN *et al.*, 2003a) while SCA effects are more important than GCA effects under low N conditions (BETRÁN *et al.*, 2003a; DIALLO *et al.*, 2003). The findings in this study contradict other studies perhaps because the germplasm under study were OPVs which were broad-based. Being elite and broad-based the OPVs had little complementation (heterosis) to offer under optimal conditions. While under stress, the lack of drought tolerance among some of the OPVs per se, may have improved their performance in combination with drought tolerant OPVs thus manifesting in higher specific combining ability than general combining ability. Heterosis under optimal conditions was lower than heterosis under stress, similar to the findings by BETRÁN *et al.* (2003b).

### **Heterotic relationships**

Biplots were constructed separately for sites of group 1 (Fig. 2) and sites of group 2 (Fig. 3) using the mean grain yield across each of these groups to visualize relationships among parental OPVs in hybrid combinations and determine heterotic groupings. PC1 for the biplot for stress sites explained 64% of the variation and PC2 explained 23% of the variation. PC1 for the biplot for optimal sites explained 62% of the variation and PC2 explained 25% of the variation. These biplots helped in graphic visualization of potentially good hybrid combinations. The biplot for stress suggested that P9/P20 (yield  $3.1 \text{ t ha}^{-1}$ ) and P2/P7 (yield  $2.7 \text{ t ha}^{-1}$ ) were very good hy-

TABLE 5 - Partial results (showing the top 30 hybrids based on average grain yield rank) for grain yield, GCA, SCA and heterosis of a 20 parent OPV diallel evaluated across 6 locations in Zimbabwe.

| Entry          | Name                          | G1 (Stress Sites) |    |               |            |            |              |              |              |                    |                    | G2 (Optimal Sites) |            |              |              |              |              |              |              |              |      |
|----------------|-------------------------------|-------------------|----|---------------|------------|------------|--------------|--------------|--------------|--------------------|--------------------|--------------------|------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|------|
|                |                               | Parent            |    | Across Stress |            | Heterosis  |              | SCA          |              | GCA                |                    | Across Optimal     |            | Heterosis    |              | SCA          |              | GCA          |              |              |      |
|                |                               | 1                 | 2  | Hybrid        | Parent     | 1          | 2            | Parent       | %            | t ha <sup>-1</sup> | t ha <sup>-1</sup> | 1                  | 2          | Parent       | High         | Parent       | 1            | 2            | Parent       | 1            | 2    |
| 88             | 99SADVEB-F2//CML312/CML442    | 6                 | 9  | 3.6           | 2.7        | 3.1        | 3.1          | 13.7         | 1.03         | -0.05              | 0.25               | 8.2                | 6.1        | 9.9          | -17.1        | 0.37         | 0.19         | 1.24         | 1.24         | 1.24         | 1.24 |
| 125            | CML395/CML444//CML312/CML442  | 9                 | 10 | 3.3           | 3.1        | 2.7        | 2.7          | 4.8          | 0.41         | 0.25               | -0.14              | 8.9                | 9.9        | 8.7          | -10.5        | -0.11        | 1.24         | 1.24         | 1.62         | 1.62         |      |
| 71             | 99SADVEA-F2/99SADVEB-F2       | 5                 | 6  | 3.6           | 2.7        | 2.7        | 34.3         | 0.48         | 0.27         | -0.05              | 7.8                | 6.7                | 6.1        | 17.5         | 0.75         | 0.05         | 0.19         | 0.19         | 0.19         | 0.19         |      |
| 44             | P401c2//CML395/CML444         | 3                 | 10 | 3.3           | 2.1        | 2.7        | 23.5         | 0.36         | 0.49         | -0.14              | 7.7                | 5.3                | 8.7        | -11.5        | -0.48        | -0.11        | 1.62         | 1.62         | 1.62         | 1.62         |      |
| 114            | ZM421FB//CML395/CML444        | 8                 | 10 | 2.8           | 2.7        | 2.7        | 4.2          | 0.32         | 0.28         | -0.14              | 8.1                | 6.1                | 8.7        | -7.9         | 0.45         | 0.04         | 1.62         | 1.62         | 1.62         | 1.62         |      |
| 139            | CML395/CML444//EEComposite    | 10                | 14 | 4.1           | 2.7        | 1.9        | 52.3         | 1.54         | -0.14        | -0.02              | 8.1                | 8.7                | 4.5        | -7.4         | 0.00         | 1.62         | -0.80        | -0.80        | -0.80        | -0.80        |      |
| 101            | ZM421FA//CML312/CML442        | 7                 | 9  | 3.4           | 1.3        | 3.1        | 8.1          | 0.30         | -0.04        | 0.25               | 8.0                | 5.2                | 9.9        | -19.7        | -0.23        | 0.05         | 1.24         | 1.24         | 1.24         | 1.24         |      |
| 128            | CML312/CML442//Syn01E3        | 9                 | 13 | 4.1           | 3.1        | 1.8        | 31.4         | 1.09         | 0.25         | -0.01              | 8.4                | 9.9                | 5.7        | -15.5        | -0.32        | 1.24         | -0.06        | -0.06        | -0.06        | -0.06        |      |
| 85             | Syn01E2/99SADVEA-F2           | 5                 | 20 | 3.6           | 2.7        | 3.7        | -3.0         | 0.36         | 0.27         | 0.17               | 8.1                | 6.7                | 7.2        | 11.6         | 0.65         | 0.05         | 0.24         | 0.24         | 0.24         | 0.24         |      |
| 135            | Syn01E2//CML312/CML442        | 9                 | 20 | 3.1           | 3.1        | 3.7        | -18.6        | 0.13         | 0.25         | 0.17               | 7.9                | 9.9                | 7.2        | -20.3        | -0.02        | 1.24         | 0.24         | 0.24         | 0.24         | 0.24         |      |
| 74             | 99SADVEA-F2//CML312/CML442    | 5                 | 9  | 4.1           | 2.7        | 3.1        | 29.6         | 0.12         | 0.27         | 0.25               | 8.8                | 6.7                | 9.9        | -10.8        | 0.19         | 0.05         | 1.24         | 1.24         | 1.24         | 1.24         |      |
| 136            | CML395/CML444//ZM301c1F2      | 10                | 11 | 2.9           | 2.7        | 2.6        | 7.4          | 0.15         | -0.14        | 0.11               | 8.3                | 8.7                | 5.9        | -4.9         | 0.50         | 1.62         | -0.21        | -0.21        | -0.21        | -0.21        |      |
| 43             | P401c2//CML312/CML442         | 3                 | 9  | 3.5           | 2.1        | 3.1        | 12.3         | 0.23         | 0.49         | 0.25               | 7.7                | 5.3                | 9.9        | -21.9        | -0.03        | -0.11        | 1.24         | 1.24         | 1.24         | 1.24         |      |
| 111            | Ac99TZEComp4DMRSR-BC2/ZM421FA | 7                 | 19 | 3.0           | 1.3        | 1.6        | 80.3         | 0.73         | -0.04        | -0.31              | 7.4                | 5.2                | 4.5        | 43.7         | 1.04         | 0.05         | -0.13        | -0.13        | -0.13        | -0.13        |      |
| 8              | ZEWac1F2//CML312/CML442       | 1                 | 9  | 2.9           | 2.4        | 3.1        | -7.7         | -0.04        | -0.11        | 0.25               | 7.7                | 6.2                | 9.9        | -22.8        | 0.05         | -0.12        | 1.24         | 1.24         | 1.24         | 1.24         |      |
| 113            | ZM421FB//CML312/CML442        | 8                 | 9  | 2.8           | 2.7        | 3.1        | -10.1        | -0.15        | 0.28         | 0.25               | 7.9                | 6.1                | 9.9        | -20.0        | 0.37         | 0.04         | 1.24         | 1.24         | 1.24         | 1.24         |      |
| 102            | ZM421FA//CML395/CML444        | 7                 | 10 | 2.6           | 1.3        | 2.7        | -2.5         | -0.10        | -0.04        | -0.14              | 8.1                | 5.2                | 8.7        | -6.9         | 0.37         | 0.05         | 1.62         | 1.62         | 1.62         | 1.62         |      |
| 26             | ZEWBc1F2//CML312/CML442       | 2                 | 9  | 2.7           | 2.4        | 3.1        | -14.8        | -0.03        | -0.11        | 0.25               | 8.1                | 6.1                | 9.9        | -18.0        | 0.81         | -0.21        | 1.24         | 1.24         | 1.24         | 1.24         |      |
| 89             | 99SADVEB-F2//CML395/CML444    | 6                 | 10 | 2.8           | 2.7        | 2.7        | 4.4          | 0.52         | -0.05        | -0.14              | 7.9                | 6.1                | 8.7        | -9.7         | -0.20        | 0.19         | 1.62         | 1.62         | 1.62         | 1.62         |      |
| 126            | CML312/CML442//ZM301c1F2      | 9                 | 11 | 2.8           | 3.1        | 2.6        | -11.8        | -0.42        | 0.25         | 0.11               | 7.8                | 9.9                | 5.9        | -21.2        | 0.37         | 1.24         | -0.21        | -0.21        | -0.21        | -0.21        |      |
| 59             | P402c2//CML312/CML442         | 4                 | 9  | 2.8           | 1.7        | 3.1        | -9.2         | -0.25        | 0.21         | 0.25               | 7.5                | 4.8                | 9.9        | -24.4        | 0.45         | -0.71        | 1.24         | 1.24         | 1.24         | 1.24         |      |
| 166            | TZEComp3c3/Syn01E3            | 13                | 17 | 3.3           | 1.8        | 2.6        | 26.6         | 0.60         | -0.01        | -0.30              | 7.6                | 5.7                | 5.6        | 33.5         | 0.82         | -0.06        | -0.13        | -0.13        | -0.13        | -0.13        |      |
| 78             | 99SADVEA-F2/Syn01E3           | 5                 | 13 | 3.3           | 2.7        | 1.8        | 20.0         | 0.52         | 0.27         | -0.01              | 7.0                | 6.7                | 5.7        | 5.2          | 0.10         | 0.05         | -0.06        | -0.06        | -0.06        | -0.06        |      |
| 138            | CML395/CML444//Syn01E3        | 10                | 13 | 2.6           | 2.7        | 1.8        | -3.9         | 0.05         | -0.14        | -0.01              | 8.0                | 8.7                | 5.7        | -8.7         | 0.21         | 1.62         | -0.06        | -0.06        | -0.06        | -0.06        |      |
| 10             | ZEWac1F2/ZM301c1F2            | 1                 | 11 | 3.6           | 2.4        | 2.6        | 39.9         | 0.83         | -0.11        | 0.11               | 6.8                | 6.2                | 5.9        | 9.7          | 0.03         | -0.12        | -0.21        | -0.21        | -0.21        | -0.21        |      |
| 103            | ZM421FA/ZM301c1F2             | 7                 | 11 | 3.4           | 1.3        | 2.6        | 33.9         | 0.73         | -0.04        | 0.11               | 7.3                | 5.2                | 5.9        | 23.7         | 0.22         | 0.05         | -0.21        | -0.21        | -0.21        | -0.21        |      |
| 75             | 99SADVEA-F2//CML395/CML444    | 5                 | 10 | 2.2           | 2.7        | 2.7        | -19.9        | -0.78        | 0.27         | -0.14              | 8.2                | 6.7                | 8.7        | -5.7         | 0.71         | 0.05         | 1.62         | 1.62         | 1.62         | 1.62         |      |
| 143            | AK95DMR-ESRW//CML395/CML444   | 10                | 18 | 2.5           | 2.7        | 1.0        | -7.8         | 0.14         | -0.14        | -0.26              | 7.9                | 8.7                | 3.7        | -9.1         | 0.27         | 1.62         | -0.16        | -0.16        | -0.16        | -0.16        |      |
| 55             | P402c2/99SADVEA-F2            | 4                 | 5  | 4.2           | 1.7        | 2.7        | 54.5         | 1.06         | 0.21         | 0.27               | 7.0                | 4.8                | 6.7        | 4.9          | 0.12         | -0.71        | 0.05         | 0.05         | 0.05         | 0.05         |      |
| 58             | P402c2/ZM421FB                | 4                 | 8  | 4.0           | 1.7        | 2.7        | 49.1         | 1.05         | 0.21         | 0.28               | 7.0                | 4.8                | 6.1        | 14.0         | 0.07         | -0.71        | 0.04         | 0.04         | 0.04         | 0.04         |      |
| <b>Average</b> |                               |                   |    | <b>2.7</b>    | <b>2.3</b> | <b>2.3</b> | <b>3.0</b>   | <b>0.01</b>  | <b>0.06</b>  | <b>-0.06</b>       | <b>6.7</b>         | <b>6.1</b>         | <b>5.8</b> | <b>2.5</b>   | <b>0.04</b>  | <b>0.01</b>  | <b>-0.01</b> | <b>-0.01</b> | <b>-0.01</b> | <b>-0.01</b> |      |
| <b>Min</b>     |                               |                   |    | <b>0.7</b>    | <b>1.0</b> | <b>1.0</b> | <b>-72.8</b> | <b>-1.56</b> | <b>-0.31</b> | <b>-0.31</b>       | <b>4.4</b>         | <b>3.7</b>         | <b>3.7</b> | <b>-34.5</b> | <b>-1.59</b> | <b>-0.80</b> | <b>-0.80</b> | <b>-0.80</b> | <b>-0.80</b> | <b>-0.80</b> |      |
| <b>Max</b>     |                               |                   |    | <b>4.2</b>    | <b>3.1</b> | <b>3.7</b> | <b>104.6</b> | <b>2.06</b>  | <b>0.49</b>  | <b>0.49</b>        | <b>8.9</b>         | <b>9.9</b>         | <b>9.9</b> | <b>43.7</b>  | <b>4.28</b>  | <b>1.62</b>  | <b>1.62</b>  | <b>1.62</b>  | <b>1.62</b>  | <b>1.62</b>  |      |





constitution of P9 and P10, compared to the remaining 18 entries, one might expect both these single crosses to consistently show distinct heterotic patterns. However, only P9 showed this discrimination. Inbred line CML312 was bred in Mexico for the subtropics but has proved to be very widely adapted with excellent combining ability thus featuring in many of the released hybrids even in the sub-Saharan African region. CML442 is an African bred inbred line and an excellent source of drought tolerance with good combining ability. CML312 and CML442 are both from heterotic group A and hence this within group cross, P9, has been used as a tester. Its consistent heterotic pattern across stress and non-stress justifies its use as a tester. The development of improved versions of the parents of P9 (CML312 for Maize Streak Virus resistance and CML442 for Turicum Leaf Blight resistance) is already underway. P19 (Ac99TZComp4DMRSR-BC2) and P18 (AK95DMR-ESRW) are populations from International Institute of Tropical Agriculture (IITA); streak resistant and having tropical adaptation. P12 (ZM303c1) is an early maturing population from CIMMYT-Zimbabwe improved through intra-population selection. P3 (P401c2) is a sub-tropical early maturing streak susceptible population from CIMMYT-Mexico and improved through reciprocal recurrent selection with its heterotic partner P402c2.

Yield and SCAs of the crosses of P1, P2, P5 and P6 with P9 and P10 were compared (Table 6). Under stress and optimum conditions crosses of P1, P2, P5 and P6 with P9 out yielded the crosses of P1, P2, P5 and P6 with P10. The SCAs of P2/P9 and P6/P9 were higher than that of P10 for both stress and optimum. This implied that P2 and P6 had the same heterotic pattern as P10 (i.e. were in the same group B) and were heterotic to P9 (group A). This was in confirmation with the knowledge and unpublished information within the program. Under stress P1/P9 ( $-0.04 \text{ t ha}^{-1}$ ) had lower SCA than P1/P10 ( $0.49 \text{ t ha}^{-1}$ ) thus exhibiting an A type heterotic pattern. However, under optimal conditions P1/P9 ( $0.1 \text{ t ha}^{-1}$ ) had lower SCA than P1/P10 ( $-0.8 \text{ t ha}^{-1}$ ) which showed a B heterotic pattern. Likewise, under stress P5/P9 ( $0.12 \text{ t ha}^{-1}$ ) had higher SCA than P5/P10 ( $-0.78 \text{ t ha}^{-1}$ ) showing a B heterotic pattern. Under optimal conditions P5/P9 ( $0.2 \text{ t ha}^{-1}$ ) had lower SCA than P5/P10 ( $0.7 \text{ t ha}^{-1}$ ) thus showing an A type heterotic pattern. Thus, P1 and P5 seemed to switch heterotic patterns under different conditions, perhaps suggesting a third type of heterotic pattern "AB" that was heterotic to both both A and B.

P1 and P2 were improved in a reciprocal recurrent selection scheme and are a representation of the most elite CIMMYT early germplasm of southern Africa. P5 and P6 represent an elite fraction of the early to intermediate germplasm in southern Africa. Lines derived from these populations have performed extremely well in combinations and synthetics from these have been released in several southern African countries. The popularity of these OPVs is a testimonial of the importance of this germplasm and hence understanding the heterotic patterns amongst P1, P2, P5, P6, P9 and P10 has big implications in efficiently channeling the resources in this germplasm development effort.

Heterotic groups are man-made. Hence their classification, use and exploitation are subjective and only relevant to the objectives, mandates and budgets available. While a powerful tool, lack of knowledge of heterotic groups should never be taken as a restrictive rule in germplasm development. The switching of the heterotic patterns of P1 and P5 between stress and non-stress sites is a case in point as P1 and P5 showed a more general discriminating ability rather than a specific one. In conclusion, P9 is a clear winner, with excellent discriminating ability under stress and optimum and is a distinct representative of heterotic group A. Further, the following patterns are suggested by this study and grouping and managing germplasm at CIMMYT-Zimbabwe should consider these patterns to better exploit the heterosis. P2 and P6 follow the heterotic pattern of P10 and fall into group B. A third pattern "AB" is shown by P1 and P5. A fourth group, P20, characterized by P20 is heterotic to group A. A fifth group, P7, characterized by the pattern of P7 is heterotic to B. The five others patterns suggested by the biplot for optimum sites needs to be further investigated.

The strategy of CIMMYT is to develop stable cultivars that perform well under both optimal and stress environments with the idea that in a year with optimal rainfall or in a situation where a farmer is able to access fertilizer the cultivar of choice would be as suitable in a drought hit year or for a farmer not having resources to buy fertilizer. While the maintenance and exploitation of multiple heterotic groups might prove beneficial it has cost and personnel implications. Germplasm development and exchange and training are the core mandates of CIMMYT. Several private companies in the region have been maintaining multiple heterotic groups and successfully exploiting the heterosis amongst them. In light of the findings in this study, a review

of CIMMYT-Zimbabwe's breeding model with respect to heterotic groups, keeping in mind budgetary constraints and commitments to its other mandates, would be a worthwhile exercise for the long term.

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