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Combining Ability and Heterosis in Corn (Zea mays L.) Grain Quality and Yield Traits under Different Plant Densities

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Authors' contributions

This work was carried out in collaboration between all authors. Author AMMAN designed the study, wrote the protocol and wrote the first draft of the manuscript. Authors MMMA and MAA managed the literature searches. Author ASMY managed the experimental process and performed data analyses. All authors read and approved the final manuscript.

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Original Research Article

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ABSTRACT

The objective of this study was to assess mean performance, heterosis and combining ability and their interrelationships in six maize inbreds and their 15 diallel F_1 crosses under elevated plant density (D). Three experiments were carried out in each season of 2013 and 2014, using RCBD with 3 replicates; each experiment was assigned to either low-D, medium-D or high-D (47,000, 71,200 and 95,200 plants/ha, respectively). Specific combining ability (SCA) were higher than general combining ability (GCA) mean squares for GYPP, GYPH, PYPH OYPH and SYPH) under elevated plant density, suggesting the existence of a greater portion of non-additive than additive and variance in controlling the inheritance of these traits, but the opposite was true for grain protein (GPC), grain oil (GOC) and grain starch (GSC). Out of 8 studied traits, significant correlations between means of the parents and their GCA effects existed for 6 traits, namely GPC, GYPP, GYPH, PYPF, OYPF and SYPF under all environments and GOC under high-D. These results indicate that the mean performance of a given parent for these traits is an indication of its general combining ability. Moreover, significant correlations existed between the means of crosses and their

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SCA effects in 20 out of 24 cases, suggesting that the mean performance of a cross could be used as an indicator of its SCA effects. For GOC under low-D and medium-D, GSC under low-D and high-D and GPC under low-D, the mean performance of a cross could be used as an indicator of its useful heterosis under the corresponding environments. The useful heterosis of a cross could be used as an indicator of its SCA effects for GOC under low-D and high-D and GPC under medium-D and high-D.

Keywords: Heterobeltiosis; diallel analysis; grain quality; high density stress.

1. INTRODUCTION

Egyptian maize hybrids selected under low plant density are not tolerant to high density and therefore are subject to yield losses when grown under high plant density. Thus, grain yield fed⁻¹ cannot be increased by increasing plant density using the present Egyptian cultivars. Maximum grain yield per land unit area may be obtained by growing maize hybrids that can withstand high plant density up to 100,000 plants/ha [1]. Average maize grain yield per land unit area in the USA increased dramatically during the second half of the 20th century, due to improvement in crop management practices and greater tolerance of modern hybrids to high plant densities [2-3]. Introducing high density adaptive traits to Egyptian cultivars is important to enable these cultivars to produce a higher grain yield than present cultivars. Heterosis and nature of inheritance of such traits should be studied; such information is scarce. Heterosis and combining ability are prerequisites for developing economically viable hybrid maize varieties. Information on the heterotic patterns and combining ability of maize germplasm is essential in maximizing the effectiveness of hybrid development [4].

Heterosis is the genetic expression of the superiority of a hybrid in relation to its parents [5]. This phenomenon manifests in increased size, or other parameters resulting from the increase in heterozygosity in the F1 generation of crosses between inbred lines [5,6] and is associated with stress tolerance [7]. In general, based on parents used, two major types of estimation of heterosis are reported in literature: (1) Mid-parent or average heterosis, which is the increased vigor of the F₁ over the mean of two parents. (2) Highparent or better parent heterosis, which is the increased vigor of the F₁ over the better parent [8.9]. The term heterobeltiosis has been to describe the increased suggested performance of the hybrid over the better parent [10].

Combining ability has been defined as the performance of a line in hybrid combinations [11].

Since the final evaluation of inbred lines can be best determined by hybrid performance, it plays an important role in selecting superior parents for hybrid combinations and in studying the nature of genetic variation [6,12]. Sprague and Tatum [13] introduced the concepts of general (GCA) and specific (SCA) combining ability. The authors reported that GCA and SCA is an indication of genes having largely additive and non-additive (dominance and epistasis) effects, respectively. Dass et al. [14] reported that estimates of combining abilities across environments have indicated that both GCA and SCA for most characters interacted with environmental change, but GCA was found to be more sensitive to environmental change than SCA. Inbred line traits under high plant density stress were more strongly correlated with top-cross performance under severe density stress than line traits under low density conditions [15].

Grain quality is an important objective in maize breeding [16-20]. In maize grain, a typical hybrid cultivar contains approximately 4% oil, 9% protein, 73% starch, and 14% other constituents; mostly fiber [18]. Some of the most important traits of interest in the maize market are those related to the nutritional quality of the grain, especially protein, oil and starch content [21]. Al-Naggar et al. [18-20] reported that GCA and SCA variances were significant and positive, but dominance was larger than the additive variance in magnitude and degree of dominance was over-dominance for the two characters. The additive genetic variance seems to be the main component in the control of oil content in maize [22]. However, non-additive gene effects, including dominance and epistasis had the predominant role in the inheritance of grain oil content in maize [23,24].

A wide array of biometrical tools is available to breeders for identifying proper parents and crosses and characterizing genetic control of economically important traits as a guide to decide the appropriate breeding methodology for hybrid breeding. Diallel analysis is one of the best biometrical tools to achieve that. Knowledge about heterosis and combining ability of maize kernel composition in diverse plant density environments is essential for plant breeding programs. Therefore, the objectives of this study were to estimate the following for diverse inbred lines in high plant density tolerance and their diallel crosses under elevated plant density: (i) performance, heterosis and combining ability variances and effects for maize grain quality and yield traits and (ii) correlations among inbred and hybrid *per se* performance, general and specific combining ability effects and heterosis.

2. MATERIALS AND METHODS

This study was carried out at the Agricultural Experiment and Research Station of the Faculty of Agriculture, Cairo University, Giza, Egypt (30° 02'N latitude and 31° 13'E longitude with an altitude of 22.50 meters above sea level), in 2012, 2013 and 2014 seasons.

2.1 Plant Material

Based on the results of previous experiments [15], six maize (*Zea mays* L.) inbred lines in the 8^{th} selfed generation (S₈), showing clear differences in performance and general combining ability for grain yield under high plant density, were chosen in this study to be used as parents of diallel crosses (Table 1).

2.2 Making F₁ Diallel Crosses

In the 2012 season, all possible diallel crosses (except reciprocals) were made among the six parents, so seeds of 15 direct F_1 crosses were obtained. Seeds of the 6 parents were also increased by selfing in the same season (2012) to obtain enough seeds of the inbreds in the 9th selfed generation (S₉).

2.3 Evaluation of parents and F₁'s

Three field experiments were carried out in each season of 2013 and 2014 at the Agricultural Experiment and Research Station of the Faculty of Agriculture, Cairo University, Giza. Each experiment included 21 genotypes ($15 F_1$ crosses and their 6 parents). The first experiment was done under low plant density (low-D); 47,600 plants/ha, the second experiment was done under medium plant density (medium-D); 71,400 plants/ha and the third experiment under high plant density (high-D); 95,200 plants/ha. A randomized complete block design with three replications was used in each experiment.

Each experimental plot consisted of one ridge of 4 m long and 0.7 m width, *i.e.* the experimental plot area was 2.8 m². Seeds were sown in hills at 15, 20 and 30 cm apart, thereafter (before the 1st irrigation) were thinned to one plant/hill to achieve a plant density of 47,600, 71,400 and 95,200 plants/ha, for the first, second and third experiment, respectively. Sowing date of the three experiments was on May 5 and May 8 in 2013 and 2014 seasons, respectively. The soil of the experimental site was clayey loam. All other agricultural practices were followed according to the recommendations of ARC, Egypt. The analysis of the experimental soil, as an average of the two growing seasons 2013 and 2014, indicated that the soil is clay loam (4.00% coarse sand, 30.90% fine sand, 31.20% silt, and 33.90% clay), the pH (paste extract) is 7.73, the EC is 1.91 dSm-1, soil bulk density is 1.2 g cm-3, calcium carbonate is 3.47%, organic matter is 2.09%, the available nutrient in mg kg-1are Nitrogen (34.20), Phosphorous (8.86), Potassium (242), hot water extractable B (0.49), DTPA extractable Zn (0.52), DTPA - extractable Mn (0.75) and DTPA - extractable Fe (3.17).

 Table 1. Designation, origin and most important traits of six inbred lines used for making diallel crosses of this study

| Inbred designation | Origin | Institution (country) | Prolificacy | Productivity under high plant density | Leaf angle |
|-----------------------|----------------|--------------------------|--------------|--|---------------|
| L20-Y | SC 30N11 | Pion. Int.Co. | Prolific | High | Erect |
| L53-W | SC 30K8 | Pion. Int.Co. | Prolific | High | Erect |
| Sk 5-W | Teplacinco - 5 | ARC-Egypt | Prolific | High | Erect |
| L18-Y | SC 30N11 | Pion. Int.Co. | Prolific | Low | Wide |
| L28-Y | Pop 59 | ARC-Thailand | Non-Prolific | Low | Wide |
| Sd 7-W | A.E.D. | ARC-Egypt | Non-Prolific | Low | Erect |

ARC = Agricultural Research Center, Pion. Int. Co. = Pioneer International Company in Egypt, SC = Single cross, A.E.D. = American Early Dent; an old open-pollinated variety, W = White grains and Y = Yellow grains Meteorological variables in the 2013 and 2014 growing seasons of maize were obtained from Agro-meteorological Station at Giza, Egypt. For May, June, July and August, mean temperature was 27.87, 29.49, 28.47 and 30.33 °C, maximum temperature was 35.7, 35.97, 34.93 and 37.07 ℃ and relative humidity was 47.0, 53.0, 60.33 and 60.67%, respectively, in 2013 season. In 2014 season, mean temperature was 26.1, 28.5, 29.1 and 29.9°C, maximum temperature was 38.8, 35.2, 35.6 and 36.4 °C and relative humidity was 32.8, 35.2, 35.6 and 36.4%, respectively. Precipitation was nil in all months of maize growing season for both seasons. Sibbing was carried out in each entry for the purpose of determining the grain contents of protein, oil and starch.

2.4 Data Recorded

Grain yield per plant (GYPP in g) estimated by dividing the grain yield per plot (adjusted at 15.5% grain moisture) on number of plants /plot at harvest. Grain yield per hectare (GYPH) in ton, by adjusting the grain yield/plot to grain yield per hectare. Grain protein content (%) (GPC%). Grain oil content (%) (GOC%). Grain starch content (%) (GSC%). Grain protein content (%), grain oil content (%) and grain starch content (%) were determined using the non-destructive grain analyzer, Model Infratec TM 1241 Grain Analyzer, ISW 5.00 valid from S/N 12414500, 1002 5017/Rev.1, manufactured by Foss Analytical AB, Hoganas, Sweden. Protein yield per hectare (PYPH), by multiplying grain protein content x grain yield per hectare. Oil yield per hectare (OYPH), by multiplying grain oil content x grain yield per hectare. Starch yield per hectare (SYPH), by multiplying grain starch content x grain yield per hectare.

2.5 Biometrical and Genetic Analyses

Analysis of variance of the RCBD was performed on the basis of individual plot observation using GENSTAT 10th addition windows software. Combined analysis of variance across the two seasons was also performed if the homogeneity test was nonsignificant. Least significant differences (LSD) values were calculated to test the significance of differences between means according to Steel et al. [25]. Diallel crosses were analyzed to obtain general (GCA) and specific (SCA) combining ability variances and effects for studied traits according to Griffing [26] Model I (fixed effect) Method 2. The significance of the various statistics was tested by "t" test, where "t" is a parameter value divided by its standard error. However, for making comparisons between different effects, the critical difference (CD) was calculated using the corresponding comparison as follows: $CD = SE \times t$ (tabulated).

Heterobeltiosis was calculated as a percentage of F₁ relative to the better-parent (BP) values as follows: Heterobeltiosis (%) = $100[(\overline{F}_1 - \overline{BP})/\overline{BP}]$ Where: \overline{F}_1 = mean of an F_1 cross and \overline{BP} = mean of the better parent of this cross. The significance of heterobeltiosis was determined as the least significant differences (L.S.D) at 0.05 and 0.01 levels of probability according to Steel et al. [25] using the following formula: LSD $_{0.05} = t_{0.05}(edf) x$ SE, LSD $_{0.01} = t_{0.01}(edf) \times SE$, Where: edf= the error degrees of freedom, SE= the standard error, SE for heterobeltiosis = $(2MS_e/r)^{1/2}$ Where: $t_{0.05}$ and $t_{0.01}$ are the tabulated values of 't' for the error degrees of freedom at 0.05 and 0.01 levels of probability, respectively. MSe: The mean squares of the experimental error from the analysis of variance Table. r: Number of replications.

Rank correlation coefficients were calculated between per se performance of inbred lines and their GCA effects; between per se performance of F₁ crosses and their SCA effects and between SCA effects and heterobeltiosis of F1 crosses for studied traits under low-D, medium-D and high-D conditions by using SPSS 17 computer software and the significance of the rank correlation coefficient was tested according to Steel et al. [25]. The correlation coefficient (r_s) was estimated for each pair of any two parameters as follows: $r_s = 1- (6 \sum d_i^2)/(n^3-n)$, Where, d_i is the difference between the ranks of the ith genotype for any two parameters, n is the number of pairs of data. The hypothesis Ho: $r_s = 0$ was tested by the r-test with (n-2) degrees of freedom.

3. RESULTS AND DISCUSSION

3.1 Analysis of Variance

Combined analysis of variance of a randomized complete blocks design for 8 traits of 21 maize genotypes under 3 environments; representing 3 plant densities (D), *i.e.* low-D, medium-D, and high-D, across two seasons is presented in Table (2). Mean squares due to parents and crosses under all environments were highly significant for all studied traits, indicating the significance of differences among studied parents and among

 F_1 diallel crosses in all cases. Mean squares due to parents *vs.* F_1 crosses were highly significant for all studied traits under all three environments, suggesting the presence of significant heterosis for all studied cases. Mean squares due to the interactions parents × years (P × Y) and crosses × years ($F_1 \times Y$) were significant or highly significant for all studied traits under all environments, except GYPH under low-D for P x Y and $F_1 \times Y$, GPC under medium-D for $F_1 \times Y$, GOC under high-D for P x Y, GSC under low-D and high-D for P x Y, PYPH under low-D and high-D for P x Y and low-D for $F_1 \times Y$, OYPH under low-D and medium-D for P x Y and SYPH under low-D for P x Y and $F_1 \times Y$.

Mean squares due to parents *vs.* crosses × years were significant or highly significant in 12 out of 24 cases (Table 2). Such interaction was expressed in most environments for GYPP, GPC and GOC traits. This indicates that heterosis differ from season to season in these cases. It is observed from Table 2 that among genotypes under all three environments (24 cases), the

largest contributor to total variance was parents vs. F_1 's (heterosis) variance for 17 cases, followed by F_1 crosses (5 cases) and parents (2 cases).

3.2 Mean Performance

Means of studied traits of 6 inbred parents. 15 F₁ crosses under low- (47,600 plants/ha), medium-(71,400 plants/ha) and high- (95,200 plants/ha) densities combined across two years are presented in Table 3. In general, the F₁ hybrids were lower in grain protein content than inbred lines under the three plant densities. This result is in agreement with that reported by Al-Naggar et al. [18,19,27]. On the other hand, F₁ hybrids showed higher means than inbreds for GYPP, GOC. GSC. GYPH. PYPH. OYPH and SYPH under all densities, indicating that heterozygotes exhibit better (more favorable) values for most studied traits than homozygotes, which is logic and could be attributed to heterosis phenomenon.

| | | | %Sum of squares | | | | | | | | | |
|-------------------------|----|---------|-----------------|---------|---------|---------|---------|---------|---------|---------|--|--|
| SOV | df | Low-D | Med-D | High-D | Low-D | Med-D | High-D | Low-D | Med-D | High-D | | |
| | | | GPC | | | GOC | | | GSC | | | |
| Р | 5 | 14.22** | 32.44** | 16.74** | 18.01** | 10.26** | 12.05** | 7.93** | 30.17** | 14.49** | | |
| F ₁ | 14 | 10.27** | 6.80** | 11.90** | 19.84** | 32.27** | 22.66** | 36.19** | 19.72** | 18.63** | | |
| P vs F ₁ | 1 | 42.39** | 14.05** | 53.24** | 7.37** | 14.90** | 15.84** | 1.54* | 1.60** | 1.02* | | |
| Ρ×Υ | 5 | 2.05* | 13.45* | 0.68* | 3.33** | 6.07** | 1.97 | 2.67 | 14.73** | 3.35 | | |
| $F_1 \times Y$ | 14 | 2.31* | 0.99 | 4.36** | 17.06** | 9.02** | 13.50** | 15.69** | 7.30** | 18.87** | | |
| P vs F ₁ × Y | 1 | 9.14** | 0.67 | 2.92** | 6.62** | 1.39** | 0.50* | 0.26 | 0.20 | 5.23** | | |
| | | | GYPP | | | GYPH | | | РҮРН | | | |
| Р | 5 | 5.50** | 6.07** | 3.53** | 4.98** | 7.82** | 4.46** | 5.60** | 7.73** | 5.11** | | |
| F ₁ | 14 | 9.66** | 12.07** | 10.52** | 13.70** | 13.63** | 11.35** | 16.94** | 14.89** | 12.97** | | |
| P vs F ₁ | 1 | 75.18** | 71.22** | 71.13** | 75.76** | 73.60** | 80.53** | 71.64** | 72.08** | 76.20** | | |
| Ρ×Υ | 5 | 0.37** | 0.26** | 0.20* | 0.12 | 0.15* | 0.76** | 0.25 | 0.33 | 1.31** | | |
| $F_1 \times Y$ | 14 | 1.91** | 1.88** | 1.22** | 0.42 | 0.53** | 0.89** | 0.38 | 0.79* | 2.10** | | |
| P vs F ₁ × Y | 1 | 0.01 | 0.38** | 0.55** | 0.01 | 0.05* | 0.02 | 0.38** | 0.01 | 0.03 | | |
| | | | ОҮРН | | | SYPH | | | | | | |
| Р | 5 | 3.86** | 5.72** | 2.75** | 5.01** | 8.21** | 4.68** | | | | | |
| F ₁ | 14 | 17.45** | 13.80** | 14.92** | 12.72** | 13.65** | 10.71** | | | | | |
| P vs F ₁ | 1 | 73.06** | 74.08** | 75.93** | 76.43** | 72.80** | 80.92** | | | | | |
| Ρ×Υ | 5 | 0.10 | 0.10 | 0.48** | 0.11 | 0.22** | 0.77** | | | | | |
| $F_1 \times Y$ | 14 | 1.83** | 0.96** | 2.65** | 0.41 | 0.57** | 0.84** | | | | | |
| P vs F ₁ × Y | 1 | 0.05 | 0.25** | 0.03 | 0.01 | 0.03 | 0.06* | | | | | |

Table 2. Combined analysis of variance of RCBD across two years for studied traits of 6 parents (P) and 15 crosses (F₁) and their interactions with years (Y) under three plant densities

Al-Naggar et al.; JABB, 8(4): 1-19, 2016; Article no.JABB.28127

| | GPC | | | GOC | | | GSC | | | GYPP | | |
|--------------|-------|-------|--------|-------|-------|--------|-------|-------|--------|--------|--------|--------|
| | Low-D | Med-D | High-D | Low-D | Med-D | High-D | Low-D | Med-D | High-D | Low-D | Med-D | High-D |
| | | | | | | Pai | rents | | - | | | |
| L20 | 10.97 | 10.63 | 11.65 | 4.23 | 3.90 | 3.82 | 71.00 | 72.17 | 72.23 | 106.58 | 92.85 | 71.48 |
| L53 | 11.82 | 10.97 | 11.47 | 4.15 | 4.20 | 4.13 | 70.48 | 71.17 | 70.87 | 132.05 | 93.69 | 71.70 |
| Sk5 | 12.80 | 12.82 | 12.80 | 3.48 | 3.52 | 3.68 | 71.25 | 70.97 | 70.70 | 77.56 | 64.94 | 52.97 |
| L18 | 13.52 | 14.38 | 13.43 | 4.03 | 4.15 | 4.05 | 70.35 | 69.48 | 71.02 | 46.69 | 27.23 | 20.07 |
| L28 | 12.88 | 13.35 | 12.85 | 4.55 | 4.28 | 4.48 | 69.93 | 68.87 | 69.92 | 44.37 | 35.38 | 30.45 |
| Sd7 | 12.57 | 9.30 | 11.38 | 4.40 | 4.28 | 4.28 | 70.75 | 70.85 | 71.28 | 55.10 | 29.14 | 32.87 |
| Average | 12.43 | 11.91 | 12.26 | 4.14 | 4.05 | 4.07 | 70.63 | 70.58 | 71.00 | 77.06 | 57.20 | 46.59 |
| | | | | | | Cro | sses | | | | | |
| L20 x L53 | 9.73 | 9.50 | 9.57 | 4.38 | 4.32 | 4.22 | 71.67 | 71.48 | 71.52 | 277.36 | 238.19 | 191.55 |
| L20 XSK5 | 10.55 | 10.33 | 10.28 | 4.80 | 4.68 | 4.40 | 70.12 | 70.33 | 70.87 | 221.68 | 182.28 | 153.06 |
| L20 x L18 | 10.95 | 10.47 | 10.55 | 4.05 | 4.17 | 4.25 | 71.63 | 71.53 | 71.37 | 219.17 | 193.75 | 178.07 |
| L20 x L28 | 10.63 | 10.70 | 10.50 | 4.38 | 4.40 | 4.65 | 71.15 | 70.85 | 70.52 | 232.77 | 186.52 | 156.26 |
| L20 x Sd7 | 10.33 | 11.40 | 10.63 | 4.50 | 4.27 | 4.37 | 70.97 | 70.68 | 70.63 | 226.70 | 182.42 | 159.88 |
| _ L 53 x Sk5 | 10.58 | 10.30 | 10.30 | 4.12 | 4.20 | 4.10 | 70.80 | 71.13 | 71.63 | 245.53 | 224.51 | 184.72 |
| L53 x L18 | 10.57 | 10.47 | 10.70 | 4.27 | 4.30 | 4.35 | 70.75 | 70.92 | 70.53 | 197.48 | 147.69 | 138.34 |
| L53 x L28 | 10.63 | 10.37 | 10.58 | 4.53 | 4.87 | 4.53 | 70.77 | 70.55 | 71.02 | 237.53 | 168.89 | 165.70 |
| L53 X Sd7 | 10.50 | 10.28 | 10.80 | 4.57 | 4.77 | 4.67 | 70.87 | 70.55 | 70.40 | 240.96 | 219.13 | 181.5 |
| Sk5 X L18 | 11.35 | 10.87 | 11.03 | 4.10 | 4.05 | 4.03 | 71.13 | 71.75 | 71.35 | 234.83 | 197.02 | 165.10 |
| Sk5 X L28 | 11.42 | 10.68 | 10.58 | 4.40 | 4.17 | 4.50 | 70.40 | 71.08 | 70.58 | 223.20 | 201.32 | 167.12 |
| Sk5 X Sd7 | 10.83 | 11.00 | 10.63 | 4.68 | 4.58 | 4.78 | 70.00 | 70.20 | 70.17 | 207.22 | 157.58 | 145.21 |
| L18 x L28 | 11.57 | 11.58 | 11.65 | 4.45 | 4.87 | 4.60 | 70.72 | 69.82 | 70.55 | 171.09 | 124.38 | 122.94 |
| L18 X Sd7 | 10.85 | 10.05 | 10.52 | 4.42 | 4.42 | 4.58 | 71.07 | 71.12 | 70.48 | 213.29 | 161.79 | 148.59 |
| L28 X Sd7 | 10.67 | 10.20 | 10.48 | 4.32 | 4.58 | 4.57 | 70.77 | 71.22 | 70.17 | 227.64 | 183.46 | 165.78 |
| Average | 10.74 | 10.55 | 10.59 | 4.40 | 4.44 | 4.44 | 70.85 | 70.88 | 70.79 | 225.10 | 184.60 | 161.62 |
| | | GYPH | | | PYPH | | | ОҮРН | | | SYPH | |
| | | | | | | Pai | rents | | | | | |
| L20 | 4.95 | 6.41 | 6.64 | 541.8 | 680.6 | 771.7 | 209.5 | 249.7 | 253.1 | 3513 | 4627 | 4801 |
| L53 | 6.13 | 6.47 | 6.66 | 734.6 | 705.7 | 765.5 | 252.3 | 271.5 | 275.9 | 4319 | 4610 | 4718 |
| Sk5 | 3.60 | 4.48 | 4.92 | 461.7 | 577.5 | 633.5 | 125.8 | 156.8 | 180.1 | 2566 | 3181 | 3481 |
| L18 | 2.16 | 1.85 | 1.86 | 294.5 | 264.8 | 251.3 | 86.7 | 76.6 | 75.2 | 1523 | 1285 | 1322 |

Table 3. Means of studied grain quality and yield traits of each inbred and hybrid under three plant densities across two seasons

Al-Naggar et al.; JABB, 8(4): 1-19, 2016; Article no.JABB.28127

| Table 3 continue | d | | | | | | | | | | | |
|------------------|-------|-------|-------|--------|--------|--------|-------|-------|-------|------|-------|-------|
| L28 | 2.06 | 2.44 | 2.83 | 265.2 | 325.4 | 363.4 | 93.4 | 104.7 | 126.5 | 1440 | 1681 | 1976 |
| Sd7 | 2.01 | 2.50 | 3.05 | 257.4 | 225.2 | 349.9 | 86.5 | 104.7 | 129.1 | 1423 | 1770 | 2179 |
| Average | 3.49 | 4.03 | 4.33 | 425.9 | 463.2 | 522.5 | 142.4 | 160.7 | 173.3 | 2464 | 2859 | 3080 |
| | | | | | | Cro | sses | | | | | |
| L20 x L53 | 12.88 | 16.45 | 17.05 | 1253.5 | 1561.9 | 1632.9 | 563.5 | 710.2 | 718.5 | 9230 | 11756 | 12195 |
| L20 XSK5 | 10.22 | 12.59 | 14.21 | 1081.7 | 1294.7 | 1467.3 | 491.7 | 598.5 | 626.9 | 7149 | 8829 | 10061 |
| L20 x L18 | 10.15 | 13.38 | 16.04 | 1111.1 | 1404.6 | 1693.1 | 411.5 | 558.1 | 681.5 | 7273 | 9565 | 11450 |
| L20 x L28 | 10.81 | 12.88 | 14.51 | 1149.0 | 1373.2 | 1522.9 | 473.9 | 569.5 | 674.7 | 7689 | 9121 | 10233 |
| L20 X Sd7 | 10.53 | 12.60 | 14.85 | 1087.8 | 1436.0 | 1578.4 | 473.4 | 537.5 | 648.1 | 7470 | 8903 | 10487 |
| L L53 X Sk5 | 11.40 | 15.50 | 16.47 | 1206.4 | 1596.8 | 1695.1 | 469.4 | 651.1 | 674.6 | 8072 | 11027 | 11802 |
| L53 x L18 | 8.99 | 10.20 | 12.85 | 950.4 | 1067.9 | 1374.3 | 384.1 | 438.3 | 557.9 | 6363 | 7233 | 9065 |
| L53 x L28 | 11.03 | 11.66 | 14.99 | 1172.7 | 1208.9 | 1583.8 | 500.2 | 567.6 | 680.1 | 7804 | 8227 | 10647 |
| L53 X Sd7 | 11.19 | 15.13 | 16.30 | 1174.7 | 1556.0 | 1759.6 | 510.8 | 721.1 | 759.3 | 7928 | 10674 | 11482 |
| Sk5 X L18 | 10.90 | 13.60 | 15.18 | 1237.4 | 1478.8 | 1675.5 | 447.2 | 551.1 | 611.8 | 7755 | 9761 | 10829 |
| Sk5 X L28 | 10.34 | 13.90 | 15.45 | 1180.0 | 1484.7 | 1634.2 | 455.1 | 579.1 | 694.5 | 7281 | 9880 | 10909 |
| Sk5 X Sd7 | 9.58 | 10.88 | 13.48 | 1037.6 | 1196.5 | 1431.4 | 448.4 | 498.7 | 643.5 | 6705 | 7638 | 9467 |
| L18 x L28 | 7.91 | 8.59 | 11.42 | 915.3 | 994.8 | 1330.3 | 351.7 | 418.0 | 525.3 | 5592 | 5996 | 8053 |
| L18 X Sd7 | 9.88 | 11.17 | 13.80 | 1071.8 | 1122.6 | 1451.6 | 436.3 | 493.6 | 632.1 | 7022 | 7945 | 9726 |
| L28 X Sd7 | 10.49 | 12.67 | 14.67 | 1116.4 | 1292.3 | 1540.5 | 462.7 | 599.7 | 682.6 | 7405 | 8999 | 10278 |
| Average | 10.42 | 12.75 | 14.75 | 1116.4 | 1338.0 | 1558.0 | 458.7 | 566.1 | 654.1 | 7382 | 9037 | 10445 |

D= Density, G = Genotype, GPC= Grain protein content, GOC= Grain oil content, GSC= Grain starch content, GYPP= Grain yield per plant, PYPH= Protein yield/ha, OYPH= Oil yield/ha, SYPH= Starch yield/ha, GYPH= Grain yield/ha

For grain protein content (GPC), the inbreds another, especially when comparing poor with showed remarkable variability. Three inbreds (L18, L28 and Sk5) exhibited the highest (14.38, percentage 13.35 and 12.82%, respectively), while the lowest GPC (9.30%) was recorded by the inbred Sd7, all under medium density. For the F1 crosses, variability in GPC was much less than in inbreds; i.e. from 9.5% for L20 × L53 to 11.58% for L18 × L28 under medium density. The cross L18 × L28 recorded the highest GPC, while the cross L20 × L53 recorded the lowest percentage under the three plant densities. Out of 15 crosses, 9 crosses showed the highest GPC under low density, four under medium density and two under high density, assuring that in general, there is a tendency of reduction of grain protein percentage due to elevated plant density in most studied genotypes.

For grain oil content, the range of variability was between 3.48% for Sk5 under low density to 4.55% for L28 under low density for inbreds and from 4.03% (Sk5 × L18) to 4.87% (L18 × L28 and L53 × L28) under medium density for crosses. The range of variability in grain oil content in the present study is similar to that found in the literature for normal maize, which was between 3.5 and 4.5% [27]. In another study on the genetic variation for oil content in maize with normal endosperm. Mittelmann [28] found values between 3.77 and 5.10%. The F1 crosses were generally higher than their parental inbred in grain oil content under the three densities, suggesting the superiority of heterozygotes to homozygotes in maize grain oil content. Similar conclusion was reported by previous investigators [20,29,30]). Heterosis for grain oil content of maize was also reported by several investigators [18,20,31-33]). The variability for grain starch content ranged from 68.87% (L28) under medium density to 72.23% (L20) under high density for inbreds and from 69.82% (L18 × L28) under medium density to 71.75% (Sk5 x L18) under medium density for F_1 crosses.

In general, GYPP of three inbreds, viz. L53, L20 and Sk5 was higher than that of the other three inbreds (L18, L28 and Sd7) under all densities. Reduction due to elevated plant density was the highest in the inbred L18 under high-density (57.0%), and the lowest in inbred L20 under medium density (12.9%). The highest GYPP of all inbreds was achieved under low density, where competition between plants is at minimum. The effect of the first order interaction $(G \times D)$ was clearly shown by the F₁ crosses, where the rank of crosses was changed from one plant density to PYPH, OYPH and SYPH.

good environments.

The second highest GYPP of studied crosses was obtained under the medium plant density. The highest GYPP in this experiment (277.36 g) was obtained from the cross L20 × L53 under lowdensity followed by the crosses L53 × Sk5 (245.53 g), L53 × Sd7 (240.96 g) and L53 × L28 (237.53 g) under the same density. These crosses could therefore be considered responsive to the good environment. The highest GYPP under the most severe stress (high density, *i.e.* 95,400 plants/ha) was obtained by the crosses L20 × L53 (191.55 g), L53 \times Sk5 (184.72 g), L53 \times Sd7 (181.95 g) and L20 × L18 (178.07 g); these crosses were considered tolerant to high density stress. The three crosses L20 × L53, L53 × Sk5 and L53 × Sd7 were tolerant to high density stress and responsive to low density.

The rank of inbred parents for GYPH was approximately similar under all the three densities, indicating less effect of interaction between inbreds and plant density on GYPH. The percent reduction in GYPH due to density stress relative to low-density was smaller for the inbred lines L20, L28 and L53 than the inbreds L18, Sk5 and Sd7 in low-performing ones, which could be attributed to the higher potential yield of the first group of lines than the second one, under good environmental conditions. Regarding GYPH of the F₁ crosses, the rank varied from one plant density level to another, indicating that for GYPH the interaction between genotype and plant density plays a role in its expression.

Comparing with the non-stressed environment (low density), all 15 F1 crosses showed an increase in their GYPH ranging from 5.75 to 35.99% under medium density and from 32.42 to 58.0% under high density. The increase in GYPH of these crosses under medium and high density over that under low density could be attributed to the elevation of plant density. This indicates that the increase of GYPH due to the increase in plant density could compensate the reduction in GYPP due to competition among plants and even this could happen in some crosses if they have more tolerance to high density stress. The best GYPH in this experiment was obtained under high density and the best crosses in this environment were L20 × L53 (17.05 ton), L53 × Sk5 (16.47 ton), L53 × Sd7 (16.30 ton) and L20 × L18 (16.04 ton). The increase in GYPH due to high plant density was accompanied with increases in

3.3 Heterobeltiosis

Estimates of better parent heterosis (heterobeltiosis) across all F₁ crosses, maximum values and number of crosses showing significant favorable heterobeltiosis for all studied traits under the three environments (plant densities) across 2011 and 2012 years are presented in Table 4. Favorable heterobeltiosis in the studied crosses was considered positive for all studied traits under all plant densities. In general, the highest average significant and positive (favorable) heterobeltiosis was shown by oil yield per hectare (186.25, 201.71, and 219.02%) under low-, medium- and high-D, respectively, followed by GYPP, SYPH, GYPH and SYPH traits. On the contrary, the lowest average significant (favorable) heterobeltiosis was shown by grain starch content (-0.09, -0.59 and -0.93%) under low-D, medium-D and high-D, respectively. The traits GPC, GSC under all environments, showed on average unfavorable heterobeltiosis. However, some crosses showed significant favorable heterobeltiosis in these cases. In general, medium-D environment, showed the largest number of crosses showing significant favorable heterobeltiosis for studied traits. For yield traits, i.e. GYPP, GYPH, PYPH, OYPH and SYPH, the high-D (the severest stressed) environment showed generally the highest maximum heterobeltiosis.

The reason for getting the highest average heterobeltiosis estimates under high-D environment could be attributed to the large reduction in grain yield of the parental inbreds compared to that of F_1 crosses due to severe

stress of high plant density and water deficit stresses existed in this environment. These results are in agreement with those of Weidong and Tollenaar [34], who reported that increasing plant density from 4 to 12 plants m⁻² resulted in increased heterosis for grain yield of maize. In general, maize hybrids typically yield two to three times as much as their parental inbred lines. However, since a cross of two extremely low vielding lines can give a hybrid with high heterosis, a superior hybrid is not necessarily associated with high heterosis [6]. This author suggested that a cross of two high yielding inbreds might exhibit less heterosis but nevertheless produce a high yielding hybrid. Besides, a hybrid is superior not only due to heterosis but also due to other heritable factors that are not influenced by heterosis. On the contrary, the low-D (non-stressed) environment showed the lowest average favorable heterobeltiosis for all yield traits, GYPP (151.79%), GYPH (162.31%), OYPF (168.25%), PYPF (129.70%), SYPF (162.95%) and for GOC (0.97%) (Table 4).

The largest significant favorable heterobeltiosis for GYPP in this study (455.28%) was shown by the cross (L18 × Sd7) under medium density environment (Table 5). This cross showed also the highest significant and favorable heterobeltiosis under high-D for GYPH (809.62%), PYPH (716.71%), OYPH (848.98%) SYPH (800.93%). The and highest heterobeltiosis for GOC trait under low, medium and high-D (13.39, 20.09 and 15.28%, respectively) was exhibited by the cross L20 x Sk5.

| Parameter | Low-D | Med-D | High-D | Low-D | Med-D | High-D | Low-D | Med-D | High-D |
|-----------|--------|--------|--------|--------|--------|--------|-------|--------|--------|
| | | GPC | | | GOC | | | GSC | |
| Average | -17.11 | -18.64 | -17.01 | 0.97 | 5.29 | 4.37 | -0.09 | -0.59 | -0.93 |
| Max | -11.38 | 7.21 | -5.81 | 13.39 | 20.09 | 15.28 | 0.94 | 1.1 | 1.08 |
| Min | -21.82 | -30.09 | -21.71 | -5.13 | -2.72 | -0.81 | -1.75 | -2.54 | -2.38 |
| No. | 0 | 0 | 0 | 1 | 6 | 4 | 0 | 1 | 0 |
| | | GYPP | | | GYPH | | | PYPH | |
| Average | 151.79 | 176.63 | 191.31 | 162.31 | 168.74 | 186.52 | 129.7 | 143.15 | 154.27 |
| Max | 313.14 | 455.28 | 404.32 | 409.27 | 407.55 | 380.66 | 321 | 323.94 | 323.92 |
| Min | 49.55 | 57.64 | 92.96 | 46.71 | 57.64 | 92.96 | 29.38 | 51.33 | 79.53 |
| No. | 15 | 15 | 15 | 15 | 15 | 15 | 15 | 15 | 15 |
| | | OYPH | | | SYPH | | | | |
| Average | 186.25 | 201.71 | 219.02 | 162.95 | 167.92 | 184.47 | | | |
| Max | 402.92 | 472.56 | 428.88 | 414.13 | 408.44 | 371.75 | | | |
| Min | 52.24 | 61.43 | 102.24 | 47.32 | 56.92 | 92.11 | | | |
| No. | 15 | 15 | 15 | 15 | 15 | 15 | | | |

Table 4. Estimates of average (Aver), maximum (Max) and minimum (Min) heterobeltiosis and number (No.) of crosses showing significant favorable heterobeltiosis for quality traits under three plant densities conditions across two seasons

| Parameter | Low-D | Med-D | High-D | Low-D | Med-D | High-D | Low-D | Med-D | High-D |
|------------|----------|----------|----------|----------|----------|----------|----------|----------|----------|
| | | GOC | | | GYPP | | | GYPH | |
| L20 X L53 | 3.54 | 2.78 | 2.02 | 110.04** | 154.23** | 167.17** | 110.04** | 154.23** | 156.13** |
| L20 X Sk5 | 13.39** | 20.09** | 15.28** | 107.99** | 96.33** | 114.13** | 106.46** | 96.33** | 114.13** |
| L20 X L18 | -4.33 | 0.40 | 4.94 | 105.63** | 108.68** | 149.12** | 105.16** | 108.68** | 141.68** |
| L20 X L28 | -3.66 | 2.72 | 3.72 | 118.39** | 100.89** | 118.60** | 118.39** | 100.89** | 118.60** |
| L20 X Sd7 | 2.27 | -0.19 | 1.95 | 112.69** | 96.48** | 123.68** | 112.69** | 96.48** | 123.68** |
| L 53 X Sk5 | -0.80 | 0.00 | -0.81 | 85.93** | 139.64** | 157.64** | 85.93** | 139.64** | 147.39** |
| L53 X L18 | 2.81 | 2.38 | 5.24 | 49.55** | 57.64** | 92.96** | 46.71** | 57.64** | 92.96** |
| L53 X L28 | -0.37 | 13.62** | 1.12 | 79.87** | 80.27** | 131.11** | 79.87** | 80.27** | 125.11** |
| L53 X Sd7 | 3.79 | 11.50** | 8.95** | 82.47** | 133.89** | 153.78** | 82.47** | 133.89** | 144.90** |
| Sk5 X L18 | 1.65 | -2.41 | -0.41 | 202.76** | 203.37** | 211.68** | 202.76** | 203.37** | 208.55** |
| Sk5 X L28 | -3.30 | -2.72 | 0.37 | 187.76** | 209.98** | 215.49** | 187.19** | 209.98** | 214.11** |
| Sk5 X Sd7 | 6.44 | 7.21* | 11.67** | 167.16** | 142.63** | 174.13** | 165.98** | 142.63** | 174.13** |
| L18 X L28 | -2.20 | 13.62** | 2.60 | 266.42** | 251.59** | 303.74** | 265.32** | 251.93** | 303.74** |
| L18 X Sd7 | 0.38 | 3.31 | 7.00* | 287.11** | 455.28** | 352.04** | 356.40** | 347.60** | 352.04** |
| L28 X Sd7 | -5.13 | 7.00* | 1.86 | 313.14** | 418.62** | 404.32** | 409.27** | 407.55** | 380.66** |
| | | PYPH | | | ОҮРН | | | SYPH | |
| L20 X L53 | 70.64** | 121.34** | 111.60** | 123.35** | 161.57** | 160.46** | 113.71** | 154.04** | 154.00** |
| L20 XSK5 | 99.66** | 90.21** | 90.15** | 134.74** | 139.69** | 147.73** | 103.51** | 90.79** | 109.56** |
| L20 X L18 | 105.10** | 106.36** | 119.40** | 96.42** | 123.51** | 169.30** | 107.04** | 106.70** | 138.48** |
| L20 X L28 | 112.08** | 101.75** | 97.35** | 126.22** | 128.07** | 166.58** | 118.91** | 97.11** | 113.13** |
| L20 X Sd7 | 100.78** | 110.98** | 104.54** | 126.00** | 115.23** | 156.11** | 112.67** | 92.40** | 118.42** |
| L 53 X Sk5 | 64.21** | 126.28** | 121.45** | 86.02** | 139.80** | 144.52** | 86.88** | 139.23** | 150.12** |
| L53 X L18 | 29.38** | 51.33** | 79.53** | 52.24** | 61.43** | 102.24** | 47.32** | 56.92** | 92.11** |
| L53 X L28 | 59.63** | 71.32** | 106.91** | 98.24** | 109.07** | 146.51** | 80.68** | 78.48** | 125.64** |
| L53 X Sd7 | 59.91** | 120.50** | 129.87** | 102.44** | 165.59** | 175.23** | 83.56** | 131.57** | 143.35** |
| Sk5 X L18 | 167.99** | 156.08** | 164.47** | 255.40** | 251.41** | 239.76** | 202.27** | 206.88** | 211.10** |
| Sk5 X L28 | 155.57** | 157.11** | 157.95** | 261.65** | 269.26** | 285.69** | 183.79** | 210.62** | 213.40** |
| Sk5 X Sd7 | 124.72** | 107.20** | 125.94** | 256.38** | 218.03** | 257.34** | 161.35** | 140.14** | 171.97** |
| L18 X L28 | 210.84** | 205.68** | 266.09** | 276.44** | 299.04** | 315.23** | 267.23** | 256.62** | 307.53** |
| L18 X Sd7 | 263.99** | 323.94** | 314.92** | 402.92** | 371.38** | 389.72** | 361.15** | 348.87** | 346.43** |
| L28 X Sd7 | 321.00** | 297.10** | 323.92** | 395.26** | 472.56** | 428.88** | 414.13** | 408.44** | 371.75** |

Table 5. Estimates of heterobeltiosis (%) for selected traits of diallel F1 crosses under three plant densities across 2013 and 2014 seasons

Under the three density environments, the highest estimates of GYPP, GYPH, PYPH, OYPH and SYPH heterobeltiosis were generally obtained by the cross (L28 × Sd7), followed by the cross L18 × Sd7 and the cross L18 × L28. These crosses could therefore be recommended for maize breeding programs as good genetic material.

3.4 Combining Ability Variances

Estimates of variances due to general (GCA) and specific (SCA) combining ability of the diallel crosses of maize for combined data across two seasons under three environments (three plant densities) are presented in Table 6. Mean squares due to GCA and SCA were significant (P≤ 0.01 or 0.05) for all studied traits (except for GOC and GSC) under all three environments (35 out of 48 cases), suggesting that both additive and non-additive gene effects play important roles in controlling the inheritance for most studied cases (72.9%). The exceptions were GOC under low and medium-D and GSC under the three densities, where GCA and SCA variances were not significant. A similar conclusion was reported by several investigators [35-37].

In the present study under all environments, the magnitude of SCA mean squares was higher than that of GCA mean squares (the ratio of GCA/SCA mean squares was lower than unity) for five traits (GYPP, GYPH, PYPH OYPH and SYPH) under the three environments, GPC under high-D and GSC under low-D, suggesting the existence of a greater portion of non-additive than additive and additive x additive variance in controlling the inheritance of these traits under respective environments. A similar conclusion was reported by many investigators [38-45].

On the contrary, the magnitude of GCA mean squares was higher than that of SCA mean squares (the GCA/SCA ratio was higher than unity) for the rest of cases, namely GPC, GOC and GSC under most studied environments. These results are in agreement with those reported by several investigators [36,41-44, 46-48].

Results in Table (6) indicate that mean squares due to the SCA \times year and GCA x year interactions were highly significant for GSC, GYPP, GYPH, PYPF, OYPF and SYPF under all environments (except GSC under high-D for GCA x year), GPC and GOC under medium-D, indicating that additive and non-additive variances for these cases were affected by years. This was not true for the rest of case, suggesting that additive and non-additive variances for these cases were not affected by years.

The mean squares due to SCA × year was higher than those due to GCA × year for OYPF and GOC under all environments and GYPP, GYPH, PYPF and SYPF in all environments, except under low-D, suggesting that SCA (nonadditive variance) is more affected by years than GCA for these cases. On the contrary, mean squares due to GCA × year was higher than those due to SCA × year for GPC under medium-D, GSC under low and medium-D and GYPP, GYPH, PYPH, OYPH and SYPH under low-D, indicating that GCA (additive) variance is more affected by years than SCA (non-additive) variance for these traits under the respective environments.

3.5 GCA Effects

Estimates of general combining ability (GCA) effects of parental inbreds for studied traits under the three environments across two seasons are presented in Table 7. The best parental inbreds were those showing positive and significant GCA effects for all studied traits. For GYPP, GYPH, PYPH, OYPH and SYPH, the best inbred in GCA effects was L53 in all environments followed by L20 and Sk5. These best general combiners for grain yield (L53, L120 and Sk5) were also the best ones in per se performance for the same traits under the respective environments (Table 3). On the contrary, the inbred lines L18, L28 and Sd7 were the worst in GCA effects (Table 7) and the worst in *per se* performance for the same traits under the three environments (Table 3).

For the grain quality traits, *i.e.* GPC, GOC and GSC, the magnitude of GCA effects was small and not significant in most cases. However, the largest values of GCA effects were exhibited by L18 under low and medium-D and L28 under high-D for GPC, Sd7 under low and medium-D and L18 under high-D for GOC and L20 under low and medium-D and L18 under high-D for GSC trait. In previous studies [37,49], the inbred lines L53, L20 and Sd5 were also the best general combiners for GYPP and GYPH under high and low plant densities.

| Parameter | Low-D | Med-D | High-D | Low-D | Med-D | High-D | Low-D | Med-D | High-D |
|-------------|---------|----------|---------|-----------|------------|------------|----------|----------|----------|
| | | GPC | | | GOC | | | GSC | |
| GCA | 7.48* | 14.64* | 5.43** | 0.64 | 0.81 | 0.88 | 1.24 | 5.54 | 3.86 |
| SCA | 5.14** | 7.15** | 5.57** | 0.42 | 0.57 | 0.38 | 1.33 | 2.79 | 1.24 |
| GCA/SCA | 1.45 | 2.05 | 0.97 | 1.52 | 1.42 | 2.32 | 0.93 | 1.98 | 3.11 |
| GCA×Y | 0.94 | 5.03** | 0.27 | 0.28 | 0.24** | 0.16 | 1.68* | 2.33** | 1.08 |
| SCA×Y | 1.23* | 1.73* | 0.65 | 0.38 | 0.37** | 0.24 | 1.33* | 1.66** | 2.02** |
| GCA×Y/SCA×Y | 0.76 | 2.90 | 0.42 | 0.74 | 0.64 | 0.66 | 1.26 | 1.40 | 0.54 |
| | | GYPP | | | GYPH | | | PYPH | |
| GCA | 12189** | 12513* | 5180* | 247.12** | 527* | 359.6** | 37811.00 | 88860** | 54631* |
| SCA | 39215** | 30650** | 23841** | 777.60** | 1293** | 1743.2** | 153673** | 253511** | 340543** |
| GCA/SCA | 0.30 | 0.41 | 0.22 | 0.32 | 0.41 | 0.21 | 0.25 | 0.35 | 0.16 |
| GCA×Y | 1067** | 1241** | 590.3** | 21.91** | 53** | 31.0** | 8262** | 4706** | 7696** |
| SCA×Y | 797.8** | 1581.4** | 689.0** | 16.85** | 68** | 36.7** | 5116** | 15991** | 12660** |
| GCA×Y/SCA×Y | 1.30 | 0.78 | 0.86 | 1.30 | 0.78 | 0.84 | 1.62 | 0.29 | 0.61 |
| | | OYPH | | | SYPH | | | | |
| GCA | 9470* | 17940* | 10161* | 2476627** | 5331906* | 3773304** | | | |
| SCA | 31507** | 53410** | 72138** | 7696247** | 12817768** | 17099676** | | | |
| GCA/SCA | 0.30 | 0.34 | 0.14 | 0.30 | 0.42 | 0.22 | | | |
| GCA×Y | 1428** | 3425** | 2133** | 185787** | 532035** | 275576** | | | |
| SCA×Y | 1757** | 6014** | 3445** | 138944** | 599804** | 323073** | | | |
| GCA×Y/SCA×Y | 0.80 | 0.57 | 0.62 | 1.30 | 0.89 | 0.85 | | | |

Table 6. Mean squares due to general (GCA) and specific (SCA) combining ability and their interactions with years (Y) for studied characters under three plant density across 2013 and 2014 seasons

Table 7. Estimates of general combining ability (GCA) effects of parents for studied characters under three plant densities across 2013 and 2014 seasons

Med-D Genotype Low-D Med-D High-D Low-D High-D Low-D Med-D High-D GPC GOC GSC L20 -0.51* 0.56** -0.38 -0.08 0.03 -0.14 -0.10 0.32 0.12 -0.05 L53 -0.43 -0.46 -0.03 0.10 0.06 0.15 -0.20 0.06 Sk5 0.25 -0.10 0.03 -0.45 0.11 0.05 -0.13 -0.10 0.03 L18 0.39 0.47 0.17 -0.18 -0.22** -0.10 0.26 0.42* 0.18 L28 0.30 0.24 0.20 0.02 0.06 0.17 -0.12 -0.18 -0.22 Sd7 -0.14 -0.06 0.05 0.12 0.16 0.10 -0.15 -0.50** -0.16 SE g_i-g_i 0.52 0.12 0.56 0.38 0.52 0.50 0.60 0.29 0.52

| | | GYPP | | | GYPH | | | РҮРН | | |
|-----------------------------------|----------|----------|----------|----------|----------|----------|----------|----------|----------|--|
| L20 | 13.05** | 17.64** | 15.05** | 1.86** | 2.54** | 3.12** | 10.62 | 21.91 | 39.95** | |
| L53 | 18.35** | 20.21** | 18.86** | 2.54** | 2.78** | 3.91** | 18.47* | 39.90** | 31.67** | |
| Sk5 | 1.74 | 1.43 | 9.93** | 0.26 | 0.24 | 2.06** | 16.91 | 2.89 | 37.96** | |
| L18 | -22.40** | -22.47** | -24.59** | -3.19** | -3.06** | -5.09** | -31.07** | -34.01** | -65.23** | |
| L28 | -8.31** | -12.73** | -14.60** | -1.14** | -1.78** | -3.02** | -5.10 | -20.10 | -35.27** | |
| Sd7 | -2.42 | -4.07* | -4.65 | -0.33 | -0.71 | -0.97 | -9.84 | -10.60 | -9.08 | |
| SE g _i -g _i | 3.08 | 3.00 | 3.99 | 0.42 | 0.63 | 0.78 | 13.23 | 21.74 | 13.58 | |
| | | OYPH | | | SYPH | | | | | |
| L20 | 12.68** | 9.97* | 15.03** | 199.3** | 271.7** | 313.8** | | | | |
| L53 | 14.15** | 19.59** | 27.05** | 260.8** | 269.8** | 391.9** | | | | |
| Sk5 | 1.94 | 2.84 | 5.01 | 5.2** | 19.50 | 204.8** | | | | |
| L18 | -27.57** | -25.80** | -39.02** | -305.4** | -288.6** | -491.9** | | | | |
| L28 | -5.23 | -7.87 | -10.16** | -119.9** | -184.9** | -310.9** | | | | |
| Sd7 | 4.03 | 1.27 | 2.09 | -40.1** | -87.5* | -107.7* | | | | |
| SE g _i -g _i | 4.97 | 7.58 | 5.92 | 0.71 | 64.55 | 81.39 | | | | |

Table 8. Estimates of specific combining ability (SCA) effects for studied characters under three plant densities across 2013 and 2014 seasons

| Cross | Low-D | Med-D | High-D | Low-D | Med-D | High-D | Low-D | Med-D | High-D | | |
|--------------------------------------|-------|-------|--------|-------|--------|--------|-------|--------|--------|--|--|
| | | GPC | | | GOC | | | GSC | | | |
| L20 × L53 | -0.20 | -0.27 | -0.51 | -0.02 | -0.15 | -0.09 | 0.35 | 0.20 | 0.43 | | |
| L20 ×SK5 | -0.07 | 0.08 | -0.24 | 0.34 | 0.10 | 0.47 | -0.60 | 0.00 | -0.69 | | |
| L20 × L18 | 0.20 | -0.34 | -0.17 | -0.20 | -0.18 | -0.08 | 0.21 | 0.95* | 0.35 | | |
| L20 × L28 | -0.03 | 0.15 | 0.04 | -0.07 | 0.37** | -0.12 | 0.10 | -0.79* | 0.07 | | |
| L20 × Sd7 | 0.10 | 0.38 | 0.89 | -0.05 | -0.15 | -0.18 | -0.05 | -0.36 | -0.16 | | |
| L 53 × Sk5 | 0.01 | 0.00 | 0.10 | -0.28 | 0.02 | -0.17 | 0.26 | -0.28 | 0.17 | | |
| L53 × L18 | -0.14 | -0.02 | 0.20 | 0.08 | 0.26 | -0.10 | -0.51 | -0.59 | -0.20 | | |
| L53 × L28 | 0.02 | 0.06 | 0.07 | 0.14 | -0.09 | 0.20 | -0.12 | 0.16 | -0.17 | | |
| L53 × Sd7 | 0.32 | 0.22 | 0.14 | 0.08 | -0.04 | 0.16 | 0.02 | 0.51 | -0.23 | | |
| Sk5 × L18 | -0.04 | 0.02 | 0.03 | -0.15 | -0.23 | -0.16 | 0.48 | 0.60 | 0.66 | | |
| Sk5 × L28 | 0.12 | -0.10 | -0.18 | -0.05 | -0.19 | -0.31 | 0.12 | 0.38 | 0.40 | | |
| Sk5 × Sd7 | -0.03 | 0.00 | 0.29 | 0.14 | 0.30 | 0.17 | -0.25 | -0.69 | -0.55 | | |
| L18 × L28 | 0.13 | 0.41 | 0.66 | 0.21 | 0.08 | 0.36 | -0.28 | -0.62 | -1.02 | | |
| L18 × Sd7 | -0.15 | -0.07 | -0.72 | 0.07 | 0.06 | -0.03 | 0.10 | -0.33 | 0.21 | | |
| L28 × Sd7 | -0.24 | -0.52 | -0.60 | -0.23 | -0.17 | -0.13 | 0.18 | 0.87* | 0.72 | | |
| SE S _{ii} – S _{ik} | 0.97 | 0.66 | 0.90 | 0.89 | 0.21 | 0.87 | 1.05 | 0.50 | 0.90 | | |
| SE S _{ii} – S _{kl} | 0.79 | 0.54 | 0.73 | 0.73 | 0.17 | 0.71 | 0.85 | 0.41 | 0.73 | | |

| | | GYPP | | | GYPH | | | РҮРН | |
|--------------------------------------|----------|----------|----------|-----------|-----------|-----------|----------|---------|----------|
| L20 × L53 | 20.88** | 30.32** | 19.69** | 2.97** | 4.26** | 4.08** | 28.52 | 50.87* | 22.43 |
| L20 ×SK5 | -18.21** | -26.79** | -27.29** | -2.73** | -3.66** | -5.65** | -42.12* | -52.26* | -96.11** |
| L20 × L18 | 3.43 | 12.38** | 18.70** | 0.53 | 1.38 | 3.87** | 18.25 | 14.02 | 53.25** |
| L20 × L28 | 2.93 | -7.74* | 1.48 | 0.44 | -0.96 | 0.31 | 8.15 | -8.10 | 10.11 |
| L20 × Sd7 | -9.03* | -8.17* | -12.57* | -1.22* | -1.02 | -2.60* | -12.81 | -4.54 | 10.31 |
| L 53 × Sk5 | 0.34 | 6.80* | 11.12* | 0.14 | 0.79 | 2.30* | 2.41 | 12.36 | 39.07* |
| L53 × L18 | -23.56** | -33.38** | -31.18** | -3.62** | -4.49** | -6.46** | -57.09** | -68.40* | -79.87** |
| L53 × L28 | 2.40 | -10.39* | -19.96** | 0.43 | -1.25 | -4.14** | 10.29 | -14.15 | -50.60** |
| L53 × Sd7 | -0.06 | 6.65* | 20.32** | 0.09 | 0.69 | 4.21** | 15.87 | 19.32 | 68.98** |
| Sk5 × L18 | 30.40** | 30.18** | 27.08** | 4.39** | 3.99** | 5.61** | 64.97** | 64.41* | 86.40** |
| Sk5 × L28 | 4.67 | 14.00** | 21.39** | 0.65 | 1.94* | 4.43** | 14.91 | 26.17 | 58.95** |
| Sk5 × Sd7 | -17.21** | -24.19** | -32.30** | -2.45** | -3.07** | -6.69 | -40.17* | -50.68* | -88.31** |
| L18 × L28 | -23.29** | -15.37** | -21.03** | -3.20** | -2.01* | -4.36** | -48.29** | -24.93 | -43.63* |
| L18 × Sd7 | 13.02** | 6.20 | 6.43 | 1.90** | 1.13 | 1.33 | 22.17 | 14.90 | -16.15 |
| L28 × Sd7 | 13.28** | 19.50** | 18.12** | 1.68** | 2.27** | 3.75** | 14.94 | 21.00 | 25.17 |
| SE S _{ii} – S _{ik} | 5.34 | 5.20 | 6.91 | 0.72 | 1.09 | 1.35 | 22.91 | 37.66 | 23.53 |
| SE S _{ii} – S _{kl} | 4.36 | 4.24 | 5.64 | 0.59 | 0.89 | 1.10 | 18.71 | 30.75 | 19.21 |
| | | ОҮРН | | | SYPH | | | | |
| L20 × L53 | 17.23* | 18.49* | 18.42* | 315.91** | 435.87** | 436.06** | | | |
| L20 ×SK5 | -0.73 | -16.21 | -6.44 | -302.79** | -367.99** | -605.99** | | | |
| L20 × L18 | -4.94 | 2.45 | 20.62* | 59.90** | 168.15* | 399.83** | | | |
| L20 × L28 | -1.06 | 6.30 | -3.45 | 49.39** | -121.46 | 32.52 | | | |
| L20 × Sd7 | -10.50 | -11.02 | -29.16** | -122.41** | -114.56 | -262.42* | | | |
| L 53 × Sk5 | -11.60* | 6.80 | 3.61 | 23.36** | 65.78 | 239.20* | | | |
| L53 × L18 | -17.88** | -17.98* | -41.72** | -383.72** | -467.02** | -657.59** | | | |
| L53 × L28 | 8.52 | -11.18 | -16.26* | 35.93** | -119.00 | -421.09** | | | |
| L53 × Sd7 | 3.73 | 3.89 | 35.95** | 8.52** | 84.37 | 403.41** | | | |
| Sk5 × L18 | 20.81** | 15.77 | 27.68** | 456.77** | 417.21** | 591.25** | | | |
| Sk5 × L28 | 1.78 | 4.65 | 10.57 | 72.15** | 207.03* | 460.21** | | | |
| Sk5 × Sd7 | -10.26 | -11.01 | -35.42** | -249.48** | -322.04** | -684.67** | | | |
| L18 × L28 | -12.14* | -9.07 | -13.05* | -326.89** | -218.57* | -474.41** | | | |
| L18 × Sd7 | 14.14* | 8.84 | 6.46 | 193.95** | 100.23 | 140.92 | | | |
| L28 × Sd7 | 2.90 | 9.31 | 22.18** | 169.42** | 252.00** | 402.77** | | | |
| SE S _{ij} – S _{ik} | 8.61 | 13.13 | 10.25 | 1.22 | 111.81 | 140.98 | | | |
| SE S _{ii} – S _{kl} | 7.03 | 10.72 | 8.37 | 1.00 | 91.29 | 115.11 | | | |

Al-Naggar et al.; JABB, 8(4): 1-19, 2016; Article no.JABB.28127

3.6 SCA Effects of Diallel Crosses

Estimates of specific combining ability effects (SCA) of F1 diallel crosses for studied traits under the six environments are presented in Table (8). The best crosses in SCA effects were considered those exhibiting significant positive SCA effects for all studied traits. For GYPP, GYPH and SYPH, the largest positive and significant SCA effects were recorded by the cross Sk5 × L18 followed by L20 × L53 and L28 × Sd7 under the three environments. For OYPH, the highest (favorable) positive and significant SCA effects were exhibited by the crosses Sk5 x L18 and L20 × L53 under the 3 environments and L20 × L18 under high-D. For PYPH, the highest positive and significant SCA effects were shown by the cross Sk5 x L18 under all environments followed by L20 x L18, L53 x Sd7 under high-D, L20 x L53 under medium-D. These crosses may be recommended for maize breeding programs for the improvement of tolerance to high plant density [50-52].

It is worthy to note that for the studied traits, most of the best crosses in SCA effects for a given trait included at least one of the best parental inbred lines in GCA effects for the same trait. The same conclusion was confirmed previously by some investigators [37,49].

For grain chemical composition traits (GPC, GOC and GSC), the values of SCA effects were mostly non-significant and small in magnitude. However, the highest positive SCA effects were shown by L18 x L28 and L20 x Sd7 under medium and high-D L53 x Sd7 under low-D, for GPC, L20 x Sk5 under all environments except medium-D, L20 x L28 and Sk5 x Sd7 under medium-D, L18 x L28 under low and high-D for GOC and Sk5 x L18 under the three environments, L28 x Sd6 and L20 x L18 under medium-D for GSC trait.

In this study, it could be concluded that the F_1 cross Sk5 x L18 is superior to other crosses in SCA effects for the yield traits, GYPH, PYPH, OYPH, SYPH under stressed and non-stressed environments. The crosses L20 x L53, L18 x Sd7 and L28 x Sd7 follow the cross Sk5 x L18 in superiority for such traits. These crosses could be offered to plant breeding programs for improving tolerance to high plant density tolerance at flowering.

3.7 Correlations among Performance, GCA and SCA Effects and Heterosis

Rank correlation coefficients calculated between mean performance of inbred parents (\overline{x}_{p}) and their GCA effects, between mean performance of F_1 's (\overline{x}_c) and their SCA effects and heterobeltiosis and between SCA effects and heterobeltiosis, for studied characters are presented in Table (9). Out of 8 studied traits, significant (P≤ 0.05 or 0.01) correlations between \overline{x}_{p} and GCA effects existed for 6 traits, namely GPC, GYPP, GYPH, PYPF, OYPF and SYPF under all environments and GOC under high-D. Such significant correlations between (\overline{x}_{p}) and their GCA effects in this investigation representing 75.0% of all studied cases (18 out of 24 cases) suggest the validity of this concept in the majority of studied traits, under all environments. These results indicate that the highest performing inbred lines are also the highest general combiners and vice versa for the previously mentioned traits and therefore, the mean performance of a given parent for these traits under the most studied environments is an indication of its general combining ability. This conclusion was previously reported by many investigators [53-56].

The trait which did not show any correlation between \overline{x}_p and GCA effects under all the six environments were GSC. In general, the environment high-D (the most stressed environment) showed significant correlations between \overline{x}_p and GCA effects for most studied traits (7 out 8 characters). The strongest correlation (highest in magnitude) between \overline{x}_p and GCA effects was shown by SYPH, GYPH and GYPP traits.

For F_1 crosses, rank correlation coefficients calculated between mean performance of crosses (\bar{x}_c) and their SCA effects (Table 9) showed that out of 8 studied traits, significant (P≤ 0.05 or 0.01) correlations existed for 5 traits under all environments, namely GYPP, GYPH, PYPF, OYPF and SYPF. Moreover, significant correlations existed in some environments for three traits, namely GPC under medium and high-D, GOC under low-D and GSC under low and medium-D. Such significant correlations between (\bar{x}_c) and SCA effects in this investigation representing 83.3% of all studied cases (20 out of 24 cases) suggest the validity of this concept in the majority of studied traits and

| Parameter | Low-D | Med-D | High-D | Low-D | Med-D | High-D | Low-D | Med-D | High-D |
|------------------------------|--------|--------|--------|--------|--------|--------|--------|--------|--------|
| | | GPC | | | GOC | | | GSC | |
| 🏅 vs. GCA | 0.89* | 0.71* | 0.70* | 0.23 | 0.17 | 0.93** | -0.27 | 0.18 | 0.55 |
| 🗓 <i>vs.</i> SCA | 0.33 | 0.66** | 0.57* | 0.82** | 0.28 | 0.39 | 0.65** | 0.57* | 0.32 |
| [™] c <i>vs.</i> H. | 0.52* | 0.32 | 0.34 | 0.65** | 0.91** | 0.45 | 0.85** | 0.35 | 0.56* |
| SCA vs.H | 0.37 | 0.52* | 0.61** | 0.66** | 0.27 | 0.67** | 0.33 | 0.27 | 0.24 |
| | | GYPP | | | GYPH | | | PYPH | |
| [™] <i>vs.</i> GCA | 0.91* | 0.94** | 0.97** | 0.88* | 0.97** | 0.97** | 0.77* | 0.90** | 0.93** |
| 🗓 <i>vs.</i> SCA | 0.67** | 0.68** | 0.71** | 0.68** | 0.67** | 0.71** | 0.83** | 0.67** | 0.82** |
| [™] c <i>vs.</i> H. | -0.36 | -0.16 | -0.20 | -0.28 | -0.13 | -0.30 | -0.18 | -0.21 | -0.27 |
| SCA vs.H | 0.27 | 0.42 | 0.32 | 0.30 | 0.46 | 0.29 | 0.21 | 0.39 | 0.12 |
| | | OYPH | | | SYPH | | | | |
| [™] <i>vs.</i> GCA | 0.72* | 0.87* | 0.92** | 0.89** | 0.98** | 0.97** | | | |
| ະ vs. SCA | 0.53* | 0.53* | 0.58* | 0.69** | 0.69** | 0.70** | | | |
| [™] c <i>vs.</i> H. | -0.25 | -0.12 | -0.12 | -0.27 | -0.12 | -0.32 | | | |
| SCA vs.H | 0.33 | 0.41 | 0.28 | 0.30 | 0.46 | 0.29 | | | |

Table 9. Rank correlation coefficients among mean performance of inbreds (\bar{x}_p) and their GCA effects, mean performance of F₁'s (\bar{x}_c) and their SCA effects and heterosis (H) and each of \bar{x}_c and SCA effects under three plant densities across 2013 and 2014 seasons

environments. All correlations between (\overline{x}_{c}) and SCA effects in the present study, were positive for all traits. These results indicate that the highest performing crosses are also the highest specific combiners and vice versa for the previously mentioned traits and therefore, the mean performance of a given cross for these traits under the respective environments is an indication of its specific combining ability. This conclusion was previously reported by Srdic et al. [57] and Al-Naggar et al. [49]. In general, the environment high-D (the most stressed environment) showed significant correlations between (\bar{x}_{c}) and SCA effects for 7 out of 8 studied traits. This conclusion was also reported by Le Gouis et al. [54] and Yildirim et al. [55] under stress conditions.

Significant correlations between mean performance of crosses (\overline{x}_{c}) and heterobeltiosis (Table 9) were exhibited only in 5 out of 24 cases (20.83%), namely GOC (except E3), and GSC (except E2), GPC under low-D. For these traits, the mean performance of a cross could be used as an indicator of its useful heterosis under the corresponding environments. The traits GYPP, GYPH, PYPF, OYPF and SYPF; i.e. yield traits did not exhibit any correlation between χ_{c} and heterobeltiosis under all (three) environments and therefore. SCA effects of crosses could not be expected from their per se performance in such cases.

Significant correlations between crosses SCA effects and heterobeltiosis (Table 9) were

exhibited only in 4 out of 24 cases (16.66%), namely GOC under low and high-D, GPC under medium and high-D. For these traits, the useful heterosis of a cross could be used as an indicator of its SCA effects under the corresponding environments. The traits GSC, GYPP, GYPH, PYPF, OYPF and SYPF; i.e. yield traits, and grain starch content did not exhibit any correlation between SCA effects and heterobeltiosis under all (three) environments and therefore. SCA effects of crosses could not be expected from their heterobeltiosis values in such cases.

4. CONCLUSIONS

The present study identified three inbreds (L53, L20 and Sk5) and three F1 crosses (L20 x L53, L53 x Sk5 and L53 x Sd7) of good performance for all yield traits (GYPP, GYPH, PYPH OYPH and SYPH) under high as well as low plant density. These genotypes could be offered to plant breeding programs for improving tolerance to elevated plant density. For GYPP, GYPH, PYPH OYPH and SYPH under elevated plant density, the non-additive variance was more important than additive variance, suggesting that the heterosis breeding method is the best choice for improving these traits, but the opposite was true for grain protein (GPC), grain oil (GOC) and grain starch (GSC), indicating that the selection in segregating generations would be effective in improving such traits. Correlation analyses of this investigation concluded that for most studied yield traits in this investigation under the three

plant densities, the mean performance of a given parent could be considered an indication of its general combining ability and the mean performance of a given cross could be considered an indication of its specific combining ability. But the mean performance of a given cross could not be considered an indication of its heterobeltiosis, and the heterobeltiosis of a given cross could not be used as an indication of its SCA effects, except in few cases.

COMPETING INTERESTS

Authors have declared that no competing interests exist.

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