

Full Length Research Paper

Genotype by environment interactions for grain yield in bread wheat (*Triticum aestivum* L.)

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Accepted 27 May, 2013

The combined ANOVA analysis for grain yield of ten wheat genotypes at 12 environments showed that bread wheat grain yield was significantly affected by environment, which explained 75.01% of the total treatment (genotype + environment + genotype by environment interactions) variation, whereas the G and GEI were significant and accounted for 9.48 and 15.5%, respectively. The additive main effects and multiplicative interactions (AMMI) analysis indicated that three principal component analysis (PCA) were significant ($P < 0.01$). PCA 1, 2 and 3 accounted for 65.49, 17.10 and 10.11% of the genotype + environment (GE) interaction, respectively. Graphical display of genotype by environment interaction (GGE-biplot) based on genotype-focused scaling was depicted in order to detect the locations of genotypes, whereas the wheat genotypes were divided into four groups based on their scores of PCA 1 and 2: Three stable and high yielding genotypes (G2, 10 and 6), two unstable high yielding genotypes (G4 and 1), three stable low yielding genotypes (G5, 7 and 8) and two low yielding unstable genotypes (G9 and 3). The correlation coefficients among the twelve test environments and the vector view of the GGE-biplot provided a succinct summary of the interrelationship between the environments whereby only 38 of the 67 correlation coefficients were significant. All environments were positively correlated except the environment E5 which was negatively correlated with E9, 12 and 10. The G10 (Giza 168) is adaptable for a wide range of environment conditions.

Key words: Additive main effects and multiplicative interactions (AMMI), additive main effects and multiplicative interaction, bread wheat, genotype by environment interaction (GEI), genotype x environment interaction, principal component analysis (PCA).

INTRODUCTION

Globally, wheat is an important cereal crop which is receives the most attention of specialists in plant breeding and production. However, its production is limited by the adverse environmental conditions. Meanwhile, genotype by environment interaction (GEI) refers to the differential responses of different genotypes across a range of environments (Kang, 2004). This is a universal issue relating to all living organisms, from bacteria to plants to humans (Kang, 1998), and it is important in agricultural, genetic, evolutionary, and statistical research. In breeding programs, genotype x

environment interaction (G x E) interactions cause many difficulties, whereas the environmental factors such as temperature and drought stress affect the performance of genotypes. Genotype + environment (GE) interaction reduces the genetic progress in plant breeding programs through minimizing the association between phenotypic and genotypic values (Comstock and Moll, 1963). Multi-environment yield trials are essential in estimation of genotype by environment interaction (GEI) and identification of superior genotypes in the final selection cycles (Kaya et al., 2006 and Mitrovic et al., 2012).

The use of different planting dates allow for subjecting the plant at different developmental stages to various temperature regimes. However, high temperatures which lead to heat stress during the grain filling period are a major environmental factor which drastically reduces wheat production in upper Egypt (Kheiralla et al., 2001). The heat stress also limits wheat (*Triticum aestivum* L.) productivity in arid, semiarid, tropical and subtropical regions of the world (Ashraf and Harris, 2005).

Consequently, development of heat-tolerant cultivars is of importance in wheat breeding programs. A detailed understanding of the genetics and physiology of heat tolerance as well as the use of the proper germplasm and selection methods will facilitate the development of heat tolerant cultivars (Mohammadi et al., 2007). Selection for high yield potential has frequently led to some yield improvements under stress conditions (Araus et al., 2002, 2008). In these cases, the breeders select plants characterized by high yield potential and high yield stability, with the latter being attributed to a minimal G x E interaction. This implies that the traits which maximize productivity in the absence of stress could still sustain a significant yield improvement under mild to moderate stress (Slafer et al., 2005; Tambussi et al., 2005). Phenotypes are a mixture of genotype (G) and environment (E) components and interactions (G x E) between them. G x E interactions complicate the process of selecting genotypes with superior performance. Consequently, Multi-environment trials (METs) are widely used by plant breeders to evaluate the relative performance of genotypes for target environments (Delacy et al., 1996).

Numerous methods have been developed to reveal patterns of GxE interaction, such as joint regression (Finlay and Wilkinson, 1963; Perkins and Jinks, 1968), sum of squared deviations from regression (Eberhart and Russel, 1966), stability variance (Shukla, 1972), coefficient of determination (Pinthus, 1973), coefficient of variability (Francis and Kanneberg, 1978), and Type B genetic correlation (Burdon, 1977).

These methods are commonly used to analyze MET data to reveal patterns of GE interaction. Alternatively, the additive main effects and multiplicative interaction (AMMI) model have led to more insight in the complicated patterns of genotypic responses to the environment (Gauch and Zobel, 1988; Zobel et al., 1988; Gauch, 1992; 2006). These patterns have been successfully related to biotic and abiotic factors.

Yan et al. (2000) proposed another methodology known as GGE-biplot for graphical display of GE interaction pattern of MET data with many advantages. GGE biplot is an effective method based on principal component analysis (PCA) which fully explores MET data. It allows visual examination of the relationships among the test environments, genotypes and the GE interactions. The first two principle components (PC1 and 2) are used to produce a two dimensional graphical display of genotype by environment interaction (GGE-biplot). If

a large portion of the variation is explained by these components, a rank-two matrix, represented by a GGE-biplot, is appropriate (Yan and Kang, 2003). Using a mixed model analysis may offer superior results when the regression of genotype by environment interaction on environment effect does not explain all the interaction (Piepho, 1997; Yan and Rajcan, 2002).

In this work, we have attempted to describe G x E interaction of grain yield by characterizing genotypic responses to a set of contrasting environmental conditions. To provide insight into G x E, external genotypic and environmental information has been incorporated into statistical models that allow a direct interpretation of G x E (Denis, 1988; Van Eeuwijk et al., 1996). As a preliminary exploratory tool, AMMI (additive main effects and multiplicative interaction) models were used to represent an additive component, and the effect of interaction (Gauch, 1992). GGE-biplots representing mean vs. stability and "ideal" genotype was constructed with genotype focus scaling for comparison the genotypes with the ideal genotype.

MATERIALS AND METHODS

This study was carried out in 2010/2011 and 2011/2012 seasons at the Research Farm of Faculty of Agriculture, Sohag University, Egypt. The soil was reclaimed with top layer (25 cm) of clay-loam. Ten genetically diverse wheat cultivars differing in adaptation to heat and drought stress were used in this study Table 1. Field experiments were carried out in 12 environments; 2 years, 2 sowing dates and 3 drought treatments Table 2. The experimental layout at each environment was a completely randomized block design with three replicates. In each environment, plot size was 10.5 m², the drought treatments were normal irrigation, withholding water from tillering up to anthesis and from anthesis to maturity and the two sowing dates used were 15 November and 5 December in both seasons. All other agricultural practices were applied as recommended. The grain yield (t/ha) was obtained by converting plot grain yield (kg) to productivity tons per hectare.

Statistical analysis

Analysis of variance is calculated using the model:

$$Y_{ij} = \mu + G_i + E_j + GE_{ij}$$

Where Y_{ij} is the corresponding variable of the i-th genotype in j-th environment, μ is the total mean, G_i is the main effect of i-th genotype, E_j is the main effect of j-th environment, GE_{ij} is the effect of genotype x environment interaction.

The AMMI model used was:

$$Y_{ij} = \mu + g_i + e_j + \sum_{k=1}^N \lambda_k Y_{ik} \delta_{jk} + \varepsilon_{ij}$$

Where Y_{ij} is the grain yield of the i-th genotype in the j-th environment, μ is the grand mean, g_i and e_j are the genotype and environment deviation from the grand mean, respectively, λ_k is the eigenvalue of the principal component analysis (PCA) axis k, Y_{ik} and δ_{jk} are the genotype and environment principal component

Table 1. List of Egyptian Bread wheat entries and their pedigree which were evaluated in 12 environments.

| Code G | Name | Pedigree |
|--------|------------|---|
| 1 | Giza 164 | Kavkas/Buho "s"//Kal/Bluebird =Veery #5 |
| 2 | Sakha 8 | Indus/Norteno "s" |
| 3 | Sakha 69 | Inia - RL 4220//Siete Cerros/Yaqui 50 |
| 4 | Gemmeiza 3 | Bb/Siete Cerros/Yaqui 50/Kal*3//Sakha 8/4/Prv/WW/3/3/Bg"s"ON CGM- 4024-1-GM-2GM-0GM |
| 5 | Gemmiza 7 | CMH74 A. 630/5x//Seri 82/3/Agent |
| 6 | Sids 1 | HD2172/Pavon "s"//1158.57/Maya74 "s" |
| 7 | Gemmeiza 1 | Maya "s"/On//1160 147/3/Bluebird/Gal 1/4/Chat "s" |
| 8 | Sahel 1 | N.S.732/Pim /Vee"s"Sd735-4sd-1sd-)sd |
| 9 | Giza 165 | Ciano/ Maris Fundin//Mantaro |
| 10 | Giza 168 | MRL/BUC//Seri.z |

Table 2. Characterization of the 12 environments used in this investigation.

| Code E | Sowing date | Drought stress stage | Cropping season |
|--------|-------------|--|-----------------|
| 1 | 15 November | S ₀ : Normal irrigation | 2010 - 2011 |
| 2 | 15 November | S ₁ : Withholding water from tillering up to anthesis | 2010 - 2011 |
| 3 | 15 November | S ₂ : Withholding water from anthesis up to maturity | 2010 - 2011 |
| 4 | 5 December | S ₀ : Normal irrigation | 2011 - 2012 |
| 5 | 5 December | S ₁ : Withholding water from tillering up to anthesis | 2011 - 2012 |
| 6 | 5 December | S ₂ : Withholding water from anthesis up to maturity | 2011 - 2012 |
| 7 | 15 November | S ₀ : Normal Irrigation | 2010 - 2011 |
| 8 | 15 November | S ₁ : Withholding water from tillering up to anthesis | 2010 - 2011 |
| 9 | 15 November | S ₂ : Withholding water from anthesis up to maturity | 2010 - 2011 |
| 10 | 5 December | S ₀ : Normal irrigation | 2011 - 2012 |
| 11 | 5 December | S ₁ : Withholding water from tillering up to anthesis | 2011 - 2012 |
| 12 | 5 December | S ₂ : Withholding water from anthesis up to maturity | 2011 - 2012 |

scores for axis k, N is the number of principal components retained in the model, and ϵ_{ij} is the residual term.

GGE-biplot methodology, which is composed of 2 concepts, the biplot concept (Gabriel, 1971) and the GGE concept (Yan et al., 2000) was used to visually analyze the METs data. This methodology uses a biplot to show the factors (G and GE) that are important in genotype evaluation and that are also the source of variation in GEI analysis of METs data (Yan et al., 2000; 2001). The GGE-biplot shows the first 2 principal components derived from subjecting environment centered yield data (yield variation due to GGE) to singular value decomposition (Yan et al., 2000). In the current study, genotype-focused scaling was used in visualizing for genotypic comparison, with environment-focused scaling for environmental comparison. The statistical analysis was conducted using GenStat 12th edition (Glaser, 2010).

RESULTS AND DISCUSSION

The combine ANOVA and AMMI analysis for grain yield at 12 environments showed that bread wheat grain yield was significantly affected by E, which explained 75.01% of the total treatment (G+E+GEI) variation, whereas the G and GEI were significant and accounted for 9.48 and

15.5%, respectively (Table 3). Similar findings have been reported in previous studies (Kaya et al., 2006; Farshadfar et al., 2012). According to Gauch and Zobel (1996, 1997), in standard multi-environment trials (METs), environment effect contributes 80% of the total sum of treatments and 10% effect of genotype and interaction. In additive variance, the portioning of GEs data matrix by using AMMI analysis indicated that three PCAs were significant ($P < 0.01$). PCA 1, 2, and 3 accounted for 65.49, 17.10 and 10.11% of the GE interaction, respectively representing a total of 92.70% of the interaction variation (Table 3).

Similar results have been reported in earlier studies Mohammadi and Amri (2009). The large yield variation explained by environments indicated that the environments were diverse, with large differences between environmental means contributing most of the variation in grain yield. Grain yield of environments ranged from 2.331 t/ha in E4 to 5.751 t/ha in E1. Genotype grain yield ranged from 3.394 t/ha in G9 to 5.087 t/ha in G10 (Table 4).

A GGE-biplot based on genotype-focused scaling was depicted in order to detect the locations of genotypes,

Table 3. AMMI analysis of variance for grain yield (t/ha) of 10 bread wheat genotypes grown at 12 environments.

| Source | df | SS | MS | F | % SS | Prob. |
|---------------|-----|--------|-------|--------|-------|-------|
| Block | 24 | 9.24 | 0.385 | 1.40 | | N.S |
| Treatment | 119 | 611.30 | 5.14 | 18.69 | | ** |
| Genotypes | 9 | 57.95 | 6.44 | 23.42 | 9.48 | ** |
| Env. | 11 | 458.57 | 41.69 | 151.60 | 75.01 | ** |
| Gen. and Env. | 99 | 94.75 | 0.96 | 3.491 | 15.5 | ** |
| IPCA 1 | 19 | 62.05 | 3.26 | 11.85 | 65.49 | ** |
| IPCA 2 | 17 | 16.20 | 0.95 | 3.45 | 17.10 | ** |
| IPCA 3 | 15 | 9.58 | 0.64 | 2.33 | 10.11 | ** |
| IPCA 4 | 13 | 5.31 | 0.41 | 1.49 | 5.56 | NS |
| Residual | 35 | 1.51 | 0.043 | 0.156 | 1.59 | NS |
| Error | 216 | 59.40 | 0.275 | | | |
| Total | 359 | 679.94 | 1.71 | | | |

**Significant at the 0.01 level of probability; Gen., genotype; Env., environment.

Table 4. Average grain yield of 10 bread wheat genotypes tested across 12 environments.

| Gen / Env | E1 | E2 | E3 | E4 | E5 | E6 | E7 | E8 | E9 | E10 | E11 | E12 | Mean |
|-----------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|--------|
| 1 | 6.103 | 5.235 | 3.154 | 2.99 | 3.543 | 5.605 | 4.980 | 3.424 | 3.441 | 6.262 | 5.276 | 5.313 | 4.611 |
| 2 | 5.789 | 4.146 | 3.178 | 2.575 | 5.711 | 5.21 | 4.369 | 3.233 | 2.822 | 5.722 | 5.215 | 5.117 | 4.424 |
| 3 | 5.344 | 3.945 | 2.711 | 2.306 | 3.768 | 4.664 | 3.800 | 2.799 | 2.663 | 3.318 | 4.403 | 4.44 | 3.847 |
| 4 | 6.590 | 4.349 | 3.181 | 1.992 | 6.322 | 5.676 | 4.678 | 3.384 | 2.044 | 6.477 | 5.784 | 5.682 | 4.68 |
| 5 | 5.486 | 3.867 | 2.453 | 2.346 | 5.061 | 4.662 | 3.777 | 2.522 | 2.749 | 5.531 | 4.991 | 4.507 | 3.996 |
| 6 | 5.727 | 3.915 | 3.676 | 2.184 | 4.463 | 5.202 | 4.224 | 3.714 | 2.209 | 5.416 | 4.336 | 5.091 | 4.18 |
| 7 | 6.124 | 3.143 | 2.865 | 1.825 | 4.153 | 4.291 | 2.627 | 2.785 | 1.995 | 5.761 | 4.175 | 4.118 | 3.655 |
| 8 | 4.604 | 3.383 | 3.205 | 2.284 | 4.589 | 4.331 | 3.613 | 2.625 | 2.614 | 4.533 | 4.114 | 4.179 | 3.628 |
| 9 | 5.231 | 2.993 | 1.842 | 1.631 | 4.974 | 3.943 | 2.765 | 1.846 | 1.992 | 5.185 | 4.51 | 3.821 | 3.394 |
| 10 | 6.509 | 4.635 | 4.198 | 3.177 | 6.336 | 5.902 | 4.941 | 4.193 | 3.307 | 6.294 | 5.610 | 5.828 | 5.078 |
| Mean | 5.751 | 3.961 | 2.992 | 2.331 | 4.892 | 4.949 | 3.977 | 3.053 | 2.584 | 5.65 | 4.841 | 4.81 | 4.1493 |

Gen., genotype; Env., environment.

where the genotypes that had PC1 scores > 0 were identified as higher yielding, while the genotypes that had PC1 scores < 0 were identified as lower yielding (Figure 1 and Table 4). In contrast PC2, which was related to genotypic stability or instability, divided the genotypes of interest into four groups based on their scores. The first group included three stable genotypes (G2, 10 and 6) that were the highest yielding, since near-zero PC2 scores showed genotypic stability. Group 2 included two unstable genotypes (G4 and 1) that were higher yielding, as absolute larger PC2 scores were associated with genotypic stability, while the group 3 (G5, 7 and 8) were low yielding and stable genotypes, and Group 4 consist of 2 genotypes (G9 and 3) that were low yielding and genotypic instability. These results are in agreements with those obtained by Kaya et al. (2006).

The estimation of yield and stability of genotypes (Figure 2) was done by using the average coordinates of the environment (AEC) methods (Yan, 2001; Yan and

Hunt, 2001). The average environment is defined by the average values of PC1 and 2 for the all environments and it is presented with a circle. The average ordinate environment (AOE) defined by the line which is perpendicular to the AEA (average environment axis) line and pass through the origin. This line divides the genotypes in to those with higher yield than average and in to those lower yield than average. By projecting the genotypes on AEA axis, the genotypes are ranked by yield, where the yield increases in the direction of arrow. In this study the highest yield had genotypes G10, 4, 1, 2, 6 and the lowers had G9, 7, 8, 3 and 5. Stability of the genotypes depends on their distance from the AE abscissa. Genotypes closer to abscissa are more stable than others. In this study, the greatest stability in the high yielding group had genotypes G10, 2 and 6, while the most stable of all was G10.

The genotype ranking is shown on the graph of genotype so-called "ideal" genotype (Figure 3). An ideal

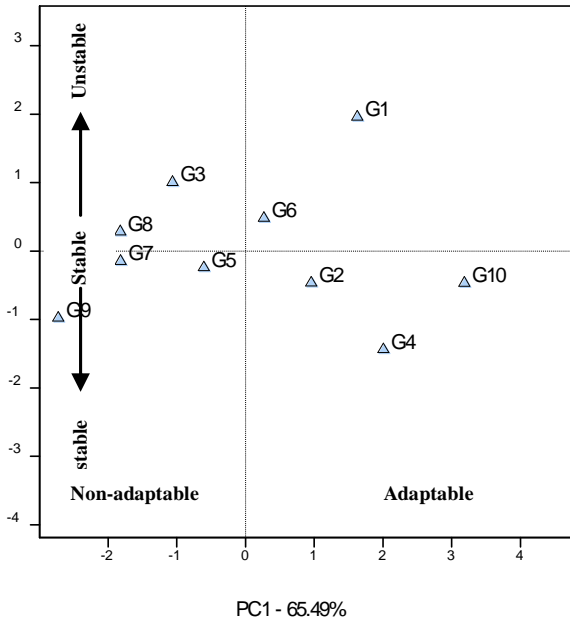


Figure 1. GGE-biplot based on genotype-focused scaling for genotype. PC and G stand for principal component and genotypes, respectively.

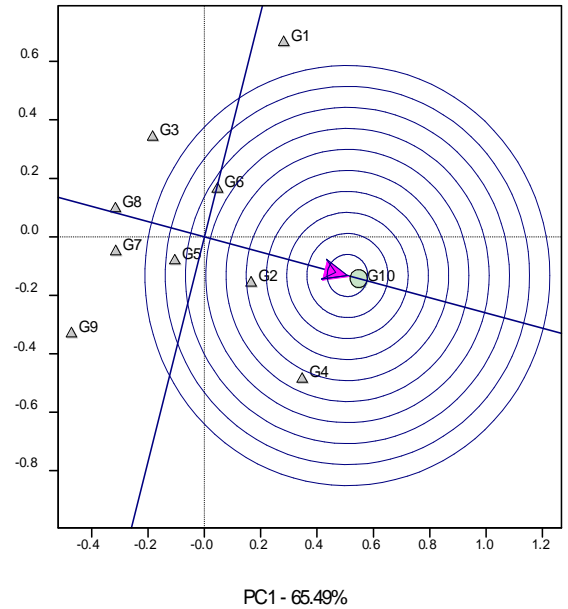


Figure 3. GGE-biplot based on genotype-focused scaling for comparison the genotypes with the ideal genotype. PC and G stand for principal component and genotypes, respectively.

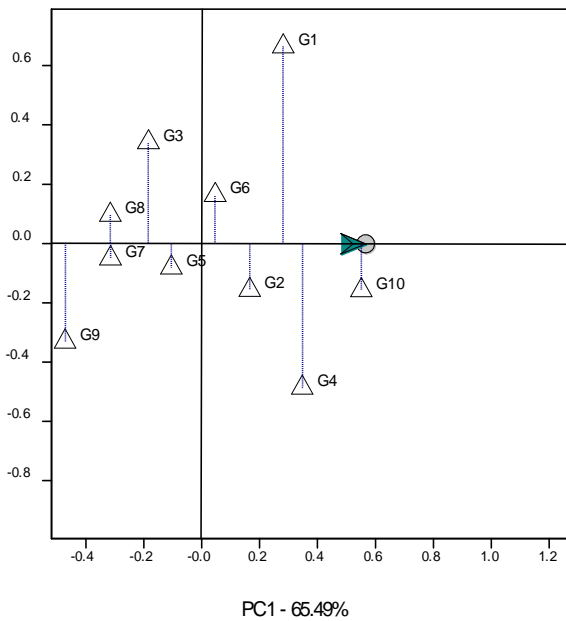


Figure 2. The “mean vs. stability” view of the GGE-biplot of 10 bread wheat genotypes across 12 environments.

genotype is defined as one that is the highest yielding across test environments and it’s absolutely stable in performance (that ranks the highest in all test environments) (Yan and Kang, 2003; Farshadfar et al., 2012). Although such an “ideal” genotype may not exist in reality, it could be used as a reference for genotype evaluation (Mitrovic et al., 2012). A genotype is more

desirable if it is located closer to “ideal” genotype (Kaya et al., 2006 and Mitrovic et al., 2012). The closer to the “ideal” genotype was G10 (Giza168).

The ideal test environment should have large PC1 scores (more power to discriminate genotypes in terms of the genotypic main effect) and small (absolute) PC2 scores (more representative of the overall environments). Such an ideal environment was represented by an arrow pointing to it (Figure 4). Although such an ideal environment may not exist in reality, it can be used as a reference for genotype selection in the METs. An environment is more desirable if it is located closer to the ideal environment. Thus, using the ideal environment as the center, concentric circles were drawn to help visualize the distance between each environment and the ideal environment (Yan et al., 2000; Yan and Rajcan, 2002).

Figure 4 indicated that E6, which fell into the center of concentric circles, was an ideal test environment in terms of being the most representative of the overall environments and the most powerful to discriminate genotypes. Favorable environments were E12, 7, 1, 2, 11, 5 and 10 while the unfavorable ones were E8, 9, 3, and 4. The favorable environments, together with E6, showed high yield potential ($> 4.00 \text{ t ha}^{-1}$, except E2 and 7), whereas the unfavorable ones had low yield potential ($< 3.00 \text{ t ha}^{-1}$ except E8) (Table 4).

The correlation coefficients among the 12 test environments (Table 5) and the vector view of the GGE-biplot (Figure 5) provided a succinct summary of the interrelationship between the environments. Table 5

Table 5. Correlation coefficients among 12 test environments.

| | E1 | E2 | E3 | E4 | E5 | E6 | E7 | E8 | E9 | E10 | E11 | E12 |
|----|---------|---------|---------|---------|--------|---------|---------|---------|---------|---------|---------|-----|
| 1 | 1 | | | | | | | | | | | |
| 2 | 0.534 | 1 | | | | | | | | | | |
| 3 | 0.640** | 0.582* | 1 | | | | | | | | | |
| 4 | 0.342 | 0.742** | 0.659** | 1 | | | | | | | | |
| 5 | 0.415 | 0.082 | 0.330 | 0.105 | 1 | | | | | | | |
| 6 | 0.734** | 0.653** | 0.823** | 0.805** | 0.408 | 1 | | | | | | |
| 7 | 0.831** | 0.884** | 0.732** | 0.792** | 0.331 | 0.796** | 1 | | | | | |
| 8 | 0.864** | 0.675** | 0.367 | 0.432 | 0.294 | 0.464 | 0.808** | 1 | | | | |
| 9 | 0.164 | 0.710** | 0.4267 | 0.410 | -0.248 | 0.324 | 0.462 | 0.436 | 1 | | | |
| 10 | 0.435 | 0.459 | 0.449 | 0.815** | -0.085 | 0.735** | 0.628* | 0.499 | 0.782** | 1 | | |
| 11 | 0.705** | 0.837** | 0.853** | 0.723** | 0.379 | 0.962** | 0.876** | 0.657** | 0.388 | 0.767** | 1 | |
| 12 | 0.733** | 0.632** | 0.608* | 0.632** | -0.131 | 0.770** | 0.749** | 0.416 | 0.752** | 0.874** | 0.743** | 1 |

*Significant at the 0.05 level of probability; **Significant at the 0.01 level of probability.

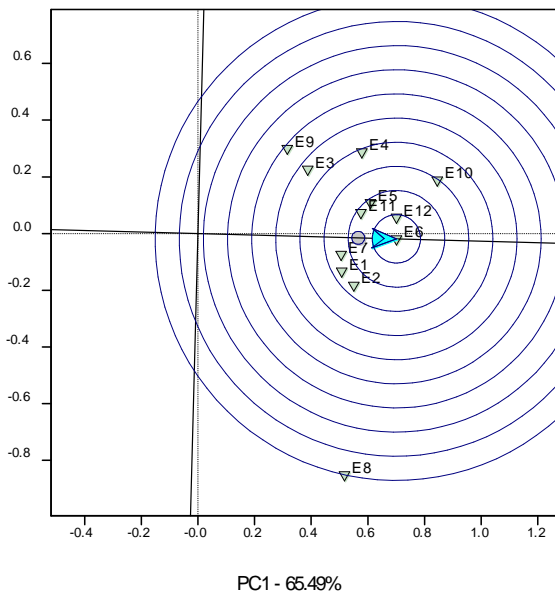


Figure 4. GGE-biplot based on the ranking of environments relative to an ideal environment. PC and E stand for principal component and environments, respectively.

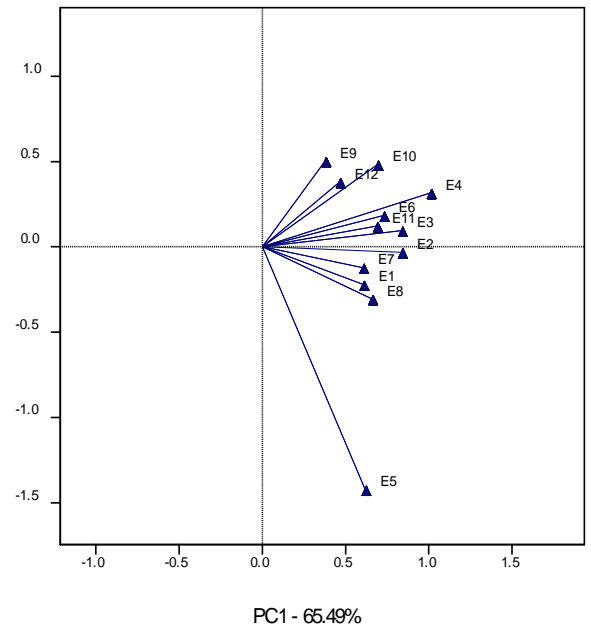


Figure 5. GGE-biplot based on environment-focused scaling for environments. PC and E stand for principal component and environments, respectively. Details of environments are given in Table 2.

contained 67 correlation coefficients, 38 of which were significant. All environments were positively correlated because all angles among them were smaller than 90°C except that environment E5 was negatively correlated with E9, 12 and 10, whereas the angles between them were more than 90°C (Figure 5). Farshadfar et al. (2012) in their study noted that the environments ER3 and EI3 which represented rain fed and irrigated conditions in 2011 cropping seasons, respectively, made an obtuse angle with each other, which indicated a negative correlation between the response of genotypes to rain fed and irrigated conditions in 2011 cropping season.

Indirect selection could be applied in the case where

the same character was measured on the same genotypes in different environments. Where there are no correlations of error effects among environments, the phenotypic correlation between environments maybe used to investigate indirect response to selection (Cooper and Delacy, 1994). Indirect selection for grain yield canbe partial across the tested environments for instance, the genotypes adaptable or higher productivity in E3 may also show similar responses to E4, 6, and 7 as well. However, indirect selection from one environment to another may not be sufficiently successful, considering

that 38 out of 67 environmental pair wise correlations were significant.

In our research both of AMMI and GGE-biplot models were successful in assessing the performance of genotypes and the selection of best genotypes was identical in both of them. Mitrovic et al. (2012) used both models to analyze 19 maize hybrids in 12 environments and reported that, the AMMI and GGE-biplot models were very useful in estimating the performance of maize genotypes, and there was no difference in the results obtained by both models. Similar results have been reported by Stojaković et al. (2010).

Conclusion

Based on the two analysis AMMI and GGE-biplot models, G10 (Giza 168), G2 (Sakha 8) and G6 (Sids 1) characterized by high yield and stability, therefore, the G10 (Giza 168) close to ideal genotype, so this variety is adaptable to a wide range for drought and heat stress conditions. In contrast G3 (Sakha 69) and G9 (Giza 165) were exhibited a lower score for both yield and stability, the present study suggested that Giza 168 variety is the most appropriate in the adverse environment conditions.

ABBREVIATIONS

PC, Principal component; **GEI**, genotype by environment interaction; **METS**, multi environment trials; **T**, ton; **Ha**, hectare; **AEC**, average coordinates of the environment; **AOE**, average ordinate environment; **AEA**, average environment axis; **G**, genotype; **E**, environment.

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