

Genotype × environment interaction by AMMI and GGE biplot analysis in three consecutive generations of wheat (*Triticum aestivum*) under normal and drought stress conditions

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Abstract

Thirty six wheat genotypes derived from diallel crosses from F₁ to F₃ and their parents were evaluated in six different environments for the stability of performance. Performance was measured by seed yield per plant under drought and non-drought stress conditions. The experiment was conducted as a randomised complete block design with three replications in over one year. Additive main effects and multiplicative interaction (AMMI) and Genotype main effect and genotype × environment interaction (GGE) were employed in the evaluation of genotypes; AMMI analyses showed significant ($P < 0.01$) G × E, (genotype × environment interaction) with respect to plant seed yield. The AMMI stability value (ASV) revealed that cross number 14 (Irena × Veery) is stable. GGE-biplot models showed that the six environments used for the study belonged to two mega-environments. The GGE results also confirmed crosses number 11 (Irena × Chamran) and 17 (S-78-11 × Chamran) as the most stable, and recommended for the creation of hybrids. Based on environment 3 (F₃ population, drought) with an inbreeding depression effect, hybrid number 17 (S-78-11 × Chamran) was identified as the best line due to its stability and high yield.

Keywords: Stability; GGE biplot; Wheat yield; AMMI analysis.

Abbreviation: AMMI - Additive main effects and multiplicative interaction; GGE - Genotype main effects and genotype × environment interaction effects; AEC - average environment coordinate; PCA - Principal components analysis; SVD- Singular value decomposition; GEI - Genotype-environment interaction.

Introduction

In segregated generations with allelic variation, individuals may be expressed differently in response to environments, so it is essential to develop varieties possessing stable performance. Therefore, by exploiting the good adaptation and stability of yield and its components in durum wheat genotypes, it would be possible to develop/identify high yielding and well adapted varieties. The development of high yielding cultivars with wide adaptability is the ultimate aim of plant breeders. However, attaining this goal is made more complicated by (GEI) genotype-environment interactions (Gauch and Zobel., 1996). Different methods are presented for statistical analysis, including parametric and non-parametric, to estimate the nature of genotype interactions with the environment and their control, but a method that has been approved by everyone has not still been introduced (Kaya et al., 2006). Two frequently used statistical analyses are the additive main effects and multiplicative interaction (AMMI) model and the genotype main effects and genotype × environment interaction effects (GGE) model (Gauch, 2006). These two statistical analyses (AMMI and GGE) have broader relevance for agricultural researchers because they pertain to any two-way data matrices, and such data emerge from many kinds of experiments. Concerning the use of

AMMI in multi-environmental trials (MET) data analysis, which partitions the GEI matrix into individual genotypic and environmental scores, an example was provided by Zobel et al. (1988). Purchase et al. (2000) developed a quantitative stability value to rank genotypes through the AMMI model, namely the AMMI Stability Value (ASV). In analysis of cultivar stability they found a significant correlation between the stability measures ASV, Shukla, Wricke (Wi) and Eberhart and Russel (S²d), but Finlay and Wilkinson (b) and Linn and Binns (Pi) showed limited association with any of the other methods. The developed ASV was considered to be the most appropriate single method of describing the stability of genotypes. The difference from AMMI is that GGE biplot analysis is based on environment-centred PCA, whereas AMMI analysis refers to double-centred PCA. For the research purpose of delineating mega-environments, both AMMI and GGE are suitable, and comparisons so far indicate similar results, as expected. For the research purpose of gaining accuracy, AMMI and GGE (as well as the shifted multiplicative model, etc.) are all equally capable (Gauch et al, 2008). Gruneberg et al. (2005) showed that AMMI, the multivariate tool, was highly effective for the analysis of MET. In recent years, this method has often been used by

international agricultural development agencies. On the other hand they consider the use of regression analysis questionable for MET. In comparing Tai's stability, AMMI and regression analysis, Manrique and Hermann (2002) concluded that regression analysis did not effectively identify stable clones, but did provide information on clone performance under improving environments. The most recent method, the GGE (genotype main effect (G) plus G x E interaction) biplot model, provides breeders a more complete and visual evaluation of all aspects of the data by creating a biplot that simultaneously represents mean performance and stability, as well as identifying mega-environments (Ding et al., 2007; Kang, 1993; Yan, 2001; Yan and Kang, 2003). The GGE biplot can be useful to display the which-won-where pattern of the data that may lead to identify high-yielding and stable cultivars and discriminating and representative test environments (Yan et al., 2001). The goal of this study was to evaluate the G x E interaction using AMMI and GGE biplot analysis for the plant grain yield of wheat crosses that were obtained from diallele crosses, in order to identify stable hybrids in stress and non-stress conditions.

Results and discussion

AMMI analysis

The combined analysis of variance showed that there are highly significant differences for environment, genotype and their interactions; combined analysis of variance and AMMI analysis is shown in Table 2. The combined ANOVA showed that bread wheat grain yields were significantly affected by the environment because of significant variance at 1% level (Table 2), which explained 51% of the total (G + E + GEI) variation, while G x E interaction captured 14.9% of the total sum of squares. A large sum of squares for environments indicated that the environments were diverse, with large differences among environmental means causing variation in the plant grain yields. The AMMI model demonstrated the presence of G x E interactions, and this has been partitioned among the first and second IPCA (Interaction Principal Components Axes). The plant grain yield variation is due to genotypic and environment factors, as shown in Table 1. Results from AMMI analysis (Table 2) also show that the first principal component axis accounted for 71.07% and the second accounted for 17.7%. Table 3 shows the AMMI model IPCA1 and IPCA2 scores of plant grain yield for each genotype and the AMMI stability value (ASV) for 36 wheat genotypes. According to ASV ranking, genotype number 14 (Irena x Veery) had the lowest value and the most stable genotype, while genotype numbers 1 and 30 (S-78-11 and Chamran x Hirmand) were unstable. Purchase et al. (2000) developed a quantitative stability value to rank genotypes through the AMMI model, named the AMMI Stability Value (ASV). During the analysis of cultivar stability they found a significant correlation between the stability measures ASV, Shukla, Wricke (Wi) and Eberhart and Russel (S^2d), but Finlay and Wilkinson (b) and Linn and Binns (Pi) showed limited correspondence with any of the other methods. The developed ASV was considered to be the most appropriate single method of describing the stability of genotypes.

Visualisation of mean performance and stability for seed yield

Visualisation of the which-won-where pattern of MEYTs data is important for studying the possible existence of different mega-environments (ME) in a region (Gauch and

Table 1. Drought stressed and normal environments

Environment	Generation	Moisture status
E1	F1	DS
E2	F2	DS
E3	F3	DS
E4	F1	N
E5	F2	N
E6	F3	N

DS:Drought stress, N:Normal

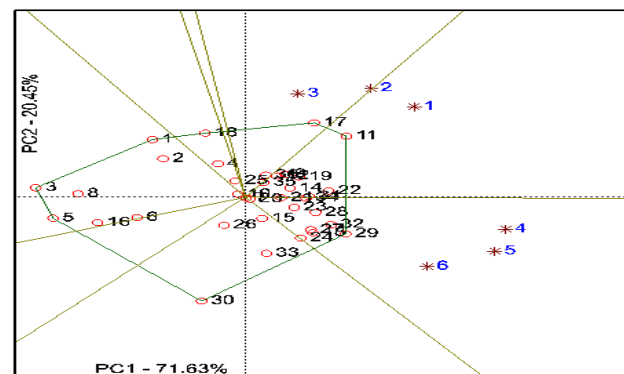


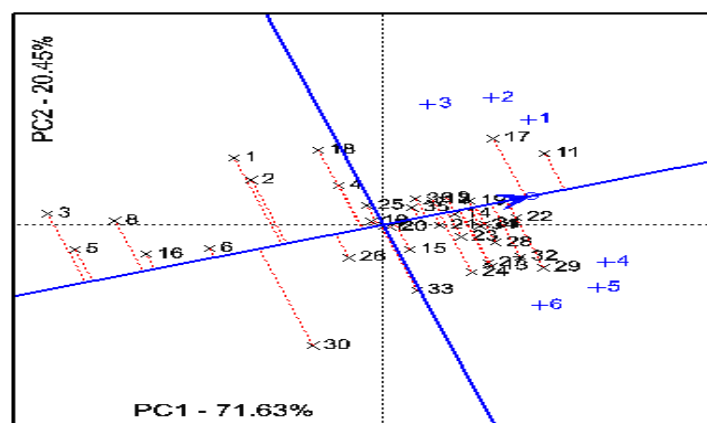
Fig 1. Polygon views of the GGE-biplot based on symmetrical scaling for the which-won-where pattern for genotypes and environments. Black and blue numbers stand for genotypes and environments, respectively.

Zobel, 1997; Yan et al., 2000, 2001). The polygon view of a GGE-biplot explicitly displays the which-won-where pattern, and, hence, is a succinct summary of the GEI pattern of a MEYT data set (Fig 1). By connecting the markers of the genotypes and the rays as depicted, the rays in Figure 1 are lines that are perpendicular to the sides of the polygon or their extensions. Ray 1 is perpendicular to the side that connects genotype numbers 17 and 11. These 8 rays divide the biplot into 9 sectors, but environments fall into three of them, so the genotype(s) vertex in these sectors may have higher or the highest yield compared to other parts in all environments (Yan, 2002). 2 environments (1 and 2) fell into sector 1 but environment (2) has a joint point between sector 1 and 9 and the vertex genotype for this sector was 11 (Irena x Chamran), suggesting a higher yielding cross for this environment. Three environments, 4, 5 and 6 (normal environments), fell into sector 2, which was delineated by Rays 2 and 3, and the vertex genotype for this sector was 29 (Chamran x Veery), suggesting that this is a higher-yielding genotype for these 3 environments. Environment 3, along with environment 2, fell into sector 9, which was delineated by Rays 1 and 8, and the higher yielding for this sector was identified by cross number 17 (S-78-11 x Chamran). These results were particularly interesting because of the participation of Chamran as a parent. At a glance there are two crosses for drought stress conditions, crosses 11 and 17, and one cross for non-stress conditions, number 29. The yield stability of genotypes was evaluated by an average environment coordination (AEC) method (Yan, 2001; Yan and Hunt, 2000; Yan, 2002). In this method, the average principal components will be used in all environments, as depicted in (Fig 2). A line is then drawn through this average environment and the biplot origin; this line is called the average environment axis and serves as the abscissa of the AEC. Unlike the AEC abscissa, this has one direction, with the arrow pointing to a greater genotype main effect; the AEC ordinate and either direction away from the biplot origin

Table 2. AMMI analysis of variance over six environments.

Source	DF	SS	MS	% Total SS	% TRT
Treatments	215	5205	24.21**	92.6	
Genotypes	35	1453	41.51**		25.8
Environments	5	2911	582.25**		51.9
Block	12	18	1.48		
Genotypes× Environments	175	840	4.80**		14.9
IPCA1	39	597	15.31**		71.07
IPCA2	37	149	4.02**		17.7
Residuals	99	94	0.95		
Error	420	394	0.94	7.4	
Total	647	5616	8.68		

**significant at 1% level.

**Fig 2.** Average environment coordination (AEC) views of the GGE-biplot based on environment-focused scaling for the means performance and stability of genotypes. Black and blue numbers stand for genotypes and environments, respectively.

indicates greater GEI effect and reduced stability. The AEC ordinate separates genotypes with below-average means from those with above-average means. Genotypes with above-average means were from 11 to 15, while genotypes with below-average means were from 25 to 3. Genotypic stability is quite crucial in addition to genotype yield mean; genotypes 14, 19, 20, 21 and 22 were more stable as well as having appropriate yield, while, conversely, 17, 24, and 29 were more variable. The ideal genotype should have the highest mean performance and be absolutely stable (Yan and Kang, 2003), which is represented by the dot with an arrow pointing to it (Fig 3). Such an ideal genotype is defined by having the greatest vector length of the high yielding genotypes and with zero GEI. Concentric circles were drawn to help visualise the distance between each genotype and the ideal genotype; a genotype is more desirable if it is located closer to the ideal genotype, so cross number 11 (Irena × Chamran), which fell into the centre of the concentric circles, was ideal in terms of higher yielding ability and stability. The remaining genotypes, like 22 (Tajan × Chamran) and 19 (S-78-11 × Moghan3) were situated in the next grades. Based on these results, cultivar chamran was identified as having a main role in producing adaptable genotypes. The vector view of the GGE-biplot (Fig 5) provides a succinct summary of the interrelationships among the environments; all environments were positively correlated because all of the angles among them were smaller than 90° and correlation within the drought stress environment groups (1, 2 and 3) and non-stress groups (4, 5 and 6) was more than between them, suggesting that indirect selection for grain yield can be practical across the test environments. For instance, adaptable genotypes or higher yielding in environment 1 may also show similar responses to environments 2 and 3, as well as indirect selection for non-stress environments (4, 5 and 6). An

environment is more desirable if it is located closer to the ideal environment. Thus, using the ideal environment as the centre, concentric circles were drawn to help visualise the distance between each environment and the ideal environment (Yan et al., 2000; Yan and Rajcan, 2002). Figure 4 shows that environment 4 was an ideal test environment in terms of being the most representative of the overall environment, based on inbreeding depression and importance of drought stress a compare was done among genotypes for environment 3, results showed that cross number 17 (S-78-11 × Chamran) has greater stability and high yielding in this environment, and that hybrid number 30 (Chamran × Hirmand) was a low yielding genotype (Fig 6).

Materials and methods

Trial

28 F₁, F₂ and F₃ hybrids and their eight parents, including 1-Irena/Babax/Pastor, 2-S-78-11, 3-Tajan, 4-Chamran, 5-Moghan3, 6-Hamoon, 7-Veery/Nacozari and 8-Hirmand, were sown in plastic pots filled with a soil mixture containing soil/sand/organic matter in a ratio of 1:1:1 in Experiments Farm of University Putra Malaysia. Four seeds were sown in each pot. The pots were irrigated after 25% (non-stress) and 75% (drought) depletion of the soil water. Each pot was filled with 3 kg of air-dried soil and the soil field capacity was calculated on the soil dry weight basis. The pots were weighed at two day intervals to compensate the water loss by evapotranspiration and irrigation was performed after 25% and 75% depletion of field capacity of soil Genotypes were arranged in a completely randomised block design with 3 replications across three generations. Two plants from each pot were harvested, and left out for sun-drying. After

Table3. Mean plant grain yield (gr), AMMI stability values (ASV), and ranking orders of the 36 hybrids and cultivar tested across six environments.

GN	E1	E2	E3	E4	E5	E6	Mean	IPCA1	IPCA2	ASV
1	7.41	7.78	7.56	8.46	7.75	7.01	7.66	-1.27	0.17	5.10
2	6.98	7.26	7.36	8.55	8.30	8.19	7.78	-0.97	0.52	3.95
3	4.58	4.79	4.39	6.29	5.59	4.68	5.06	-1.01	0.13	4.05
4	7.85	7.83	7.21	10.49	9.84	8.75	8.67	-0.63	0.12	2.53
5	3.90	4.00	4.22	6.35	6.47	6.72	5.28	-0.56	0.77	2.37
6	5.16	5.06	5.06	8.45	8.60	8.66	6.83	-0.22	0.75	1.15
7	7.27	7.08	6.97	10.92	11.06	11.03	9.06	-0.07	0.72	0.79
8	4.94	5.11	5.08	6.97	6.72	6.49	5.89	-0.79	0.50	3.23
9	9.06	8.46	6.21	13.58	11.85	8.49	9.61	-0.08	-0.86	0.93
10	7.89	7.23	4.94	12.66	10.98	7.61	8.56	0.02	-0.84	0.85
11	10.64	10.37	8.86	14.04	12.73	10.35	11.17	-0.45	-0.46	1.88
12	8.66	8.24	6.74	12.71	11.6	9.37	9.55	-0.15	-0.33	0.70
13	7.78	6.92	5.53	13.86	13.44	11.80	9.89	0.78	0.12	3.14
14	8.42	7.98	6.86	12.76	12.10	10.54	9.78	0.04	0.02	0.17
15	7.194	6.59	5.54	12.25	11.86	10.56	9.00	0.38	0.20	1.54
16	4.76	4.481	3.53	8.44	7.76	6.36	5.89	-0.22	0.04	0.89
17	10.61	10.43	8.65	13.46	11.72	8.788	10.61	-0.75	-0.78	3.12
18	8.49	8.67	7.86	10.15	9.03	7.458	8.61	-1.10	-0.20	4.45
19	8.84	8.47	7.38	12.87	12.16	10.59	10.06	-0.08	-0.007	0.36
20	7.79	7.19	5.41	12.52	11.32	8.77	8.83	0.09	-0.44	0.59
21	8.10	7.56	6.24	12.82	12.04	10.24	9.50	0.16	-0.07	0.67
22	9.21	8.44	6.33	14.55	13.21	10.24	10.33	0.31	-0.60	1.39
23	8.22	7.47	5.66	13.62	12.58	10.11	9.61	0.39	-0.35	1.61
24	7.47	6.55	4.99	13.75	13.22	11.33	9.56	0.84	0.014	3.36
25	7.90	7.54	6.09	11.74	10.62	8.43	8.72	-0.24	-0.33	1.02
26	6.57	5.96	4.73	11.6	11.03	9.43	8.22	0.33	0.05	1.34
27	7.92	6.98	5.16	14.17	13.37	11.05	9.78	0.77	-0.20	3.11
28	8.10	7.48	6.55	13.33	13.12	12.06	10.11	0.48	0.34	1.96
29	8.15	7.20	5.77	14.63	14.27	12.63	10.45	0.95	0.15	3.81
30	4.24	3.28	2.65	11.12	11.65	11.40	7.39	1.27	0.88	5.19
31	8.66	8.00	6.36	13.72	12.75	10.49	10.00	0.27	-0.27	1.12
32	8.29	7.38	5.70	14.47	13.79	11.68	10.22	0.77	-0.10	3.09
33	6.59	5.66	4.23	12.97	12.59	10.94	8.83	0.90	0.13	3.64
34	8.63	7.91	6.06	13.85	12.72	10.15	9.89	0.30	-0.41	1.29
35	8.06	7.80	7.11	11.73	11.30	10.31	9.39	-0.17	0.25	0.75
36	8.19	8.02	7.53	11.54	11.22	10.48	9.50	-0.28	0.35	1.19
Mean	7.57	7.15	6.02	11.82	11.12	9.54				

GN; genotype number; E: environment; IPCA: interaction principal component axes.

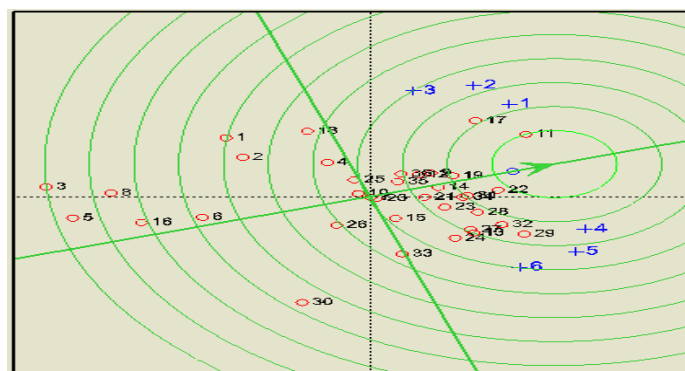


Fig 3. GGE-biplot based on genotype-focused scaling for comparison the genotypes with the ideal genotype. Black and blue numbers stand for genotypes and environments, respectively.

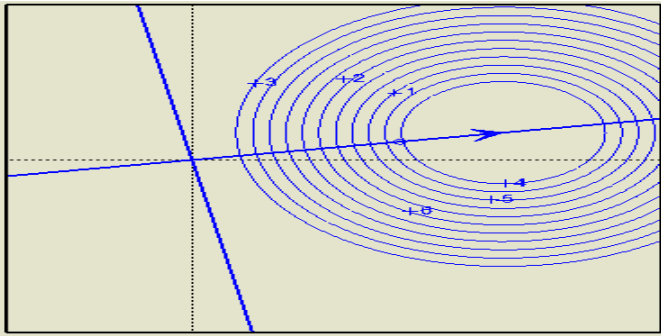


Fig 4. GGE-biplot based on environment-focused scaling for comparison the environments with the ideal environment. blue numbers stand for environments.

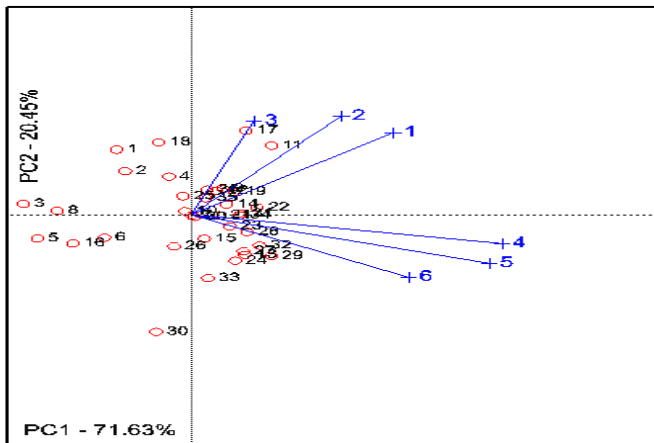


Fig 5. GGE-biplot based on environment-focused scaling for environments. Black and blue numbers stand for genotypes and environments, respectively.

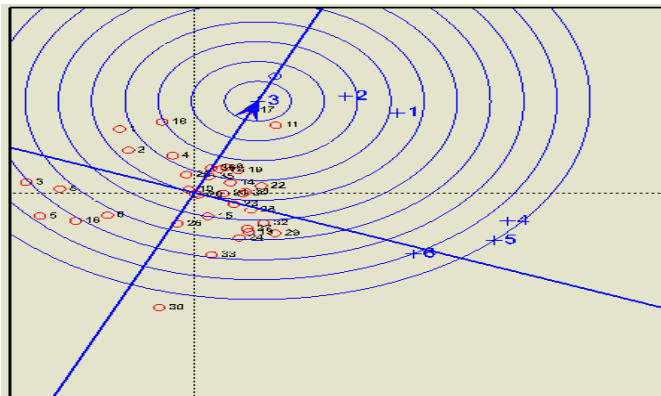


Fig 6. GGE-biplot based on environment 3 focused scaling for comparison the genotypes with more inbreeding depression. Black and blue numbers stand for genotypes and environments, respectively.

threshing samples, the grain yield per plant was recorded as an average.

AMMI and GGE biplot analysis

The number of components for a particular member of an AMMI or GGE model family can be indicated by adding that number as a suffix, such as AMMI1 with one component or GGE2 with two; the full models with all components are designated by AMMIF and GGEF. At the opposite extreme, the AMMI model with no components, which has just the

ANOVA portion of the model, is designated by AMMI0 (it has no GGE counterpart). Two additional terms, θ_{ge} and v_{ge} , will be introduced below and will serve to focus attention on the values submitted to SVD (singular value decomposition) (Guach et al, 2008). The AMMI model equation is written as: $Y_{ge} = \mu + \alpha_g + \beta_e + \sum_n \lambda_n \gamma_{gn} \delta_{en} + \rho_{ge}$. For the additive parameters, Y_{ge} is the yield for genotype (g) in environment (e), μ is the grand mean, α_g denotes genotype deviation, β_e indicates environment deviation, λ_n is the singular value for component n, γ_{gn} is the eigenvector value for g, δ_{en} is the eigenvector value for e and the residual term is ρ_{ge} . The GGE model is written as $Y_{ge} - \beta_e - \mu = v_{ge} = \sum_n \lambda_n \gamma_{gn} \delta_{en} + \rho_{ge}$ where v_{ge} is environment-centred yields, and $Y_{ge} - \beta_e$ is the nominal yields in the AMMI literature (Gauch and Zobel, 1997). The interaction G×E was analysed in an AMMI model (Zobel,1988., Guach, 1992) with a view to identify wheat crosses better adapted to different irrigation conditions. Purchase (1997) proposed the formula to calculate an AMMI's stability value (ASV) as follows:

$$ASV = \sqrt{\left[\frac{SSIPCA1}{SSIPCA2}(IPCA1SCORE)\right]^2 + (IPCA2SCORE)^2}$$

Where SSIPCA1/SSIPCA2 is the weight given to the IPCA1 value by dividing the IPCA1 SS by the IPCA2 SS; and the IPCA1 and IPCA2 scores are the genotypic scores in the AMMI model. The 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 analyse the multi-environment yield trial (MEYTs) data. This methodology uses a biplot to show the factors (G and GE) that are important in genotype evaluation and that are also sources of variation in GEI analysis of MEYTs data (Yan et al., 2000, 2001), and data is also analysed using two software programmes: Genstat.8 and SAS.9.

Conclusion

The results indicated that the yield performance of wheat was highly influenced by GE interaction effects; the magnitude of environment effect was about two times that of genotype effect. There were desirable genotypes in terms of high mean yields, for example genotype number 11. According to the GGE biplot, in drought stress conditions and inbreeding depression in the F₃ generation, crosses 17 (S-78-11 × Chamran) and 11 (Irena × Chamran), which carry the tolearnace genes, can be characterised as genotypes with the appropriate mean yield and stability in drought stress conditions (Fig 6).

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