

Genotype, environment and genotype \times environment interaction effects on the performance of maize (*Zea mays* L.) inbred lines

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ABSTRACT

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Based on principal component analysis (PCA), GGE biplot analysis is an effective method to fully assess multi-environmental yield trials (METs). Additive main effects and multiplicative interaction (AMMI) is an alternative method for assessing phenotypic stability and adaptability. In this research, MET data of 14 maize inbred lines were used to perform AMMI and GGE biplot analyses. These genotypes were evaluated under diverse climatic conditions in five Iranian locations during two cropping cycles (2007 and 2008). A genotype (inbred line) by location table was used for performing the analyses. Based on both mean grain yield and yield stability, inbred lines K3615/2, K19/1, K166B and K18 proved to be superior and also had greater mean performance among the test inbred lines. Graphic analysis was used to identify the most suitable inbred lines for each test environment. Inbred lines K3615/2, K19/1, K166B, K18, K3653/2 and K3547/5 were identified as suitable in all locations. The AMMI and GGE biplot graphics revealed three separate groups of environments, i.e., three mega-environments. Group one included three sites, Karaj, Kabootar Abad and Zarghan, while group two included only Islam Abad-e-Gharb and group three only Miandoab. Islam Abad Gharb and Miandoab were more discriminative for genotypes. The inbred lines that were most responsive to the environment were K3615/2, K166B, K19/1 and K18; the least responsive line was K3547/5.

Key words: maize, GGE biplot, AMMI, PCA, G \times E interaction

INTRODUCTION

Maize (*Zea mays* L.), one of the major field crops in Iran, is grown on more than 230,000 hectares. Phenotype is a combination of genotype (G), environment (E) and genotype \times environment interaction (G \times E). G \times E usually complicates the process of selecting superior genotypes. Consequently, multi-environment trials (METs) are widely used by plant breeders for evaluating the relative performance of genotypes over the target environments (Delacy *et al.*, 1996). Numerous methods have been developed to study and reveal the nature of G \times E interaction, e.g., joint regression (Finlay and Wilkinson, 1963; Eberhart and Russell, 1966), additive main effects and multiplicative interaction (AMMI) (Gauch, 1992) and type B genetic correlation (Burdon, 1977). These methods are commonly used to analyze MET data and have also been applied in G \times E interaction studies in maize and other crops (Bertoia *et al.*, 2006; Lee *et al.*, 2003; Ades and Garnier-Géré, 1997; Wu and Matheson, 2005; Butrón *et al.*, 2004). Setimela *et al.* (2007) analyzed grain yield data of 35 early to intermediate maturing open-pollinated maize varieties (OPVs) for five seasons across 59 locations of the Southern African Development Community.

The GGE biplot analysis of these data showed that ideal test environments could discriminate superior performing maize OPVs from poor ones, and identified six mega-environments in the target areas.

GGE biplot analysis was recently developed to simultaneously use some of the functions of these methods. In phenotypic variation, E explains most of the variation, and G and G \times E are usually small (Yan, 2002). However, only G and G \times E interaction are relevant to cultivar evaluation, particularly when G \times E interaction is determined as repeatable (Hammer and Cooper, 1996). Hence, Yan *et al.* (2000) deliberately put the two together and referred to the combination as GGE. Following the proposal of Gabriel (1971), the biplot technique was also used to display the GGE of MET data, and is referred to as a GGE biplot (Yan, 2001; Yan *et al.*, 2000).

The GGE biplot is in fact a data visualization tool that graphically displays G \times E interaction in a two-way table (Yan *et al.*, 2000). The GGE biplot is an effective tool for the following applications:

1) Mega-environment analysis (e.g.; “which-won-where” pattern), whereby specific genotypes can be recommended for specific mega-environments (Yan and Kang, 2003).

2) Genotype evaluation (mean performance and

stability), and

3) Environmental evaluation (to discriminate among genotypes in target environments).

GGE biplot analysis is increasingly being used in $G \times E$ interaction studies in plant breeding research (Butron *et al.*, 2004; Crossa *et al.*, 2002; Dehghani *et al.*, 2006; Yan and Hunt, 2002; Kaya *et al.*, 2006; Samonte *et al.*, 2005; Yan and Tinker, 2005; Yan, 2001; Yan, 2002; Yan and Kang, 2003).

AMMI is a multivariate technique for assessing the phenotypic stability and adaptability of genotypes (Pacheco and Vencovsky, 2005). This method partitions the overall variation into G , E and $G \times E$. The data structure that AMMI and GGE biplot analyses require is a two-way data matrix, such as number of genotypes tested in a number of environments. The experiment may or may not be replicated. These analyses combine two statistical procedures: analysis of variance (ANOVA) and principal component analysis (PCA) (Gauch, 2006).

Despite the diverse climatic conditions in Iran's maize growing areas and the genetic variation in maize germplasm, little has been published on $G \times E$ (especially in inbred lines). The purpose of this research was to apply GGE biplot and AMMI techniques to study the patterns of $G \times E$ interaction in maize; to graphically display means, adaptability and stability of maize inbred lines; and to identify suitable inbred lines for each location.

MATERIALS AND METHODS

The genetic materials used in this study originated from Iran's national maize breeding program. Fourteen maize inbred lines (Table 1) were evaluated in five locations during two cropping seasons (2007 and 2008) using a randomized complete block design (RCBD) with three replications. Each replication was broken into two blocks to improve uniformity. The five locations were Karaj (L1), Isalm Abad-e-Garb (L2), Kabootar Abad (L3), Miandoab (L4) and Zarghan (L5); they represent the broad range of Iranian environments where maize is commercially grown (Table 2). The same 14 inbred lines were used in each site. Fertilizer was applied at rates of 140 kg ha⁻¹ of N and 160 kg ha⁻¹ P₂O₅ at planting. An additional 140 kg ha⁻¹ of N was top-dressed 50 days after planting. Each plot consisted of two 16-hill rows, both harvested for grain yield, with 75 cm row spacing and 35 cm between hills. When the plants reached the 4- to 5-leaf stage, the plots were thinned leaving two plants per hill, to achieve a final plant density of approximately 76 000 plants/ha. Grain yield (t ha⁻¹) for each genotype was measured and adjusted to

14% grain moisture content at harvest. Bartlett's test of homogeneity of variances and the normality test for data were performed using Minitab software. The ANOVA was performed using SAS. Graphic analysis (GGE biplot and AMMI biplot) was performed using GGE biplot software (Yan, 2001). The AMMI analysis was performed using the PROC IML procedure of SAS. AMMI and GGE biplot methods were used to study the G , E and $G \times E$ effects on grain yield. These methods have been described in detail by Gabriel (1971), Yan (2002), Yan *et al.* (2001), Yan and Hunt (2002), Yan and Kang (2003) and Gauch (1992; 2006).

Table 1. Pedigree/origin of the 14 intermediate to late maturing Iranian maize inbred lines

Code	Inbred lines	Pedigree /origin
Lancaster Sure Crop (LSC) related lines		
1	MO17	CL. 187-2 × C103
2	K18	Derived from MO17 changes
3	K19/1	Derived from K19 changes
Reid Yellow Dent (RYD) related lines		
4	B73	BSSS C5(Iowa Stiff Stalk Synthetic)
5	A679	A B73 back-cross derived line [(A662 × B73)(3)]
Lines extracted from late synthetic		
6	K3615/2	SYN-Late
7	K3640/5	SYN-Late
8	K3653/2	SYN-Late
9	K3651/1	SYN-Late
Lines extracted from CIMMYT originated materials		
10	K166B	--
11	K3547/5	Srinagar 8848
12	K3544/1	--
13	K3545/6	Taltizapan-8946
14	K3493/1	Unknown from EVT 16A

RESULTS AND DISCUSSION

The ANOVA for grain yield using the AMMI method is presented in Tables 3, 4 and 5 for 2007, 2008 and the average of the two cropping seasons, respectively. There were significant differences among the genotypes, environments and $G \times E$ interaction. Significant $G \times E$ interaction explained 15.26%, 12.84% and 12.66% of the total sum of squares for 2007, 2008 and the two-year average, respectively. In the AMMI analysis, the sum of first IPCA (IPC1) and second IPCA (IPC2) explained 73%, 79% and 86% of the $G \times E$ variation for 2007, 2008 and the two-year average, respectively. The first two PCs explained 79%, 82% and 87% of the total GGE variation in data for 2007, 2008 and the two-year average, respectively. The graphical method was employed to investigate environmental variation and interpret the $G \times E$ interaction (Fig. 1 and 2).

The ranking of 14 inbred lines based on their mean grain yield and yield stability for 2007, 2008 and the two-year average, respectively, is shown in Fig. 1. It has been reported that when PC1 in a GGE biplot approximates the G (mean performance), PC2

Table 2. Summary of information on the five test locations

Trial	L1	L2	L3	L4	L5
	Karaj	Islam Abad- e -Gharb	Kabootar Abad	Miandoab	Zarghan
Latitude	35°49' E	34°08' E	32°31' E	36°58' E	29°46' E
Longitude	51° N	47°26' N	51°51' N	46°03' N	51°43' N
Elevation (masl)	1360	1346	1545	1142	1604

Table 3. Analysis of variance for grain yield of 14 maize inbred lines in five locations during the 2007 cropping season

S. O. V.	df	SS	MS	P > F	% of Total
Environment (E)	4	1007.3701	251.842**	< 0.0001	47.73
Genotype (G)	13	477.0163	36.6936**	< 0.0001	22.60
E × G	52	322.0221	6.1927**	< 0.0001	15.26
IPC1	16	134.398	8.3999**	< 0.0000	6.37
IPC2	14	99.819	7.1299**	< 0.0001	4.73
IPC3	12	66.514	5.5428**	< 0.0041	3.15
Residual	10	21.291	2.1291 ^{ns}	0.45	1.00
Error	138	296.7376	1.4868 ^{ns}	-	14.06
Total	209	2110.4049			

** : Significant at the 1% probability level.
ns: Not significant.

Table 4. Analysis of variance for grain yield of 14 maize inbred lines in five locations during the 2008 cropping season

S. O. V.	df	SS	MS	P > F	% of Total
Environment (E)	4	1069.9625	267.4906**	< 0.0001	53.57
Genotype (G)	13	217.9129	16.7625**	< 0.0001	10.91
E × G	52	256.4482	4.9317*	0.03	12.84
IPC1	16	132.298	8.2686**	0.002	6.62
Residual	36	124.151	3.4486 ^{ns}	1.494	6.22
Error	138	451.8714	3.2744 ^{ns}	-	22.62
Total	209	1997.1891			

** : Significant at the 1% probability level.
ns: Not significant.

Table 5. Analysis of variance for grain yield of 14 maize inbred lines in five locations during the 2007 and 2008 cropping seasons

S. O. V.	df	SS	MS	P > F	% of Total
Environment (E)	4	839.3680	209.842**	< 0.0001	53.6
Genotype (G)	13	320.6006	24.6616**	< 0.0001	20.48
E × G	52	198.1553	3.8107**	< 0.0001	12.66
IPC1	16	114.148	7.1342**	< 0.0000	7.29
IPC2	14	54.687	3.9062**	< 0.002	3.49
Residual	22	29.32	1.0471 ^{ns}	1.16	1.87
Error	138	205.1732	1.4868 ^{ns}	-	13.11
Total	209	1564.7894			

** : Significant at the 1% probability level.
ns: Not significant.

IPC: Interaction principle component

must approximate the $G \times E$ associated with each genotype, which is a measure of instability (Yan *et al.*, 2000; Yan, 2002). The line passing through the biplot origin and the environmental average is indicated by circles and is known as the average environment coordinate (AEC) axis, which is defined by the average PC1 and PC2 scores for all environments. Projection of genotype markers onto this axis should, therefore, approximate the mean yield of the genotypes. Thus, inbred lines 7, 4, 5, 3, 9 and 11 had higher grain yield, followed by genotypes 8, 10, 12, 13, 6, 1, 14 and 2 for all dataset. The line which passes through the origin but is perpendicular to the AEC with double arrows represents the status of the genotypes' stability. A position in either direction away from the biplot origin, on this axis, indicates greater $G \times E$ interaction and reduced stability (Yan, 2002).

Therefore, inbred lines 5, 6, 13, 8 and 9 showed a more variable and less stable performance than the other genotypes. Genotypes 4, 3, and 2 in 2007, genotypes 4 and 2 in 2008, and genotypes 7, 4, 11 and 2 in the two-year average were located close to the AEC abscissa and thus were more stable than the others (Fig. 1).

For L1, 7 was the best inbred line in all cases (Fig. 1b). For L2, 5 was the best inbred line in 2007, whereas 7 was the best in 2008 and in the two-year average. For L3, inbred line 7 was the best in 2007 and in the two-year average, and inbred lines 3 and 8 were best in the 2008 cropping season. For L4, 7 was the best inbred line in 2007 and in the two-year average, while inbred line 3 was the best in the 2008 cropping season. For L5, 5 was the best inbred line in 2007, and 7 was the best in 2008 and in the two-year average.

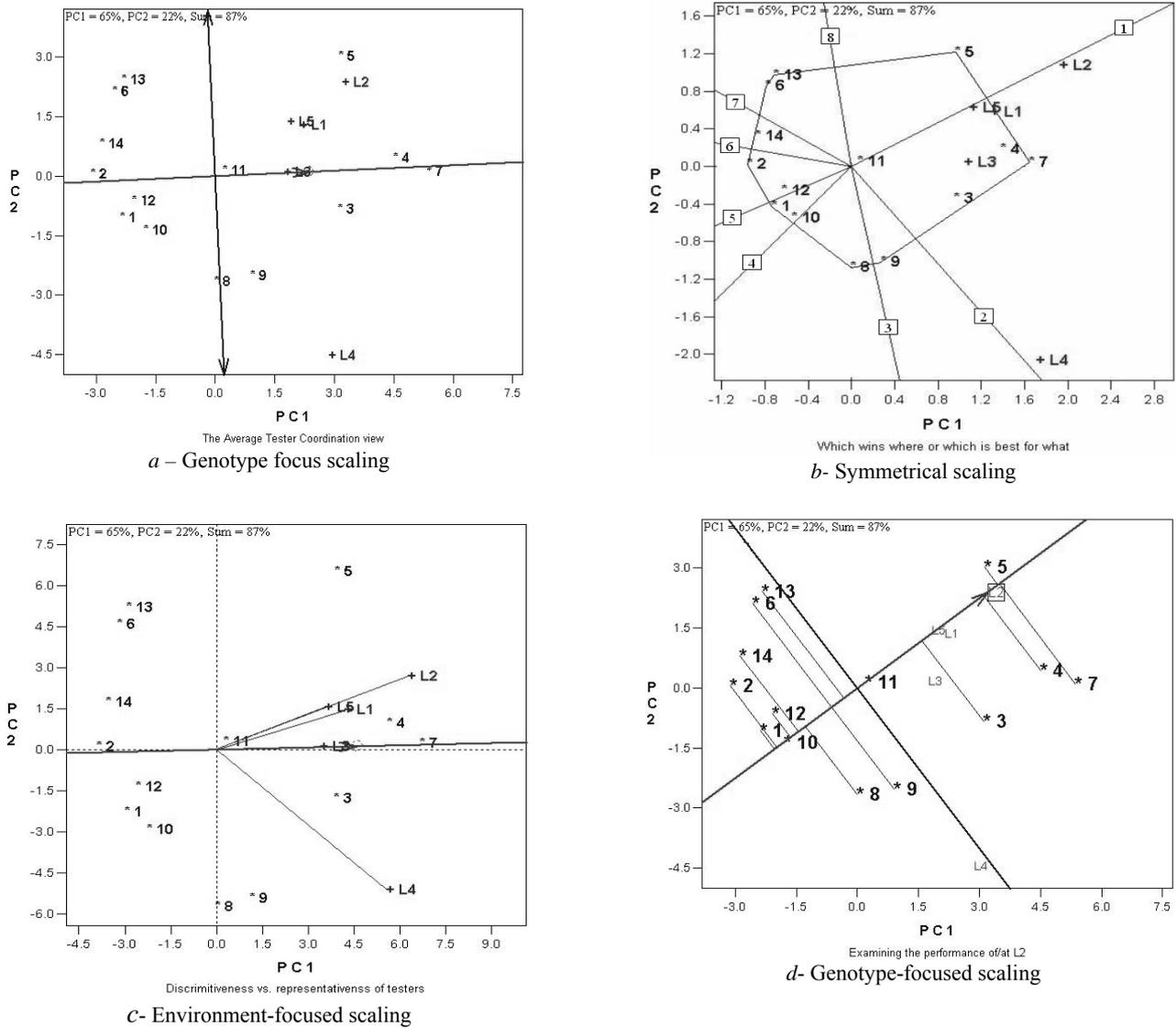


Fig. 1. GGE biplot based on the grain yield performance of 14 maize inbred lines in five environments (locations) and two cropping seasons (2007 and 2008). The 14 inbred lines are indicated by numbers and the five locations by letters and numbers (L1 – L5). *a*: average-environment coordinate (AEC) view of the GGE biplot for ranking of 14 lines based on mean yield and stability; *b*: polygon view of the GGE biplot shows the "which-won-where" pattern; *c*: the vector view of the GGE biplot shows relationships among environments; *d*: different genotypes in a given environment I2. The genotype codes are: 1= MO17, 2= B73, 3= K18, 4= K19/1, 5= K166B, 6= A679, 7= K3615/2, 8= K3640/5, 9= K3653/2, 10= K3651/1, 11= K3547/5, 12= K3544/1, 13= K3545/6, 14= K3493/1.

Fig. 1c provides a summary of the interrelationships among environments. The lines connecting the biplot origin and the markers for the environments are called environment vectors. The angle between the vectors of two environments is related to the correlation coefficient between them. The cosine of the angle between the vectors of two environments approximates the correlation coefficient between them (Kroonenberg, 1995; Yan, 2002). Based on the angles of the environment vectors, the five locations were clustered into two groups in all cases. Group one included L1, L2, L3 and L5. Group two included only L4. For example, the fact that the smallest angle is between L1 and

L5 implies that there was the highest correlation between them. The large angle between L5 and L4 indicates the poor correlation between these locations (Fig. 1c). Another interesting observation from the vector point of view of the biplot is that the length of the environment vectors approximates the standard deviation within each environment, which is a measure of its discriminating ability (Yan and Kang, 2003). Thus L2 and L4 are the most discriminative environments (Fig. 1c). Another important feature of a test environment is how much it represents the target environment. To measure representativeness using a biplot, an average environment has to be defined and used as a reference.

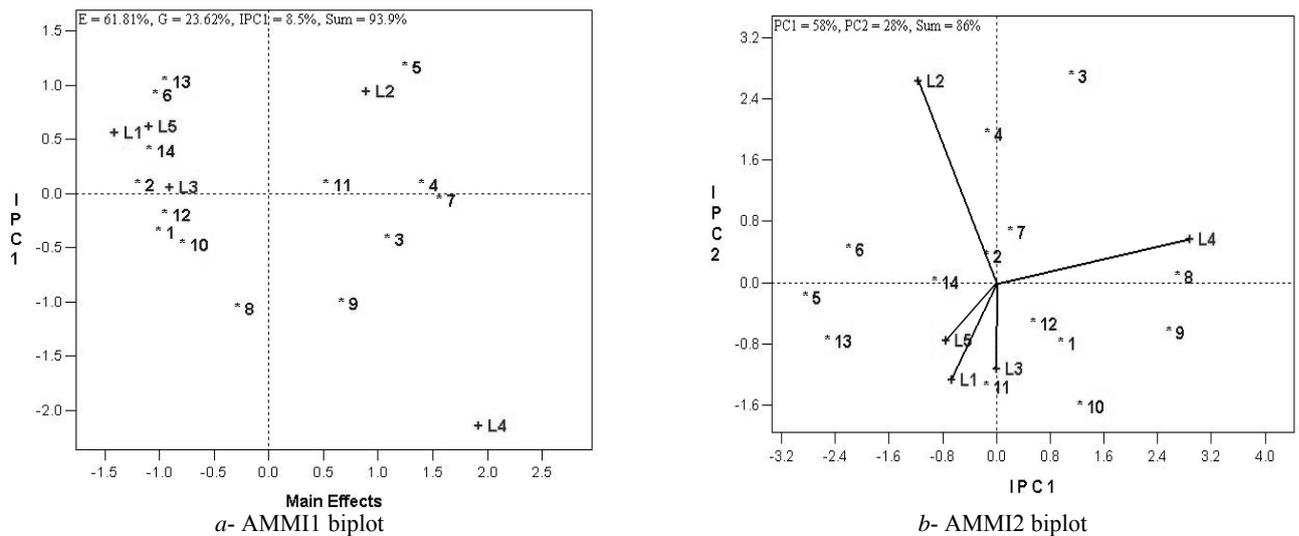


Fig. 2. Graphic displays of G and E in an AMMI biplot for yield performance in five environments (locations) and two years. The 14 lines are indicated by numbers and the 5 locations in letters and numbers (L1 – L5). *a*: AMMI1 biplot. *b*: AMMI2 biplot. The genotype codes are: 1= MO17, 2= B73, 3= K18, 4= K19/1, 5= K166B, 6= A679, 7= K3615/2, 8= K3640/5, 9= K3653/2, 10= K3651/1, 11= K3547/5, 12= K3544/1, 13= K3545/6, 14= K3493/1.

The line that passes through the biplot origin and the average environment is AEC, as discussed earlier. The angle between the vector of an environment and the AEC axis is a measure of the representativeness of the environment.

The performance of different genotypes in the L2 location is shown in Fig. 1d. The line that passes through the biplot origin and the L2 marker is the L2 axis. Genotypes are ranked according to their projections onto the L2 axis based on their performance in L2 and in the direction indicated by the arrow. Thus at L2 inbred lines 5, 4, 7 and 3 were high yielding, and inbred lines 1, 2 and 12 were low yielding. The order of inbred line performance in Fig. 1d is: 7 > 5 > 4 > 3 > 11 > 13 > 6 ≈ 9 > 8 > 14 > 12 > 10 > 2 > 1. The line perpendicular to the L2 axis which passes through the biplot origin separates inbred lines with higher grain yield than the grand mean (right side) from those with lower grain yield than the grand mean (left side) in L2 (Fig. 1d). Inbred lines 7, 5, 4, 3 and 11 had higher grain yield than the grand mean in L2. Locations could also be ranked according to one genotype. Inbred line 7 had the maximum grain yield and high yield stability (Fig 1a). The line that passes through the biplot origin to the marker of inbred line 7 is the axis of inbred line 7. Environments are ranked along this axis in the direction of the dot representing inbred line 7 in Fig. 1c. For example, the relative performance of line 7 in different environments in Fig. 1c ranks as follows: L2 > L4 > L1 > L5 > L3. The line perpendicular to the inbred line 7 axis separates environments in which inbred line 7 is below and above the mean. However, inbred line 7

is above the mean in all five locations.

AMMI biplots showing grain yields of inbred lines versus IPC1 scores (AMMI1 biplot) are presented in Fig. 2. According to Fig. 2, inbred line 4 had higher grain yield and higher yield stability. Inbred line 11 had higher grain yield than the mean and is located near the origin; hence, it also had yield stability. Lines 5 and 8 had higher grain yield than the mean, but no yield stability. AMMI biplots showing IPC1 and IPC2 scores of inbred lines and locations (AMMI2) are presented in Fig. 2. These two IPCs explain 73%, 79% and 86% of G × E variation for 2007, 2008 and the two-year average, respectively. When an inbred line is near an environment (location), this indicates it is specifically adapted to that environment. For example, inbred lines 5, 13 and 11 had specific adaptation to L1 and L5, and inbred lines 3, 7 and 8 to L4 (Fig. 2b). Inbred lines that were close to the center of the AMMI2 biplot were broadly adapted to the test locations. Inbred line 2, closest to the center, was the most widely-adapted inbred line in this study.

In conclusion, the ideal cultivar should have the highest mean performance and be highly stable. Such an ideal cultivar would have the greatest vector length of the high-yielding genotypes and zero G × E. For all datasets, inbred line 4 performed as the ideal genotype. Inbred line 4 can thus be used as a reference genotype in cultivar evaluation. The closer a line is to the ideal, the more well suited it is. Since inbred lines 3 and 7 were the closest to the ideal genotype (inbred line 4), they were the best suited of all the test inbred lines. For broad adaptation, the

ideal genotypes are those that have both high mean grain yield and high yield stability. In the GGE biplot, they are close to the positive end of AEC and have the shortest vector from the AEC. Inbred lines 7, 4, and 3 had broad adaptation in this study. For specific adaptation, the ideal genotype should have high mean grain yield and respond well to a particular environment.

When the following two criteria are fulfilled, this indicates differences in mega-environments. First, there are different top genotypes in different test locations. Second, between-group variation is significantly greater than within-group variation, a common criterion for clustering environments. Dividing the target environments into different mega-environments and deploying different genotypes in different mega-environments is the best way to utilize $G \times E$ interaction.

The polygon view of the GGE biplot (Fig. 1b) indicates the superior genotype(s) in each environment and in each group of environments (Yan and Hunt, 2002). The polygon is formed by connecting the data points of the genotypes that are farthest away from the biplot origin, such that all other genotypes are contained in the polygon. The vertex inbred lines have the longest vectors in their respective directions, which is a measure of responsiveness to environments. The vertex lines are, therefore, among the most responsive genotypes; all others are less responsive in their respective directions. An inbred line located at or close to the origin would rank the same in all environments and would not be responsive to a particular environment. We can compare two adjacent vertex genotypes within the polygon. For example, comparison of inbred lines 7 and 9 for the two-year average (Fig. 1b) indicates that inbred line 7 had higher grain yield in L4, because it was located in the L4 sector. Similarly, inbred line 8 did not perform well in any location, because it did not occur with any location in one sector. Rays are lines that are perpendicular to the sides of the polygon or their extension (Yan, 2002). Eight rays have divided the biplot into eight sections; five locations are situated in two sectors in 2007 and 2008, and in just one of them for the two-year average. The vertex lines for each sector produced the highest grain yield in environments that fall within that sector. The inbred line with the highest grain yield in all locations is line 7, followed by 4 and 3. The vertex lines with no locations in their sectors were the poorest performers in all five locations. Vertex genotypes are the most responsive genotypes, i.e., they are the best or the worst genotypes in some or all test environments.

In summary:

- The 14 maize inbred lines showed very high variation for grain yield.
- The five test locations were classified into three mega-environments.
- Inbred line K3615/2 was the best performer in all locations, followed by K19/1 and K18.
- Inbred lines K3615/2, K19/1, K3547/5 and B73 had the highest yield stability.

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