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Additive main effects and multiplicative interactions model (AMMI) and genotype main effect and genotype by environment interaction (GGE) biplot analysis of multi-environmental wheat variety trials

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Genotype by environment (G×E) interaction is associated with the differential performance of genotypes tested at different locations and in different years, and influences selection and recommendation of cultivars. Wheat genotypes were evaluated in six environments to determine the G×E interactions and stability of the genotypes. Additive main effects and multiplicative interactions (AMMI) was conducted for grain yield of both year and it showed that grain yield variation due to environments, genotypes and (G×E) were highly significant (p <0.01). Stability for grain yield was determined using genotype plus genotype by environment interaction (GGE) biplot analysis. The first two principal components (PC1 and PC2) were used to create a 2-dimensional GGE biplot. Which-won-where pattern was based on six locations in the first and five locations in the second year for all the 20 genotypes. The resulting pattern is one realization among many possible outcomes, and its repeatability in the second was different and a future year is quite unknown. A repeatability of which-won-where pattern over years is the necessary and sufficient condition for mega-environment delineations and genotype recommendation.

Key words: Additive main effects and multiplicative interactions (AMMI), genotype×environment (G×E) interactions, wheat, stability.

INTRODUCTION

The increase in population and the subsequent rise in demand for agricultural produce are expected to be greater in regions where production is already insufficient, in particular in Sub-Saharan Africa. The necessity and demand to increase agricultural production represents a huge challenge to local farming systems given it must come mainly from increased yield per unit area in addition to the limited extension of cultivated land in the country. To meet this requirement various crop improvement programmes have been initiated by the Ethiopian Institute of Agricultural Research (EIAR). Under any crop improvement programme a sample of promising genotypes are performance tested each year at a number of sites, representing major crop growing areas with the a view to identify genotypes which possess the dual qualities of high yield capacity and low sensitivity to

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adverse change in environmental condition. One of the important focuses in the current paper is to assess the performance of improved genotypes in multi environment (multi-location, multi-year or both) trials. Multi-Environment Yield Trials (MEYT) are conducted for different crops throughout the world (Yan and Rajcan, 2002; Dehghani et al., 2006) not only to identify high yielding cultivars but also to identify sites that best represent the target environment (Yan, 1999; Yan et al., 2000, 2001). As usual in MEYT, a number of genotypes are tested over a number of sites and years to see adaptation of the crop. But, it is often difficult to determine the pattern of genotypic responses across environments without the use of appropriate analytical and statistical tools such as additive main effects and multiplicative interactions (AMMI) and Genotype main effect and Genotype×Environment interaction (GGE) biplot (Gauch, 1992; Gauch and Zobbel, 1996; Yan et al., 2000; Yan, Tinker, 2006) for graphical display of data.

The measured yield of each cultivar in each test environment is a result of genotype main effect (G), and environment main effect (E) and genotype by environment (G×E) interaction (Yan and Kang, 2003). Though, E mostly accounts for about 80% of the total yield variation; it is only G and G×E interaction that are relevant to cultivar evaluation and mega environment classification (Rao et al., 2005; Yan et al., 2000; Yan, 2002; Yan and Rajcan 2002; Kaya et al., 2006). AMMI and GGE models are singular value decomposition (SVD) based statistical methods often applied to yield trial studies for visualizing the data. The methods helps in understanding complex genotype by environment(G×E) interactions, determining which genotype has been in which environments, and also helping in grouping environments with the same winner (or similar winners) into mega-environments.

Wheat is the most important cereal crop in Ethiopia and represents nearly 14% of grain crop production. It covers 71,786.86 ha of cropped land area with average productivity of 9.86 qut/ha but it is less than half of the world average yield (ECSA, 2011). Understanding genotype by environment interaction (GEI) helps plant breeders to design better breeding strategies. Therefore, the objectives of this study are to evaluate the yield performance and stability of genotypes in relation to environment (location) on year to year basis. Secondly the study will examine the possible existence of different mega environments and the wining genotype for each mega environments.

MATERIALS AND METHODS

Description of the data

The data used in the current paper are from a study carried out between 2004 and 2005 in six different research stations in Ethiopia. The locations consist of loc1 (Kulumsa),loc2(Adet), loc3 (Bekoji), loc4 (Sinana), loc5 (Holeta) and loc6 (DeberZeit). Twenty bread wheat genotypes were evaluated in each of the above locations (environments) in a randomized complete block design with four replications. These Twenty genotypes are coded from G1-G20.

The model

In terms of effects, the basic model for a multi-environment trial can be written as

$$Y_{ijl} = \mu + \alpha_i + \beta_j + \gamma_{ij} + \epsilon_{ijl} \quad (1)$$

Where Y_{ijl} is the measured yield value of the i^{th} genotype in the j^{th} environment and l^{th} replicate, μ is the grand mean, α_i is the main effect of the i^{th} genotype, β_j is the main effect of j^{th}environment, γ_{ij} is interaction between i^{th} genotype and j^{th} environment and ϵ_{ijl} is random error. Were we assume that $\epsilon_{ijl} \sim$indep $N(0,\delta_j^2)$. The ranges of indices are i=1, 2,...,20j =1, 2,..., 6 l =1, 2, 3, 4. Thus the cell mean for the model is

$$\mu_{ij} = E(Y_{ijl}) = \alpha_i + \beta_j + \gamma_{ij} + \epsilon_{ijl} \quad (2)$$

In GGE biplots genotype plus genotype × environment (*G* + *GE*) interaction are studied together and to achieve this G+GE effect is separated out from the observed mean and eventually the model becomes (omitting the random error)

$$\mu_{ij} - (\mu + \beta_j) = \alpha_i + \gamma_{ij} \quad (3)$$

However in the case of the AMMI model, the effect of genotypes is also separated out only genotype × environment (GE) interaction is studied for biplot, and eventually the model becomes

$$\mu_{ij} - (\mu + \beta_j + \alpha_i) = \gamma_{ij} \quad (4)$$

The mathematical expressions for partitioning of G+GE for GGE biplots and GE for AMMI models are similar except a difference in model formulation. The G+GE for GGE and GE for AMMI effects are partitioned into multiplicative terms by using the singular value decomposition (SVD) as

$$\mu_{ij} - \mu - \beta_j = \lambda_1 \xi'_{i1} \eta_{j1} + \lambda_2 \xi'_{i2} \eta_{j2} + \gamma_{ij}$$

and

$$\mu_{ij} - \mu - \beta_j - \alpha_i = \lambda^*_1 \xi'^*_{i1} \eta^*_{j1} + \lambda^*_2 \xi'^*_{i2} \eta^*_{j2} + \gamma^*_{ij} \quad (7)$$

respectively, where λ_1 (λ^*_1) and λ_2 (λ^*_2) are the singular values (SV) for the first and second principal component (PC1 and PC2), ξ'_{i1}(ξ'^*_{i1}) andξ'_{i2} (ξ'^*_{i2}) are eigenvectors of genotype i for PC1 and PC2, η_{j1} (η^*_{j1}) and η_{j2} (η^*_{j2}) are eigenvectors of environment j for PC1 and PC2 and γ_{ij}($\gamma_{ij}{}^*$) is the residual not explained by PC1 and PC2 for genotype i in environment j. The PC1 and PC2 eigenvectors cannot be plotted directly to construct a meaningful biplot before the singular values are partitioned into the genotype and environment eigenvectors. To generate a biplot that can be used in visual analysis of MEYT data, the SVs have to be partitioned into the genotype and environment eigenvectors so that Equation (5) can be written in the form of

$$\mu_{ij} - \mu - \beta_j = \sum_{l=1}^{k} g'_{il} e'_{lj} + \gamma_{ij} \text{and } \mu_{ij} - \mu - \beta_j - \alpha_i = \sum_{l=1}^{k} g'_{il} e'_{lj} + \gamma^*_{ij} \quad (6)$$

Table 1. ANOVA table for AMMI model.

Source	Year 2004					Year 2005				
	df	SS	MS	F	F-prob	df	SS	MS	F	F-prob
Total	479	54590	114			399	27188	68.1		
Treatments	119	41599	349.6	10.2	0	99	19806	200.1	9.93	0
Genotypes	19	1187	62.5	1.82	0.01944	19	2779	146.3	7.26	0
Environments	5	35212	7042.4	99.8	0	4	13988	3497.1	31.97	0
Block	18	1270	70.6	2.06	0.00706	15	1641	109.4	5.43	0
Interactions	95	5200	54.7	1.6	0.00134	76	3038	40	1.98	0.00003
IPCA	23	2035	88.5	2.58	0.00012	22	1459	66.3	3.29	0
IPCA	21	1588	75.6	2.21	0.00193	20	897	44.9	2.23	0.00227
Residuals	51	1577	30.9	0.9	0.66493	34	682	20.1	1	0.47979
Error	342	11721	34.3			285	5742	20.1		

The block source of variation refers to blocks within environments.

Where g'_{il} and e'_{lj} are called PCI scores for genotype i and environment j, respectively. In a biplot, genotype i is displayed as a point defined by all g'_{il} values, and environment j is displayed as a point defined by all e'_{lj} values (l = 1 and 2 for a two-dimensional biplot). Singular-value partitioning is implemented by

$$g'_{il} = \lambda_l^{f_i}\xi_{il} \text{ and } e'_{lj} = \lambda_l^{1-f_i}\eta_{lj} \quad (7)$$

where f_i is the partition factor for PCI. Theoretically, f_i can be anything between 0 and 1 although 0.5 is so far the most commonly used partition factor (Yan, 2002). In this paper we have use a value of 0.5 to give equal importance to both genotype and environment.

RESULTS AND DISCUSSION

The AMMI analysis of variance of grain yield (Table 1) showed significant effects of genotype, environment (location) and genotype by environment interaction. Location explained 84.65% of the total (G + E + GE) variation of year 2004 and 70.63% for year 2005, whereas the genotype by environment interaction and genotype captured 12.5 and 0.0029% of year 2004 and 15.34 and 14.03% for year 2005, respectively. The magnitude of genotype by environment interaction as compared to genotype suggested a possible existence of different mega environments in year 2004. The partitioning of GGE sum of squares through the GGE biplot analysis showed that PC1 and PC2 accounted 43.21 and 26.43% of GGE sum of squares of year 2004 and 58.01 and 22.14% for year 2005, respectively. The two principal components explained a total of 69.6 and 80.16% variation in the two years respectively. Nonetheless agricultural biplot literature provides no guidance concerning how much of the total variability accounted for by the first two principal components are considered adequate (Sabaghnia et al., 2012b; Yang et al., 2009). This result revealed that there was a differential yield performance among wheat genotypes across testing environment (location) due to the presence of genotype by environment interaction.

Graphical statistical methods based on GGE biplot analysis

Relationship among test environments

GGE biplot, which was based on environment focussed scaling, was used to estimate the pattern of environments (locations) as shown in Figure 1. Environment PC1 score had both negative and positive scores indicating that there was a difference in rankings of yield performance among genotypes across environments leading to cross-over G ×E interactions.

Like PC1, the environment PC2 scores had both positive and negative values. This gave rise to crossover, leading to inconsistent genotype yield performance across environment (locations). To visualize the relationship between environments, lines are drawn to connect the test environments to the biplot origin known as environment vectors. The cosine of the angle between two environments is used to approximate the correlation between them as described and used in Dehghani et al. (2009, 2010), Kaya et al. (2006), Yan and Tinker (2006).b For example locations 2,3 and 6 were positively correlated (an acute angle), location 1 and 5 were negatively correlated (an obtuse angle), and location 1 and 4 were not correlated (a right angle) in year 2004.The presence of wide obtuse angle (that is, strong negative correlations) among test environments is an indication of high cross over GEI (Yan and Tinker, 2006).

The distance between two environments measures their dissimilarity in discriminating the genotype, thus the six locations in (Figure 1a) fell into 4 apparent groups where locations 2,3 and 6 form the first group while lactations 1,4 and 5 each of them separately form their own group. The presence of close associations among some test locations in year 2004, suggest that the same

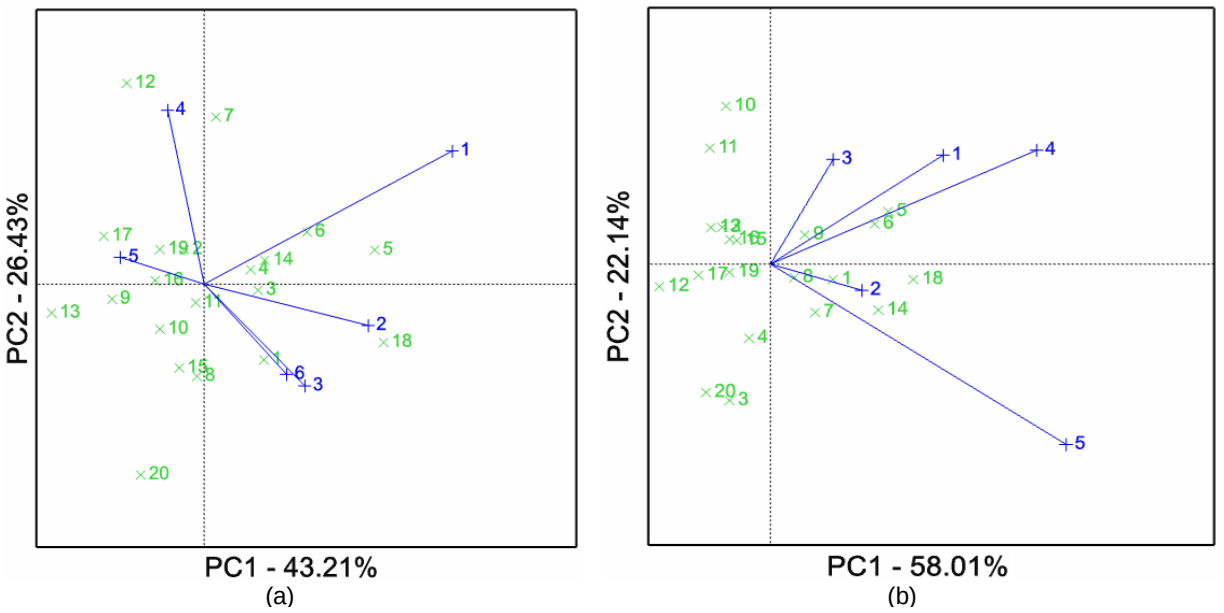

Figure 1. Scatter plot of environments (a) year 1 (b) year 2.

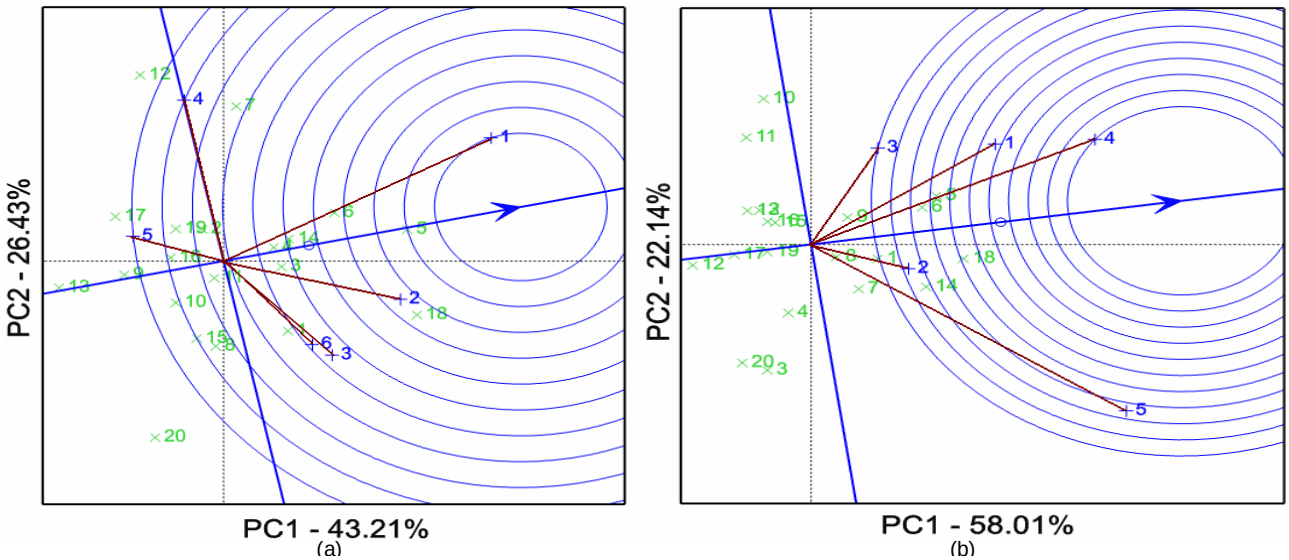

Figure 2. GGE biplot based on environment-focused scaling for comparison of the environment with ideal environment (a) year 1 (b) year 2.

information about genotypes could be obtained from fewer test locations, and hence the potential to reduce test cost (Choukan, 2010; Tukamuhabwa et al., 2012). If two test locations are closely correlated consistently across years, one of them can be drooped without loss of much in-formation about the genotypes. However, in reality the correlation consistency between the test locations vary from year to year as it shown in Figure 1. Clearly Figure 1a and Figure 2b show differing genotype and environment structure. However it should be noted that data in 2005 had only five of the location in 2004.

Discriminating ability and representativeness of the test environment

GGE biplot discriminating ability and representativeness is an important measure of the testing environments. The concentric circles on the biplot as shown in Figure 2 help to visualize the length of the environment vectors, which is proportional to the standard deviation within the respective environments and is a measure of the discriminatory ability of the environments. Therefore, among the six environments, E1 and E4 were most

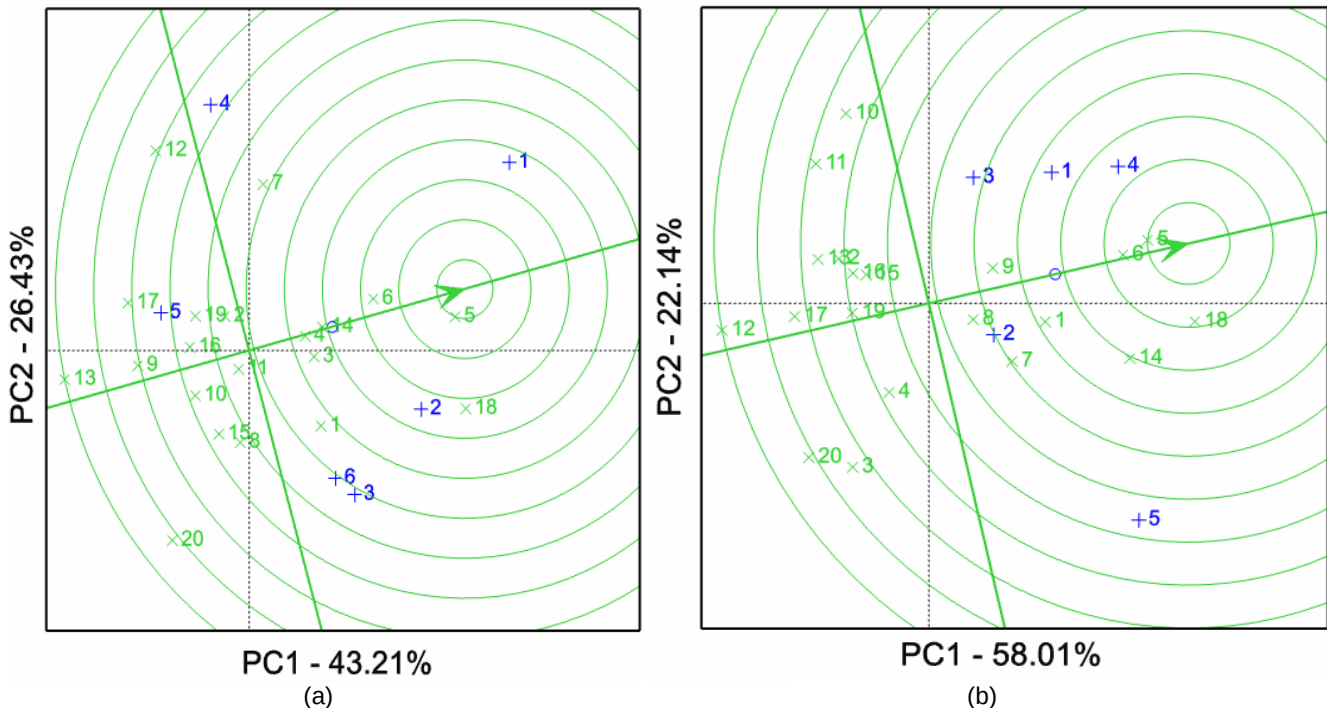

Figure 3. GGE biplot based on genotype-focused scaling for comparison of the genotype with ideal genotype (a) year 1 (b) year 2.

discriminating (informative) and E5 least discriminating in year 1; whereas in year 2 (Figure 2) E5 and E4 are most discriminating and E2 was least-discriminating. Test environments that are consistently non-discriminating (non-informative) provide little information on the genotypes and, therefore, should not be used as test environments. The average environment (represented by the small circle at the end of the arrow) has the average coordinates of all test environments, and Average-Environment Axis (AEA) or Average-Tester-Axis (ATA) (Yan, 2002) is the line that passes through the average environment and the biplot origin. A test environment that has a smaller angle with the AEA is more representative of other test environments. Thus, E1 and E4 are most representative whereas E5 and E3 least representative in their respective year. Test environments (locations) that are both discriminating and representative (e.g., E1) are good test environments for selecting generally adaptable genotypes. Discriminating but non-representative test environments like E3 are useful for selecting specifically adapt-able genotypes if the target environments can be divided into mega-environments or they are useful for culling unstable genotypes if the target environment is a single mega-environment.

Ranking genotypes relative to the ideal genotype

An ideal genotype should have the highest mean performance and be absolutely stable (that is, performs the best in all environments). Such an ideal genotype is defined by having the greatest vector length of the high yielding genotypes and with zero GEI, as represented by an arrow pointing to it (Figure 3). Although such an ideal genotype may not exist in reality, it can be used as a reference for genotype evaluation (Yan and Tinker, 2006). A genotype is more desirable if it is located closer to the ideal genotype. Thus, using the ideal genotype as the centre, concentric circles were drawn to help visualize the distance between each genotype and the ideal genotype. Because the units of both PC1 and PC2 for the genotypes are the original unit of yield in the genotype-focused scaling (Figure 3), the units of the AEC abscissa (mean yield) and ordinate (stability) should also be in the original unit of yield. The unit of the distance between genotypes and the ideal genotype, in turn, will be in the original unit of yield as well. Therefore, the ranking based on the genotype-focused scaling assumes that stability and mean yield are equally important (Farshadfar et al., 2012; Yan, 2002). Figure 3 revealed that G5, which fell into the centre of concentric circles, was the ideal genotype in terms of higher yielding ability and stability, compared with the rest of the genotypes. In addition, G6 and G14, located on the next consecutive concentric circle, may be regarded as desirable genotypes.

Mean performance and stability of the genotypes

Yield performance and stability of genotypes were

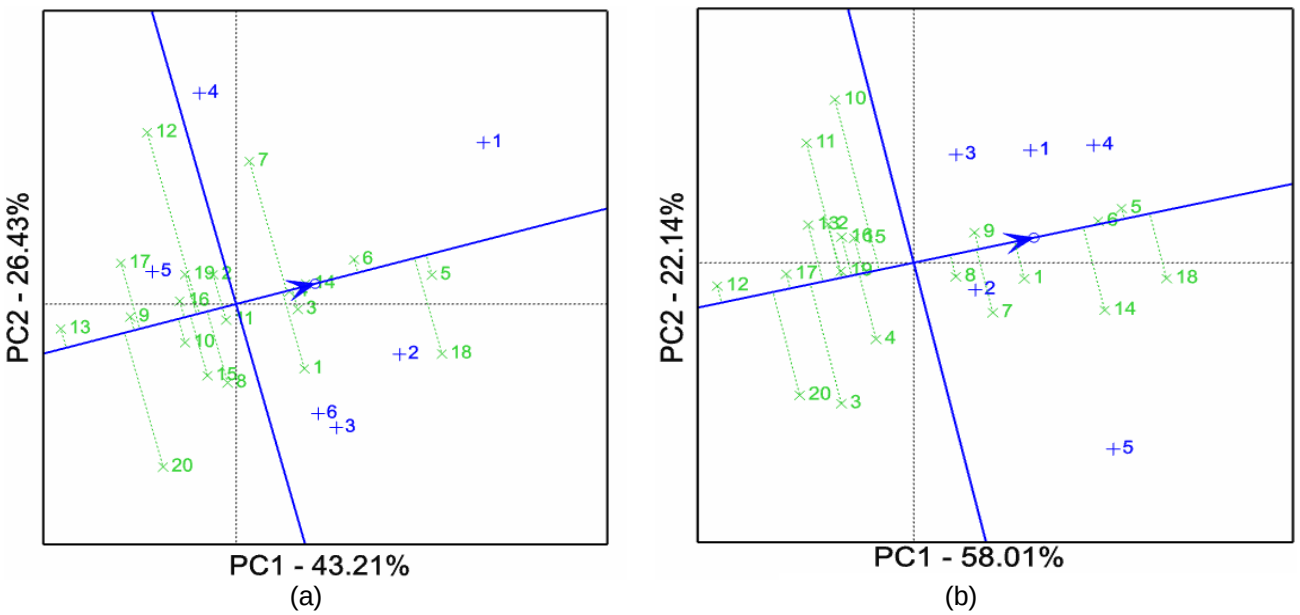

Figure 4. GGE biplot based on environment-focused scaling for mean performance and stability of the genotypes (a) year 1 (b) year 2.

evaluated by an average environment coordination (AEC) method in Farshadfar et al. (2011). Within a single mega-environment, genotypes should be evaluated on both mean performance and stability across environments. Figure 4a gives the average environment coordination (AEC) view of the GGE biplot. The single-arrowed line is the AEC abscissa, it points to higher mean yield across environments. Thus, G5, G18, G6 and G14 had the highest mean yield. The non-arrowed line is the AEC ordinate; it points to greater variability (poorer stability) in either direction. Thus, G12 and G20 ware highly unstable and below average yield, whereas G4 and G14 highly stable, were followed by G5, G6 and G3 with above average yield in the first year.

The mean performance and stability of these 20 genotypes in five locations (environment) in the second year of the trial shows some variation from the first year as it shown in Figure 4b. However G6, G5, G4 and G18 were relatively high yielding and stabile genotypes in both trial years.

Which genotype won where and mega environments with GGE bi-plot

One of the most attractive features of a GGE biplot is its ability to show the which-won-where pattern of a genotype by environment data set (Figure 5). Many researchers find this use of a biplot intriguing, as it graphically addresses important concepts such as crossover GE, mega environment differentiation, specific adaptation, etc as discussed in Yan and Tinker (2006). The polygon is formed by connecting the markers of the genotypes that are further away from the biplot origin such that all other genotypes are contained in the polygon. Genotypes located on the vertices of the polygon performed either the best or the poorest in one or more locations since they had the longest distance from the origin of biplot. The perpendicular lines are equality lines between adjacent genotypes on the polygon, which facilitate visual comparison of them. For example, the equality line between G5 and G18 in 2004 indicates that G5 was better in E1, whereas G18 was better in E2, E3 and E6. An interesting feature of this view of a GGE biplot is that the vertex genotype(s) for each sector has higher (some times the highest) yield than the others in all environments that fall in the sector (Gauch et al., 2008; Yan, 2002). These six equality lines divide the biplot into six sectors, and the environments fall into four of them (Figure 5).This pattern suggest that the target environment may consist of four different mega-environments and that different cultivars should be selected and deployed for each.

In which-win-where GGE biplot for the second year (Figure 5b), eight equality lines divide the biplot into eight sectors and the five locations fell into three of them. The mega-environment classification of these five trial location is different from the first year. This difference leads to a different wining genotype in different locations (environment) across a year.

Conclusions

The GGE biplotsof MEYT data allow visualizing the inter-relationship among genotypes including the ranking of genotypes based on both mean performance and stability, inter-relationship among environments, and

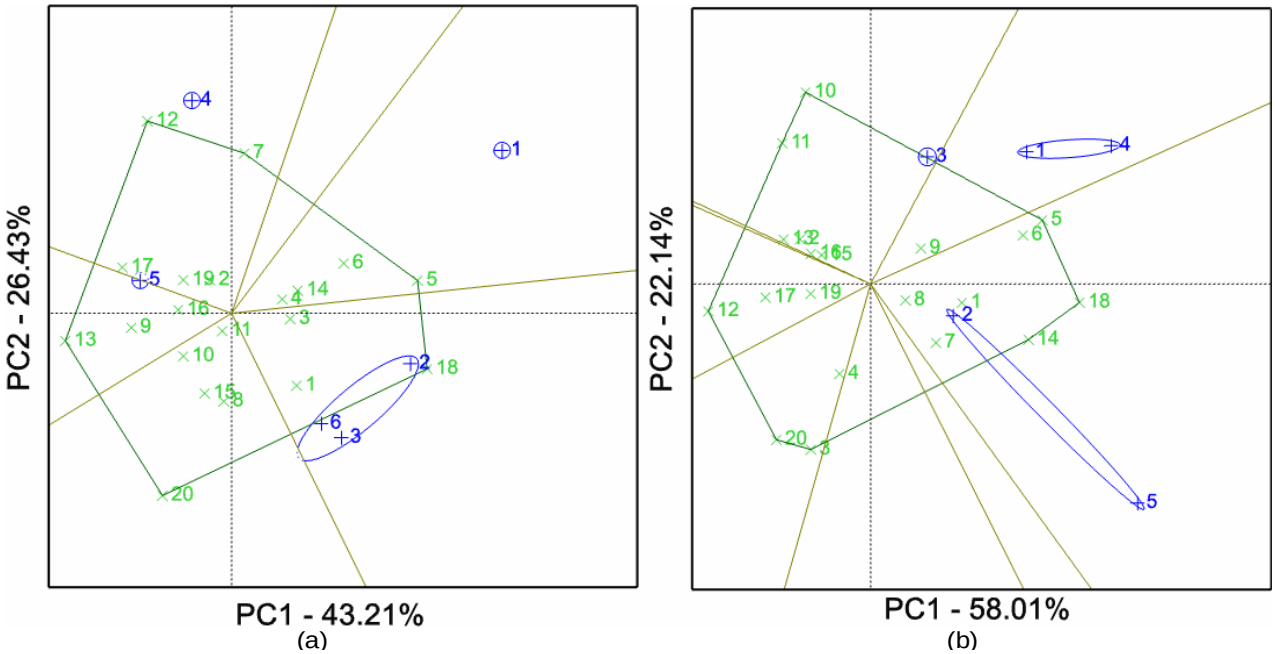

Figure 5. The which-won-where view of the GGE biplot to show which genotypes performed best in which environment (a) year 1 (b) year 2.

interaction between genotypes and environments including the which-won-where pattern. The result of this study indicated that wheat yield performance was highly influenced by the environment effect followed by the magnitude of GEI and genotype. Total yield variation by the genotype increased from 0.0029% in first year to 14.03% in the second year which had almost equal effect with the G×E interactions. These two years repeated over location data analysis result; which-win-where pattern, yield performance and stability of genotype indicate that repeatability pattern over years is the necessary and sufficient condition for mega-environment delineation and genotype recommendation. Decision making recommendation based on one year data should be done with caution.

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