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Current advances in GxE analysis models and their interpretations, an implication for genotype selection for multiple environments. A review article

Tewodros Mulualem[1]and Zelalem Bekeko*[2]

[1]Jimma Agricultural Research Center, Po Box 192, Jimma and [2]Haramaya University School of Plant Sciences, Po Box 138, Dire Dawa, Ethiopia.
*Corresponding authors: zelalembekeko@yahoo.com

Abstract

In agricultural experimentation, such as crop improvement programs a large number of genotypes are normally tested over wide ranges of environments and new genotypes generally tested at many locations and for several years before being recommended for production for a given area. To achieve this goal, multiple-environmental trials (MET) are conducted annually for all major crops throughout the world with the purpose of identifying superior genotypes for the target locations. In most cases, GE interaction is observed and need to be modelled and interpreted. The underlying statistical and genetic models used in this system are complex. In GE there are different types of models that are available for the analysis of GEI and broadly classified into four groups: the analysis of components of variance, stability analysis, multivariate methods and qualitative methods. However, multi-environment trials, is one of the most common methods in a GxE interaction to compute the simple averages across replications for a genotype in an environment and then analysing the means. An alternative method of analysing the data in a two-way table of means is the Additive Main Effects and Multiplicative Interaction (AMMI) model which combines the conventional analyses of variance for additive main effects with the principal components analysis for the non-additive residuals. Additive Main Effect and Multiplicative Interaction is frequently applied in yield trials in agricultural research when both main effects and interaction are important. The other method is the regression of genotype means on the environment for means analysis and GG E by plot analysis. Therefore, recently at an advanced level a combined model approach is used to analyse GEI for identification and selection of best genotypes. Therefore the objective of this review article is to assess recent advances in GxE analysis models, their analysis and interpretation for identification and selection of the best performing genotypes for a given area.

Keywords: AMMI; GEI; genotype; environment; model; stability

Introduction

The phenotype of an individual is determined by both the genotype and the environment, these two effects are not always additive which indicates that genotype x environment interactions (GEI) are present. The GEI result in inconsistent performances between the genotypes across environments. Significant GEI results from the changes in the magnitude of differences between genotypes in different environments or changes in the relative ranking of the genotypes (Falconer, 1952; Fernandez, 1991). The two forms of GEI are qualitative and quantitative (absolute differences between genotypes). GEI makes it difficult to select the best performing and most stable genotypes and is an important consideration in plant breeding programs because it reduces the progress from selection in any one environment.

GEI analysis is particularly important when the rank of lines selected for breeding changes in different environments (crossover GEI). Indeed, high yielding genotypes in favorable environments can have inferior performances under poor growing conditions (Ceccarelli, 1996). For this reason, understanding the causes of GEI would help in developing genotypes which show satisfactory performances in one to

several environments. For the correct analysis of multi-environmental trials, the additive main effects and multiplicative interaction (AMMI) model is a valuable tool due to the accuracy that it provides in GEI studies (Gauch, 1992; 2006). Li *et al.* (2006) tested the effectiveness of the AMMI model in comparison with correlation and path analysis to investigate GEI effects.

Annicchiarico evaluated (1997a) in comparison to the joint regression model to investigate GEI effects on crops in specific environments. Its efficiency has also been tested in specific environments for GEI effects on yield and yield components in genotypes (Voltas *et al.,* 1999a; Voltas *et al.*, 2002) and for GEI effects on quality (Rharrabtia *et al.,* 2003).

Another model that has gained importance in investigating the role of genotype, environment and GEI effects in yield-trial experiments are the genotype main effects and genotype x environment interaction (GGE) biplot (Gauch, 2006; Yan *et al.,* 2007). The AMMI results are graphically presented in the form of a biplot (Gabriel, 1971; Yan *et al.,* 2007), in which the genotypes and environment scores of the first two bilinear terms are represented by vectors in a space, with their starting points at the origin (0,0) and end points (markers) determined by their scores (Gauch and Zobel, 1996; Vargas and Crossa, 2000). To investigate the biological meaning of environment, genotype and interaction effects, the correlation coefficients between the environment IPCA (IPCAe) scores obtained from the AMMI analysis and the environment covariables were calculated, as the correlations between the genotype IPCA (IPCAg) scores and means of the recorded traits.

Additionally, the yield biplot obtained from the AMMI model was enriched by the procedure described by(van Eeuwijk, 1995; Vargas *et al.,* 1999a; Voltas *et al.,* 2002). This method helps in the interpretation of the AMMI biplot patterns by adding the directions of the greatest changes for the genotype and environment covariables, as obtained from the regression of the standardized covariables on the AMMI axes. Finally, ANOVA was performed to test whether the differences in the yield levels and in the levels of interaction for yield among groups of genotypes were significant. Measuring GEI helps to determine an optimum breeding strategy, to breed for specific or general adaptation, which depends on the expression of stability under a limited or wide range of environment (Crossa, 1990).

In multi-environment, stability analysis model is important to identify best genotypes in variable environment. It is usually refers to a genotype's ability to perform consistently, whether at high or low yield levels, across a wide range of environments. The terms phenotypic stability, yield stability and adaptation are often used in quite different senses. Most stability measures relate to either of two contrasting concepts of stability: "static" (Type-1) and "dynamic" (Type 2) (Becker and Léon, 1988; Lin *et al.*, 1986). Static stability is analogous to the biological concept of homeostasis: a stable genotype tends to maintain a constant yield across environments. The term "environmental sensitivity" has also been used in this respect, where greater sensitivity corresponds to lower stability (Falconer, 1990; Dyke *et al.*, 1995).

Dynamic stability implies for a stable genotype a yield response in each environment that is always parallel to the mean response of the tested genotypes, i.e. zero GE interaction. The measure of dynamic stability depends on the specific set of tested genotypes, unlike the measure of static stability (Lin *et al.*, 1986). Different concepts and definitions of stability have been described over the years (Lin *et al.*, 1986; Becker and Léon, 1988). There are three identified concepts of stability:

Type 1: A genotype is considered to be stable if its among-environment variance is small. Becker and Léon, (1988) called this stability a static, or a biological concept of stability. A stable genotype possesses an unchanged performance regardless of any variation of the environmental conditions. This concept of stability is useful for quality traits, disease resistance, or for stress characters like winter hardiness. Parameters used to describe this type of stability are coefficient of variability (CVi) used for each genotype as a stability parameter and the genotypic variances across environments (Si^2).

Type 2: A genotype is considered to be stable if its response to environments is parallel to the mean response of all genotypes in the trial. Becker and Léon, (1988) called this stability the dynamic or agronomic concept of stability. A stable genotype has no deviations from the

general response to environments and thus permits a predictable response to environments. A regression coefficient (*bi*) stability variance ($\sigma^2 i$) can be used to measure type 2 stability.

Type 3: A genotype is considered to be stable if the residual MS from the regression model on the environmental index is small. The environmental index implicates the mean yield of all the genotypes in each location minus the grand mean of all the genotypes in all locations. All stability procedures based on quantifying GEI effects belong to the dynamic concept (Becker and Leon, 1988), this includes the procedures for partitioning the GEI of ecovalence and stability of variance, procedures using the regression approach.

Statistical methods to measure GxE Interaction: Currently, the combined analysis of variance procedure is the most common method used to identify the existence of GEI from replicated multi-location trials. If the GEI variance is found to be significant, one or more of the various methods for measuring the stability of genotypes can be used to identify the stable genotype(s). A wide range of methods are available for the analysis of GEI and can be broadly classified into four groups: the analysis of components of variance, stability analysis, multivariate methods and qualitative methods.

The analysis of variance: Consider a trial in which the yield of G genotypes is measured in E environments each with R replicates (GER). The classic model for analyzing the total yield variation contained in GER observations is the analysis of variance (Fisher, 1925; Martin, 2004). The within environment residual mean square measures the error in estimating the genotype means due to differences in environmental factors, such as shading and competition from one plot to another. After removing the replicate effect when combining the data, the GE observations are partitioned into two sources: (i) additive main effect for genotypes and environments and (ii) non additive effects due to GEI. The analysis of variance of the combined data expresses the observed (*Yij*) mean yield of the i^{th} genotype at the j^{th} environment as:

$$Yij = \mu + Gi + Ej + GEij + eij$$

where μ is the general mean; *Gi, Ej*, and *GEij* represent the effect of the genotype, environment, and the GEI, respectively; and *eij* is the average of the random errors associated with the r^{th} plot that receives the i^{th} genotype in the j^{th} environment. The non additivity interaction as defined in the above model implies that the expected value of the i^{th} genotype in the j^{th} environment (*Yij*) depends not only on the levels of G and separately but also on the particular combination of levels of G and E.

The major limitation in this model is that the error variances over environments should be homogeneous to test for genotypic differences. If error variances are heterogeneous, this analysis is open to criticism as the F-test of the GEI mean squares against the pooled error variances is biased towards significant results. A correct test for significance, by weighting each genotype mean by the inverse of its estimated variance, has been used. This weighted analysis gives less weight to environments that have a high residual mean square. The disadvantage of weighted analysis is, however, that weights may be correlated to environment yield responses (high yielding environments showing higher error variance and low yielding sites presenting lower error variances) and this could mask the true performance of some genotypes in certain environments (Crossa, 1990).

One of the main deficiencies of the combined analysis of variance in multiplication trials is that it does not explore any underlying structure within the observed non additivity (GEI). The analysis of variance fails to determine the pattern of response of genotypes and environments. The valuable information contained in (*G-1*) (*E-1*) degrees of freedom is particularly wasted if no further analysis is done. Since the non-additive structure of the data matrix has a non-random and random component, the advantage of the additive model is lost if the pattern component of the non-additive structure is not further partitioned into functions of one variable each (Crossa, 1990).

Analysis of variance of multi-location trials is useful for estimating variance components related to different sources of variation, including genotypes and GEI. In general, variance component methodology is important in multi-location trials, since errors in measuring the yield performance of a genotype arise largely from GEI. Therefore, knowledge of the

size of this interaction is required to (i) obtain efficient estimates of the genotypic effects and (ii) determine optimum resource allocations, that is the number of plots and locations to be included in future trials. In a breeding program, variance component methodology is used to estimate the heritability and predicted gain of a trait under selection.

The ANOVA method for estimating variance components consists of equating mean squares to their expectations and solving the resulting set of simultaneous equations as shown in Tables 1 and 2 and are based on the model provided by Allard (1960), for the determination of interaction variance components. Stability analysis or parametric approach: Stability usually refers to a genotype's ability to perform consistently, whether at high or low yield levels, across a wide range of environments. Stability analysis provides a general summary of the response patterns of genotypes to change environments. The main types of stability analysis, is joint regression analysis or joint linear regression (JLR). It involves the regression of the genotypic means on an environmental index. Joint regression analysis provides a means of testing whether the genotypes have characteristic linear responses to changes in environments (Martin, 2004).

Table (1): Variance analysis and expected mean square for GEI models

Source	DF	MS	Expected mean square
Year (Y)	Y-1		
Location (L)	L-1		
YxL	(Y-1)(L-1)		
Rep in Loc and Years	Ly(R-1)		
Genotypes(G)	(G-1)	MS5	$\sigma^2 e + r s^2 gly + rl s^2 gy + ry s^2 gl + rly s^2 g$
GxL	(G-1)(L-1)	MS4	$\sigma^2 e + r s^2 gly + rl s^2 gl$
GxY	(G-1)(Y-1)	MS3	$\sigma^2 e + r s^2 gly + rl s^2 gy$
GxLxY	(G-1) (L-1) (Y-1)	MS2	$\sigma^2 e + r s^2 gly$
Error	LY(G-1)(R-1)	MS1	$\sigma^2 e$

Where, Y, L, G and R are the number of years, locations, genotypes and replications, respectively. The $\sigma^2 e$ and $\sigma^2 g$ are components of variance of error and genotypes respectively. Combinations of the subscript identify the components, for the interactions. MS1 to MS5 are the observed values of the various mean squares

Table (2): Estimates of variance components and methods of determining GEI

Variance component	Methods of Determination
Genotypes ($\sigma^2 g$)	(MS5+MS2-MS3-MS4)/*rly*
Genotype x Location ($\sigma^2 gl$)	(MS4-MS2)/ *ry*
Genotype x Year ($\sigma^2 gy$)	(MS3-MS2 /*rl*
GxLxY ($\sigma^2 gyl$)	(MS2-MS1)/ *r*
Error ($\sigma^2 e$)	MS1

Regression coefficient (*bi*) and deviation mean square ($S^2 di$): Joint linear regression is a model used for analyzing and interpreting the non-additive structure (interaction) of two-way classification data. The GEI is partitioned into a component due to linear regression (*bi*) of the i^{th} genotype on the environment mean, and a deviation (d^{ij}):

(GE)ij = biEj + dij and thus *Yij = μ + Gi + Ej + (biEj + dij)+ eij)*

This model uses the marginal means of the environments as independent variables in the regression analysis and restricts the interaction

to a multiplicative form. The method divides the (*G-1*) (*E-1*) df for interaction into *G-1* df for heterogeneity among genotype regressions and the remainder (*G-1*) (*E-2*) for deviation. Further details about interaction are obtained by regressing the performance of each genotype on the environmental means.

The regression coefficient by regressing variety mean on the environmental mean, and plotting the obtained genotype regression coefficients against the genotype mean yields. A genotype with *bi* = 0 as stable, while, a genotype with *bi* = 1 to be stable (Eberhart and Russell, 1966; Martin, 2004).

According to Finlay and Wilkinson (1963), regression coefficients approximating to 1.0 indicate average stability, but must always be associated and interpreted with the genotype mean yield to determine adaptability. When the regression coefficients are approximating to 1.0 and are associated with high yield mean, genotypes are adapted to all environments. When associated with low mean yields, genotypes are poorly adapted to all environments. Regression coefficients above 1.0 indicate genotypes with increasing sensitivity to environmental change, showing below average stability and great specific adaptability to high yielding environments. Regression coefficients decreasing below 1.0 provide a measure of greater resistance to environmental change, having above average stability but showing more specific adapted to low yielding environments.

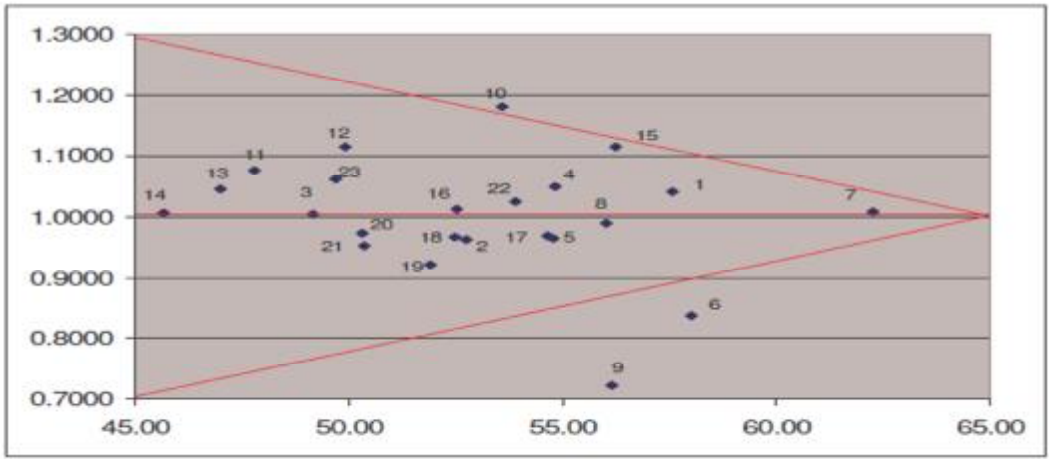

Figure (1): Regression coefficients plotted against the mean yield of maize (as an example)

In effect the residual mean squares from the regression model across environments are used as an index of stability, and a stable genotype is one in which the deviation from regression mean squares (S^2di) is small.

$S^2di = 1 / E - 2 [Ej (Xij - Xi - X j + X..)^2 – (bi –1)2 Ej (X j - X..)^2]$

There are some statistical criticism is that the genotype mean (x-variable) is not independent from the marginal means of the environments (y-variable). Regressing one set of variables on another that is not independent violates one of the assumptions of regression analysis this problem may be overcome if a large number of genotypes are used >15.

Coefficient of determination (r^2 *ij*): The coefficient of determination (r^2 *ij*) instead of deviation mean squares to estimate stability of genotypes, because ri^2 is strongly related to S^2di (Becker, 1981).

$$ri^2 = 1 - \frac{Si^2di}{S^2xi}$$

The application of ri ^{2} and di has the advantage that both statistics are dependent of units of measurement.

Ecovalence (*Wi*): The concept of covalence is defined as the contribution of each genotype to the GEI sum of squares. The covalence (*Wi*) or stability of the i^{th} genotype is its interaction with the environments, squared and summed across environments, and express as:

$$Wi = [Yij - Yi. - Y. j - Y..]^2$$

Where, *Yij* is the mean performance of genotype *i* in the j^{th} environment and *Yi.* and *Y.j* are the genotype and environment mean deviations, respectively, and *Y..* is the overall mean. For this

reason, genotypes with a low *Wi* value have smaller deviations from the mean across environments and are thus more stable. It is used to measures the contribution of a genotype to the GEI, a genotype with zero covalence is regarded as stable (Martin, 2004).

Shukla's stability variance parameter: The stability variance of genotype *i* as its variance across environments after the main effects of environmental means have been removed (Shukla, 1972; Martin, 2004). Since the genotype main effect is constant, the stability variance is thus based on the residual (*GEij* + *eij*) matrix in a two-way classification. The stability statistic □is termed "stability variance" (□*i*) and is estimated as follows:

Crossover interactions and nonparametric analysis: GEI is important in agricultural production,

when there are changes in a genotype's rank over environments. These are called crossovers or qualitative interactions, in contrast to non-crossovers or quantitative interactions. With a qualitative interaction, genotype differences vary in direction among environments, whereas with quantitative interactions, genotypic differences change in magnitude but not in direction. If significant qualitative interactions occur, subsets of genotypes are to be recommended only for certain environments, whereas with quantitative interactions the genotypes with superior means can be used in all environments. Therefore, it is important to test for crossover interactions (Martin, 2004).

The advantages of nonparametric statistics compared to parametric ones are: reduction of the bias caused by outliers, no assumptions are needed about the distribution of the analyzed values, homogeneity of variances, and additivity (linearity) of effects are not necessary requirements. Moreover, the advantages of nonparametric stability statistics are expected to be less sensitive to errors of measurement than parametric estimates and the addition or deletion of one or a few observations is not likely to cause great variation in the estimate as would be the case for stability statistics.

Multivariate analysis methods: Multivariate analysis is appropriate for analysing two-way matrices of G genotypes and E environments. The response of any genotype in E environments may be conceived as a pattern in E-dimensional space, with the coordinate of an individual axis being the yield or other metric of the genotype in one environment. Two groups of multivariate techniques have been used to elucidate the internal structure of genotype x environment interaction:

i. Ordination techniques, such as principal component analysis, principal coordinate's analysis, and factor analysis, assume that the data are continuous. These techniques attempt to represent genotype and environment relationships as faithfully as possible in a low dimensional space. A graphical output displays similar genotypes or environments near each other and dissimilar items are farther apart. Ordination is effective for showing relationships and reducing noise.

ii. Classification techniques such as cluster analysis and discriminant analysis, seek discontinuities in the data. These methods involve grouping similar entities in clusters and are effective for summarizing redundancy in the data.

Principal component analysis: Principal component analysis (PCA) is the most frequently used multivariate method. Its aim is to transform the data from one set of coordinate axes to another, which preserves, as much as possible, the original configuration of the set of points and concentrates most of the data structure in the first principal component axis. Various limitations have been noted for this technique. The linear regression method uses only one statistic, the regression coefficient, to describe the pattern of response of a genotype across environments, and most of the information is wasted in accounting for deviation. Principal component analysis (PCA) is a generalization of linear regression that overcomes this difficulty by giving more than one statistic, the scores on the principal component axes, to describe the response of a genotype (Eisemann, 1981).

Principal coordinates analysis: Principal coordinate analysis is a generalization of the PCA analysis in which any measure of similarity between individuals can be used. Its objectives and limitations are similar to those of PCA, and also has the following advantages: (a) it is trustworthy when used for data that include extremely low or high yielding sites; (b) it does not depend on the set of genotypes included in

the analysis; and (c) it is simple to identify stable varieties from the sequence of graphic displays (Martin, 2004).

Factor analysis: Factor analysis is related to PCA, the "factors" of the former being similar to the principal components of the latter. A large number of correlated variables are reduced to a small number of main factors. Variation is explained in terms of general factors common to all variables and in terms of factors unique to each variable (Crossa, 1990).

Additive main effects and multiplicative interaction (AMMI): The additive main effect and multiplicative interaction (AMMI) method integrates analysis of variance and principal components analysis into a unified approach (Gauch and Zobel, 1988; Annicchiarico, 2002). The AMMI method is used to summarize the patterns and relationships of genotypes and environments (Annicchiarico, 2002). Moreover, it combines the analysis of variance for the genotype and environment main effects with principal components analysis of the genotype environment interaction (Ceccarelli, 1996). It has proven useful for understanding complex GEI. The results can be graphed in a useful biplot that shows both main and interaction effects for both the genotypes and environments. AMMI combines analysis of variance into a single model with additive and multiplicative parameters (Annicchiarico, 1997b).

The combination of analysis of variance and principal components analysis in the AMMI model, along with prediction assessment, is a valuable approach for understanding GEI and obtaining better yield estimates (Annicchiarico, 1997a,b). The interaction is explained in the form of a biplot display where, PCA scores are plotted against each other and it provides visual inspection and interpretation of the GEI components. Integrating biplot display and genotypic stability statistics enable genotypes to be grouped based on similarity of performance across diverse environments. There are many statistical methods available to analyse the GxE interaction. Recently there are two frequently used models especially for statistical analyses of GxE. These are additive main effects and multiplicative interaction (AMMI) model and the genotype main effects and genotype × environment interaction effects (GGE) model. These two models are multivariate methods. Multivariate analysis has three main purposes: (i) to eliminate "noise" in the data set (for example, to distinguish systematic and non-systematic variation); (ii) to summarize the information and (iii) to reveal a structure in the data (Crossa *et al*., 1990).

GGE Biplot :The concept GGEbiplot Methodology: The GGE-biplot methodology consists of two concepts: biplot and 'GGE'. The concept of GGE originates from analysis of mega environment trials (MET) of crop cultivars. The yield of a cultivar (or any other measure of cultivar performance) in an environment is a mixed effect of genotype main effect (G), environment main effect (E), and genotype _ environment interaction (GE). In normal METs, E accounts for 80% of the total yield variation, and G and GE each account for about 10% (Gauch and Zobel, 1996; Yan *et al*., 2000). For the purpose of cultivar evaluation, however, only G and GE are relevant (Gauch and Zobel, 1996). Furthermore, both G and GE must be considered in cultivar evaluation, thus the term GGE (Yan *et al*., 2000).

The GGE biplot is a biplot that displays the GGE part of MET data. The recently developed GGE-biplot method provides a more elegant and useful display of mega environment trials data. It effectively addresses both the issue of mega-environment differentiation and the issue of genotype selection for a given mega-environment based on mean yield and stability. It also allows environments to be evaluated just as well as genotypes. In addition, it facilitates interpretation of GxE as genotypic factor by environmental factor interactions. GGE biplot has the advantage in that it is important in:

(i) Ranking the cultivars based on their performance in any given environment,
(ii) Ranking the environments based on the relative performance of any given cultivar,
(iii) Comparing the performance of any pair of cultivars in different environments,
(iv) Identifying the best cultivar in each environment,
(v) Grouping the environments based on the best cultivars,
(vi) Evaluating the cultivars based on both average yield and stability,
(vii) Evaluating the environments based on both discriminating ability and representativeness, and

(viii) Visualizing all of these aspects for a subset of the data by removing some of the cultivars or environments. *GGE* biplot has been applied to visual analysis of genotype environment data, genotype trait data, genotype marker data, and diallel cross data.

A GGE biplot can be generated based on Single value decomposition of: (i) environment-centred data; (ii) environment centred and within-environment standard deviation-scaled data; and (iii) environment centred and within-environment standard error-scaled data.

GGE is a linear-bilinear model *that removes the effect of location* and expresses the answer only as a function of the effect of genotypes and the GxE interaction. This model is recommended when the environments are the main source of variation in relation to the contributions of the genotypes and the GxE interaction with respect to the total variability (Balzarini *et al*., 2005). This technique allows the detection of GxE interactions in terms of the crossover effect resulting from great changes in the ranking of the genotypes across the environments. GGE biplot displays two principal component (PC1 and PC2) derived from environment centered yield data. It allows the determination of mega-environments.

Conclusion

Genotype x Environment interaction (GEI) is a common phenomenon in agricultural research. Genotypic values may increase or decrease from one environment to another which might cause genotypes responses in different environments. The association between the environment and the phenotypic expression of a genotype constitute the GEI. The GEI determines if a genotype is widely adapted for an entire range of environmental conditions or separate genotypes must be selected for different sub environments. The impact of an environmental factor on different genotypes may vary implying that the productivity of plant may also vary from one environment to the next. Breeding plans may focus on the GxE interaction to select the best genotype for a target population of environments. For the correct analysis of multi-environmental trials, the additive main effects and multiplicative interaction (AMMI) model is a valuable tool due to the accuracy that it provides in GEI studies tested the effectiveness of the AMMI model in comparison with correlation and path analysis to investigate GEI effects.

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