Special Proceeding of the 21st Annual Conference of SSCA held at SV Agricultural College (ANGRAU), Tirupati, during January 29-31, 2019; pp 131-140

AMMI Models and its Applications

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Received: 11 June 2019; Revised: 14 June 2019; Accepted: 16 June 2019

Abstract

Plant breeding programmes, usually evaluate genotypes that are mostly at the final stages of development across locations and years or make recommendations from among the well-established varieties suitable for a given region or location. Plant breeders invariably encounter genotype × environment interactions (G×E or GEI) while testing genotypes (cultivars) in multi-environment trials (METs). G×E interactions are observed as differential responses of genotypes in different environments. The presence of interaction complicates the selection of widely adapted or superior genotypes for quantitative traits in particular, and in making cultivar recommendations for the target population of environments (TPE). Conventional statistical methods such as analysis of variance (ANOVA) and principal component analysis (PCA) have shown to be inadequate in handling large data sets with complex G×E interactions that typically emerge from METs. The draw backs have been overcome using the Additive Main effects and Multiplicative Interaction (AMMI) model by combining the ANOVA of the genotype (G) and environment (E) main effects with the PCA of the G×E interaction. The main purposes of AMMI analysis are: (i) understanding complex GEI patterns, (ii) exploit specific adaptations (iii) increasing accuracy to improve heritability, selections, and therefore genetic gains. AMMI analysis and biplots are demonstrated using simulated multi-environment evaluation of genotypes.

Key words: Breeding experiments, multi-environment trials, G×E interactions, AMMI models, Biplots.

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1 Introduction

The main stages of a plant breeding programme include (i) generating genetic variability, (ii) selection and (iii) testing of experimental cultivars (Ceccarelli, 2009). The experimental cultivars in the last stage are usually tested in multi-environment trials (METs) and at the end, new varieties are recommended for cultivation. In METs, a large number of genotypes are evaluated for yield or other economically important traits in replicated field trials that are conducted across several environments. Most common environments are locations in a region and years within location. Within years and location, genotypes can be tested under different conditions / stresses, varying input levels, soil type / topography, varying field management protocols and varying abiotic stresses such as drought, submergence salinity. The pattern of conditions / stresses that the genotypes experience is

Late Professor M.N. Das Memorial Lecture delivered during the 21st Annual Conference of the SSCA held at SV Agricultural College, (ANGRAU), Tirupati during 29 – 31 January 2019
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representative of future growing environments and its performance is a prediction of its future performances.

Genotypes tested in METs respond differently across the range of environments referred to as the genotype x environment interaction (G×E). Especially, quantitative traits, which are controlled by several genes, are highly influenced by environmental factors and display a continuous variation. GEI occurs in all stages of a breeding program either in terms of changing mean performances across environments or in terms of heterogeneity of variances across environments or as lack of correlation between environments (Malosetti et al., 2013). Therefore, the main objective of METs is to estimate the effects of treatments across broad or specific environments. Plant breeders usually look for non-crossover G×E (interaction without rank changes in genotype means among environments) when selecting genotypes for broad adaptation to a wide range of environments and crossover G×E (interaction with rank changes in genotype means among environments) for specific adaptations of genotypes to subsets of environments.

Several statistical models have been proposed for studying the GxE interaction in different crops. Under broad adaptation (ignore G×E) the aim is to (i) identify varieties that have high mean across a range of environments using ANOVA and (ii) evaluate the consistency of genotypic performance across the range of environments based on regression techniques. The model for ANOVA in a single environment consists of the genotype and the design effects for the individual location. ANOVA for the combined analysis across locations extends the model for individual location by adding the location factor and the genotype x location interactions. However, the genotypes that are superior across environments might not be the best ones for specific environments. ANOVA defines if G×E is significant or not and provides a quantitative estimate of the amount of phenotypic variation associated with the interaction but does not explore the possibility of partitioning the same into interpretable components. The idea of partitioning the interaction is the basis for regression models (Finlay and Wilkinson, 1963; Eberhart and Russell, 1966; Perkins and Jinks, 1968). However, a major drawback of the regression analysis is that the method is not informative if linearity fails and is highly dependent on the set of genotypes and environments included.

On the other hand, crossover interactions are the most important for breeders as they imply that the choice of the best genotype is determined by the environment (Malosetti et al., 2013). The presence of crossover interaction implies that improvements made in one set of environments will not be carried over when the selected genotypes are grown in other environments. Therefore, under specific adaptation, the aim is (i) either to subdivide environments into groups so that there is little GEI within each group (reduce G×E) or (ii) to select different genotypes suitable for different set of environments (exploit G×E).

The Additive Main effects and Multiplicative Interaction (AMMI) model (Gauch, 1988; Zobel et al., 1988; Gauch, 1992) and the genotype + genotype by environment interaction (GGE) model (Yan et al., 2000) are based on singular value decomposition (SVD) that partition the G×E interaction into the sum of a set of multiplicative terms. The objectives of AMMI are (i) to identify genotypes with similar responses across environments, (ii) to identify environments that discriminate genotypes in a similar manner, (iii) increasing accuracy by separating signal from noise to improve recommendations, repeatability, selections and genetic gains (Gauch, 2013).

2 AMMI Model

In AMMI, the ANOVA is first applied to a two-way table of genotypes and environments. ANOVA partitions the variation into the genotype (G) and environment (E) main effects and the G×E interaction. The multiplicative principal component analysis (PCA) model is applied to the residual (*i.e.* the G×E interaction) from the additive model. Both genotypes and environments are regarded as fixed effects. The AMMI model (for the mean phenotype) is written as

$$y_{ge} = \mu + \alpha_g + \beta_e + \sum_{m=1}^{M} \lambda_m u_{gm}^{*} v_{em}^{*} + \rho_{ge} + \varepsilon_{ge} \quad (1)$$

y_{ge} is the mean phenotypic observation of the genotype g in environment e, μ is the grand mean, α_g is the effect of genotype g, β_e is the effect of environment e, λ_m is the singular value for PCA axis m, u_{gm}^{*} is the m^{th} element of the genotype eigen vector for axis m, v_{em}^{*} is the m^{th} element of the environment eigen vector for axis m, ρ_{ge} is the residual that remains if not all axes are used and ε_{ge} is the error term (Gauch, 1992). Scaling the terms in the interaction sum results in two vectors of parameters called the interaction principal component axes (IPCA) for genotypes and environments. The m^{th} IPCA for genotypes has the elements $u_{gm} = \sqrt{\lambda_m}\, u_{gm}^{*}$ and the m^{th} IPCA for the environments has elements $v_{em} = \sqrt{\lambda_m}\, v_{em}^{*}$. The choice of M, the number of axes to be retained is complicated. The fewer the components retained, the simpler and more interpretable the model, but more axes may be required to model complex interactions. Thus equation (1) is known as the AMMI model of order m or AMMIm and rewritten as

$$y_{ge} = \mu + \alpha_g + \beta_e + \sum_{m=1}^{M} u_{gm} v_{em} + \rho_{ge} + \varepsilon_{ge} \quad (2)$$

where ρ_{ge} is usually assumed to be zero

2.1 Steps in the AMMI analysis

The steps involved in the AMMI analysis according to Gauch (2013) are

(i) ANOVA
(ii) Model diagnosis
(iii) Mega-environment delineation
(iv) Selection and recommendation.

ANOVA test is first carried out to examine whether AMMI analysis is effective for the given data. AMMI analysis is said to be effective only if $SS\left(GxE_{signal}\right)$ is at least as large as that $SS\left(G\right)$ where

- $SS\left(GxE_{noise}\right) = \left(error\ mean\ sq.\right) x\ \left(d.f\ for\ GxE\right)$
- $SS\left(GxE_{signal}\right) = SS(GxE) - SS(GxE_{noise})$ (3)

Model diagnosis deals with the problem of determining the number of multiplicative terms to be retained in the AMMI model. The criteria include

(i) Statistical test of significance for the multiplicative terms (Gollob, 1968; Cornelius, 1993; Piepho, 1995) based on distributional assumptions.
(ii) Agricultural interpretability.
(iii) Predictive accuracy (Gauch, 1988; Crossa et al, 1991; Piepho, 1994; Dias and Krzanowski, 2003) based on cross validation of the model by data splitting and the root mean square prediction difference (RMSPD).

Mega-environment is a group of environments which causes groups of genotypes with similar response to a trait (Gauch and Zobel, 1997). It can also be defined as a geographical region within which a single cultivar performs the best everywhere (Yan, 2014). Mega-environment subdivision implies exploiting rather than ignoring the potential for yield increases that resides in G×E interactions. The criteria for mega-environment delineation include (Gauch and Zobel, 1997)

(i) Focuses on the variation relevant for mega environment subdivision – given by $SS(G) + SS\ (signal)$
(ii) Answers breeders and agronomists question "Which won where"? – Grouping of locations with identical winners into mega-environments and targeting suitable genotypes for each mega-environment.
(iii) Dual analysis of both genotypes and environments – should integrate both G and E into a single model (biplot analysis).

Flexibility with handling various data structures – two-way (G×L) or a three way (G× L×Year) structure, complete or incomplete factorial designs with unreplicated or replicated trials, is an interesting part of the analysis.

3 Biplot Analysis

The AMMI parameters are represented on Biplots (Gabriel, 1971). Biplots are an extensively used graphical technique to display interaction patterns, to visualize the interrelationships among genotypes, environments, and the interactions between genotypes and environments. Two dimensional biplot is a graphical approximation of a two-way G×E data table. For example, consider the factorization

$$\underset{P}{\begin{pmatrix} 20 & -9 & 6 \\ 6 & 12 & -15 \\ -10 & -6 & 9 \\ 4 & -11 & 14 \end{pmatrix}} = \underset{R}{\begin{pmatrix} 4 & 3 \\ -3 & 3 \\ 1 & -3 \\ 4 & -1 \end{pmatrix}} x \underset{C}{\begin{pmatrix} 2 & -3 & 3 \\ 4 & 1 & -2 \end{pmatrix}}$$

The biplot is a plot of this factorization where the

X-axis : First column of R and first row of C
Y axis : Second column of R and second row of C

Biplot involves two steps: (i) decomposing the two-way table into principal components (PCs) and (ii) plotting the PC1 scores against the PC2 scores for each of the rows and columns to form a biplot.

3.1 AMMI Biplot

The results of the AMMI model are interpreted using the AMMI biplots. AMMI biplots are two dimensional graphs where aspects of both genotypes and environments are plotted on the same axis (Kempton, 1984). However, a biplot is only a descriptive graphical tool and cannot be used for hypothesis testing. AMMI biplots allow graphical representation of the G×E interactions on a low dimensional space (Bradu and Gabriel, 1978; Kempton, 1984). Gauch (2013) provided a protocol for the AMMI analysis of MET data. AMMI biplots are of two major kinds

3.1.1 Rank–1 or AMMI–1 biplot

The abscissa is the main effects of genotype and environment and the ordinate constitutes the IPAC1 (interaction principal component axis) scores from SVD of the empirical interactions (*i.e.*, deviations of cell means from additive main effects of genotypes and environments (Zobel et al., 1988). AMMI-1 biplot enables a simultaneous view of the mean performance and the stability of the genotypes (Samonte et al., 2005; Asfaw et al., 2009; Rashidi et al., 2013).

1. The horizontal line shows an IPCA1 score of 0 and the vertical line indicates the grand mean.
2. Distances in the direction of abscissa show main effect differences but have similar interactions.
3. Distances in the direction of ordinate show interaction effect differences but have similar main effects.
4. For any G–E combination, AMMI estimates the yield of genotype G in environment E as

$$(overall\ mean) + (main\ effect\ of\ G) + (main\ effect\ of\ E) + (IPCA\ 1\ of\ G) + (IPCA1\ of\ E)$$

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5. IPCA = 0 showed stability and general adaptability with yield close to mean yield and negligible interaction.
6. Best genotypes that combine high yield and stable performances are adaptive.
7. Cultivars with IPCA 1 scores > 0 responded positively (adaptable) to environments that had IPCA 1 scores > 0 (*i.e*., their interaction is positive) and responded negatively to environments that had IPCA 1 scores < 0. The reverse applies for cultivars that had IPCA 1 scores < 0.
8. Adaptability of specific cultivars are assessed by plotting their nominal yields at specific environments. Nominal yields are the yield from the AMMI model equation without the environment deviation that is, based on G and IPCA1 effects only.

3.1.2 Rank–2 or AMMI–2 biplot

AMMI–2 biplot provides an easy understanding of the interaction patterns. Here the abscissa is the IPCA1 scores of genotype and environment and the ordinate is the IPCA2 scores of genotype and environment.

1. Genotype points near the origin are non-sensitive to environmental interactive forces.
2. Genotype points close to each other (close or farther from the origin) have similar interactive patterns while those distant from each other are different.
3. Sites with short spokes on the plot do not exert strong interactive forces while sites with long spokes exert strong interaction.
4. The interaction effect of a genotype in an environment is approximated by projecting the genotype point onto the line determined by the environmental vector, where distance from the origin provides information about the magnitude of the interaction.
5. Connecting the extreme genotypes on a GE biplot forms a polygon and the perpendiculars to the sides of the polygon form sectors of genotypes and sites. The genotypes at vertex are the winners in the sites included in that sector.

4 Mixed Model Analysis

In the AMMI model both genotypes and environments are regarded as fixed. The traditional linear model, coupled with ordinary least squares estimation procedures, is too restrictive to perform satisfactory data analyses majorly because of the assumption of (a) constant error variances and (b) independence of errors. Homogeneity of error variance causes most concern when carrying out analysis of variance of multiple location trials. With the Bartlett test it can be tested if the error variance of the trials is significantly different. The test requires at least two replicates at each factor level. Moreover, the Bartlett's test is oversensitive to deviations thus the heterogeneity of variances should be considered at the 99.9% level or higher (Brown and Calgari, 2008). If the error variances differ significantly the only practical solution is to transform the data (sqrt, log, scale). Experimental plots in close proximity to each other are more similar than are plots that are further apart and therefore the assumption of independence of errors does not hold. Therefore, an enhanced statistical analysis that accounts for heterogeneous field conditions would improve predictions. Thus, error structure in "real world" experiments is often more complex than assumed in standard linear models for conventional data analysis. Moreover, the variances of the genotypes often differ and the responses of some pairs of genotypes are more similar than those of others (Piepho and van Eeuwijk, 2002). Moreover, data generated from METs are highly unbalanced as the test genotypes and the test sites vary from year to year and the number of replicates varies from site to site. Therefore, plant breeding experiments require broad range of models that can be used for

- Modelling of spatially correlated residuals (correlation between adjacent plots).
- Allows each environment to have its own error variance.
- Allows each environment to have a different genetic variation.
- Allows each pair of environments to have different genetic correlations.
- Ease with which incomplete data (not all varieties in all environments) can be handled.
- Allows extrapolation of results.

Thus, mixed models are the preferred class of models for the analysis of MET data. Mixed model has two components of effects, fixed and random,

- fixed effects – these are units selected purposefully because those are the only units of interest. Only a finite set of levels that can be represented and inferences are to be made only concerning the levels defined for the study.

- random effects – there is an 'infinite' set of levels (a population of levels). The levels present in the study are a sample from that population and the population is the focus.

5 AMMI in a Mixed Model Framework

For n_g genotypes grown in n_e environments in n_r replications, the G×E model is given by

$$y_{ijl} = \mu + g_i + e_j + ge_{ij} + \epsilon_{ijl} \quad (4)$$

y_{ijl} is the l[th] observation of genotype *i* in environment *j*, g_i is the effect of the i[th] genotype e_j is the effect of the *j*[th] environment, ge_{ij} is the interaction effect between genotype *i* and environment *j* and ϵ_{ijk} is the error. Oman (1991) and Piepho (1997a, b) discussed multiplicative models from a mixed model perspective. They proposed, a covariance structure should be fit to the multiplicative interactions such that the correlation among interaction terms are accounted for, as opposed to the AMMI where the interactions are explicitly modeled as multiplicative terms.

A factor-analytic (FA) structure involving one or two multiplicative terms together with equal specific variances for the genotypes and an environment main effect in the model corresponds to the mixed model version of AMMI. The factor-analytic covariance structure is used to model the covariance of the multiplicative interactions as opposed to a Principal Components model for fixed interaction effects in AMMI models. Factor-analysis is also concerned with the pattern of relationships among variables and is a method that is closely related to the principal component analysis (PCA). While PCA assumes that new variables (principal components) are functions of observed variables, factor analysis assumes the observed variables are functions of unobserved underlying factors. PCA searches for a new set of components, which preserve as much variance of the observed variables as possible. Factor Analysis searches for a new set of factors, which contain as much of the covariance between the observed variables as possible *i.e.* in PCA, all of the observed variance is analyzed, while in factor analysis it is only the shared variances that is analyzed.

Piepho (1994, 1997b) proposed a method to obtain the best linear unbiased predictors (BLUPs) for factor scores of the factor-analytic model used to model interactions. Considering genotypes as fixed and environments as random he showed how to construct biplots using the BLUPs. Therefore, the modified AMMI model incorporating the factor-analytic structure is

$$y_{ge} = \mu + \alpha_g + \beta_e + \sum_{m=1}^{M} \lambda_{gm} w_{em} + \delta_{ge} + \varepsilon_{ge} \quad (5)$$

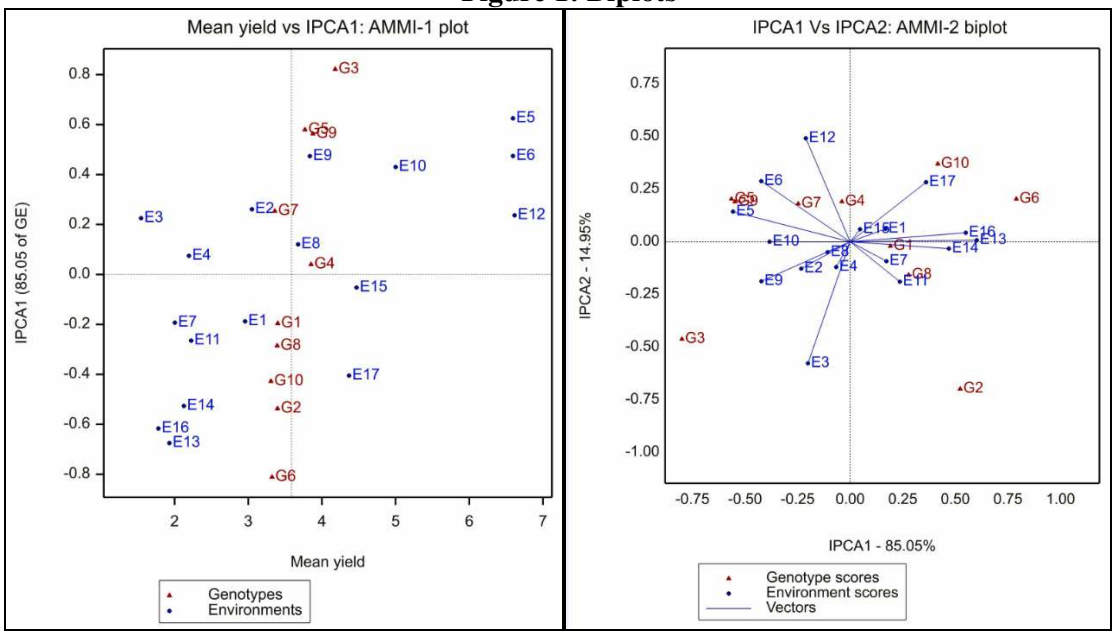
where the variance-covariance structure of genotypes within an environment is

$$\left.\begin{aligned} \mathrm{var}(y_{ge}) &= \sigma^2_{\beta} + \sum_{m=1}^{M} \lambda^2_{gm} \sigma^2_m + \sigma^2_{\varepsilon} \\ \mathrm{cov}(y_{ge}, y_{g'e}) &= \sigma^2_{\beta} + \sum_{m=1}^{M} \lambda_{gm} \lambda_{g'm} \sigma^2_m \end{aligned}\right\} \quad (6)$$

For the mixed model in (2), estimation of variance components is carried out by the Restricted Maximum Likelihood (REML) procedure.

The method is illustrated using mean yield (t/ha) data simulated for a two-way table of 10 genotypes in 17 environments. A factor-analytic-FA0(2) model is fitted using SAS PROC MIXED in which the specific variances δ_{ge} are assumed to be absent. The BLUPs of the interaction effects from the model are subject to SVD (Piepho, 1997a; Anitha, 2005; Kumar et al., 2012) to obtain the IPCA scores for the AMMI model. The interpretation of the biplots provide an insight and understanding of the interaction pattern between genotypes and environments.

Figure 1: Biplots



6 Conclusions

The models based on regression analysis are basically additive in nature and those based on multivariate models is multiplicative in nature. Each of the approaches has its own distinct characteristics with due merits and demerits. But presence of interaction effect complicates the issues involved especially in multi environmental trials of a breeding experiment and the above approaches separately have limitations to be considered for modeling the same.

Thus the use of conventional methods to study G x E interactions in METs poses additional challenges in the analysis. The interactive approach has been well developed known as Additive Main effects and Multiplicative Interaction (AMMI) model based on a combination of two simple models (i) the ANOVA (Analysis of Variance) and (ii) the PCA (Principal Components Analysis). The results of the AMMI model are well interpreted using two dimensional graphs called biplots, where aspects of both genotypes and environments are plotted. However, a biplot is only a descriptive graphical tool and cannot be used for testing any hypothesis of relevance.

Similarly, the mixed-model with factor-analytic covariance structure was also developed by assuming environments (or treatments) as random and T×E interaction is analyzed in a mixed-model framework. Similarly, graphical Biplots provide an insight and understanding of the interaction pattern between genotypes and environments.

Acknowledgements

I would like to thank Dr. Anitha Raman, IRRI, for all the support extended in the preparation of the manuscript.

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