

Use of AMMI and linear regression models to analyze genotype-environment interaction in durum wheat

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Summary. The joint durum wheat (Triticum turgidum L var 'durum') breeding program of the International Maize and Wheat Improvement Center (CIMMYT) and the International Center for Agricultural Research in the Dry Areas (ICARDA) for the Mediterranean region employs extensive multilocation testing. Multilocation testing produces significant genotype-environment (GE) interaction that reduces the accuracy for estimating yield and selecting appropriate germ plasm. The sum of squares (SS) of GE interaction was partitioned by linear regression techniques into joint, genotypic, and environmental regressions, and by Additive Main effects and the Multiplicative Interactions (AMMI) model into five significant Interaction Principal Component Axes (IPCA). The AMMI model was more effective in partitioning the interaction SS than the linear regression technique. The SS contained in the AMMI model was 6 times higher than the SS for all three regressions. Postdictive assessment recommended the use of the first five IPCA axes, while predictive assessment AMMI1 (main effects plus IPCA1). After elimination of random variation, AMMI1 estimates for genotypic yields within sites were more precise than unadjusted means. This increased precision was equivalent to increasing the number of replications by a factor of 3.7.

Key words: *Triticum turgidum* L var 'durum' – Durum wheat – Genotype-environment interaction – AMMI model – Prediction assessment

Introduction

High and stable yielding germ plasm with stress resistance and good grain quality is the main objective of CIMMYT and ICARDA joint Durum Wheat Breeding Program in the Mediterranean region. In this region the selection of suitable germ plasm is conducted with the durum wheat research programs of western Asia, northern Africa, and sourthern Europe.

The testing of Regional Durum Wheat Yield Trials for Moderate Rainfall areas (RDYT-MR) is carried out over a wide range of variable environments. Environmental variation causes differential genotypic responses that result in rank changes of genotypes. Genotype-environment (GE) interaction for the Mediterranean multilocation trials shows large variation (Nachit 1986). The large GE variation usually impairs the accuracy of yield estimation and reduces the relationship between genotypic and phenotypic values.

The predictive accuracy of yield estimate is achieved by improving experimental field techniques, by increasing the number of replications or by using a more sophisticated layout of replications, or by using better statistical analysis for GE partition and interpretation. The latter option offers considerable effectiveness in cost and accuracy of genotypic yield estimate (Gauch and Zobel 1988, 1989).

Partitioning and interpretation the GE interaction is generally based on linear regression techniques (Finlay and Wilkinson 1963; Eberhard and Russell 1966) or multivariate analyses (Kempton 1984; Gauch 1988; Zobel et al. 1988). The linear regression techniques, however, have shown several deficiencies; for example, confounding of interaction and main effects (Wright 1971) and non-linear genotypic response to the environments (Nachit 1986). However, multivariate techniques such as

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the additive main effects and mutliplicative interaction (AMMI) procedure with prediction assessment can be powerful in analyzing multilocation trials (Gauch 1988; Gauch and Zobel 1988). The AMMI model integrates the usual additive analysis of variance (ANOVA) for the additive effects with the principal components analysis (PCA) for the multiplicative effects (Gauch and Zobel 1990). The additive main effects are first extracted from the analysis, and then the principal components analysis is used to investigate the GE interaction.

The AMMI model uses two procedures to determine the number of Interaction Principal Components Axes (IPCA) to include in the analysis: postdictive and predictive assessment. The postdictive assessment uses the IPCA variation to identify the significant axes, while the predictive assessment uses the cross-validation technique to identify the axis with the most accurate yield estimates. Yield estimates of the predictive assessment are produced by adjusting the treatment's means through discarding the residual termed non-pattern variation or noise (Gauch 1990). The AMMI predictive assessment splits the data of the replications into two parts, one part for model fitting and the other part for model validation (Gauch and Zobel 1988). The sum of the squared differences between the model's fitted values and validation data over genotypes and environments is divided by the number of validation observations, and its square root is taken to give the Root Mean Square Predictive Difference (RMS PD). Smaller values of RMS PD indicate good predictive success.

The objective of this study was to: (1) determine and compare the amounts of GE interaction using the AMMI model and linear regression technique, and (2) apply the AMMI predictive accuracy assessment to estimate genotype yields.

Materials and methods

The multilocation Regional Durum Wheat Yield Trial for Moderate Rainfall areas (RDYT-MR) of the 1986/87 season had 21 durum wheat genotypes (Table 1) grown in 22 Mediterranean sites (Table 2). A randomized complete block design with three replications was used in each site. The test plot consisted of six rows 3 m long sown 0.25 m apart at a sowing rate of 100 kg ha⁻¹. The central four rows with a length of 2.5 m were harvested. Grain yield is expressed in kg ha⁻¹. The variable local checks of the sites were excluded from the analysis.

The equations of the additive main effects and multiplicative interaction (AMMI) model (Gauch 1988) and the related models of analysis of variance (ANOVA), principal components analysis (PCA), and concurrence or joint linear regression (Tukey 1949; Finlay and Wilkinson 1963) used in the statistical analysis of yields for RDYT-MR are given below.

The analysis of variance model (ANOVA) is

 $\mathbf{Y}_{\mathbf{g}\mathbf{e}} = \boldsymbol{\mu} + \boldsymbol{\alpha}_{\mathbf{g}} + \boldsymbol{\beta}_{\mathbf{e}} + \boldsymbol{\varrho}_{\mathbf{g}\mathbf{e}} ;$

$$Y_{ge} = \mu + \alpha_g + \beta_e + K \alpha_g \beta_e + \pi_g \beta_e + \eta_e \alpha_g + \varrho_{ge} ; \qquad (2)$$

 Table 1. Grain yield across-sites for 21 durum wheat genotypes of the RDYT-MR for 1987 in 22 sites

Code	Name or cross	Grain yield (kg ha ⁻ 1)
1	Stork	3,830
2	CD20632/02SPSelAp	3,993
3	CD24831AdSelAp	4,006
4	Oronte 6	4,126
5	CD6118SPSelAp	3,756
6	Scoflag	4,247
7	Sajur	3,954
8	Belikh 2	3,963
9	Ain Arous 1	3,942
10	Karasu	3,810
11	CD10549AdSelAp	3,870
12	Cham 1	4,058
13	Om Rabi 11	3,762
14	Amst 1	3,746
15	Cd20632/15SPSelAp	4,024
16	Sebou	3,952
17	ICD-79-0246	4,014
18	Oronte 1	3,874
19	CD26701SPSelAp	3,978
20	Korifla	3,940
21	Sabil 1	3,885

Table 2. Yields and geographical parameters of 22 sites where 21durum wheat genotypes of RDYT-MR for 1987 were grown

Site, country	Grain yield (kg ha ⁻¹)	Latitude (°N)	Altitude (masl)
Santa Engarcia, Spain	5,981	40.0	490
Jerez, Spain	5,334	36.4	20
Settat, Morocco	859	32.5	350
Marchouche, Morocco	3,640	33.3	400
Douyete, Morocco	3,340	35.2	500
Sidi Belabbes, Algeria	3,406	35.1	486
Beja, Tunisia	4,570	37.0	165
Kef, Tunisia	5,952	36.1	35
Khroub, Algeria	6,079	36.2	645
Viterbo, Italy	3,373	42.2	300
Marj, Lybia	4,695	30.3	310
Tessaloniki, Greece	3,696	40.4	10
Izmir, Turkey	6,674	38.3	20
Rainfed-Tll, Syria	3,599	36.0	282
Breda, Syria	1,248	35.6	300
Early Planting, Syria	3,053	36.0	282
Late Planting, Syria	872	36.0	282
Jeleen, Syria	5,329	32.4	421
Terbol, Lebanon	5,614	33.5	890
Tel Amara, Lebanon	3,837	33.6	950
Ramtha, Jordan	2,000	32.4	650
Irbid, Jordan	3,520	32.3	618

the principal components analysis model (PCA) is

$$Y_{ge} = \mu + \sum_{n=1}^{N} \lambda_n \gamma_{gn} \, \tilde{\delta}_{en} + \varrho_{ge} ;$$

(3)

and the AMMI model is

(1)

$$Y_{ge} = \mu + \alpha_g + \beta_e + \sum_{n=1}^{N} \lambda_n \gamma_{gn} \,\delta_{en} + \varrho_{ge} \,. \tag{4}$$

In the ANOVA, LR, and AMMI models (Eqs. 1, 2, and 4), Y_{ge} is the grain yield of genotype g in environment e; μ is the grand mean; α_g is the genotype mean deviation; β_e is the environment mean deviation; and ρ_{ge} , the respective residual. In LR (Eq. 2), K is the Tukey concurrence constant; π_g is the genotype slope on the environment means; and η_e is the environment slope on the genotype means. The LR techniques partitioned the GE interaction (Table 3) into joint (K $\alpha_g \beta_e$), genotypic ($\pi_g \beta_e$), and environmental regression ($\eta_e \alpha_g$), and a residual term (g_{ge}).

In PCA (Eq. 3), λ_n is the square root of the eigenvalue of the principal component axis n; γ_{gn} and δ_{en} are the genotype and environment PCA values, respectively for the axis n; N is the number of PCA axes retained in the model and ϱ_{ge} is the residual. The sum of the deviations of α and β is equal to zero ($\Sigma \alpha = \Sigma \beta = 0$), and the γ and δ eigenvector values for each PCA axis are scaled to unit vectors such that $\Sigma \gamma^2 = \Sigma \delta^2 = 1$. The eigenvalue for a given PCA axis is the sum of squares (SS) accounted for by that axis, and it equals λ^2 (Gauch and Zobel 1989).

For an AMMI model, the sum of the eigenvalues $(\Sigma \lambda^2)$ for N axes and the residual SS (g_{ge}) for a reduced model equals the GE interaction SS. The condensation of most of the GE interaction in a few interaction principal components (IPCA) axes (n=1-3) results in a reduced AMMI model with a residual term (ϱ_{ge}) ; ϱ_{ge} is of course different for each of these different models. However, when the experiment has more than one replication, an error term (ε_{ger}) is added to the above-mentioned equations: $Y_{ger} = Y_{ge} + \varepsilon_{ger}$. The degrees of freedom (*df*) for the IPCA axes are calculated according to Gollob's method (1968): df = G + E - 1 - 2n for axis n.

The additive part of the AMMI model (μ , α_{g} , and β_{e}) is estimated first with ANOVA (Eq. 1), and the multiplicative part (λ_{n}, γ_{gn} , and δ_{en}) is estimated with the PCA (Eq. 3) to explain the pattern in GE interaction (Gauch and Zobel 1989). The direct estimation of GE interaction is generated by the multiplication of a genotype IPCA score ($\lambda_{n}^{0.5} \gamma_{gn}$) by an environment IPCA score ($\lambda_{n}^{0.5} \delta_{en}$).

The inclusion of the number of axes is assessed by two procedures: the postdictive and predictive assessment. The postdictive assessment uses *F*-tests for each IPCA axis (Gauch 1988). Those IPCA axes that are not significant at 0.05 probability level are pooled into the residual term (Table 4). Whereas, the predictive assessment is determined by data splitting (Gauch and Zobel 1988): the data are divided at random into two parts, using one part of the data for model fitting (construction) and the other part for validation. For each combination of genotype and environment in RDYT-MR, two randomly selected replications were used to construct the AMMI fitting model, and the remaining replication was used to validate it. Consequently, the RDYT-MR trial had $21 \times 22 \times 2 = 924$ yield observations for fitting the model and $21 \times 22 \times 1 = 462$ yield observations for validation (Table 6).

To select the optimal number of axes to retain in the predictive assessment, cross-validation techniques were applied (Wold 1978; Krzanowski 1983). The cross-validation was used as follows: the differences between the prediction values (model's fitted values) and validation observations were first squared and summed over all genotypes and environments and divided by the number of validation observations, and then its squared root was taken to compute the Root Mean Square of the Predictive Difference (RMS PD). The squared root difference between the mean squares of prediction difference [(RMS PD)²] and fitting model error [(RMS FE)²] was used to estimate the prediction error [(RMS PE)²]. Smaller values of RMS PD indicate good predictive success (Table 5). The average RMS PD values were initially based upon 5, 10, 25, 50, 100 and 200 different random splittings. The results showed that for 462 validation observations, 25 random validation runs were adequate in this instance (Table 5).

Table 3. Pooled analysis of variance of grain yield (kg ha⁻¹) for 21 genotypes grown at 22 sites in 1987

Source of variation	df	Sum of squares $(\times 10^5)$	Mean squares $(\times 10^5)$
Total	1,385	47,767.72	34.49
Treatments	461	42,340.72	91.84**
Genotypes (G)	20	204.33	10.22**
Environments (E)	21	37,819.56	1,800.93**
GE	420	4,316.84	10.28 **
Joint regression	1	41.61	41.61 **
G regression	19	178.52	9.31*
E regression	20	223.47	11.17**
Residual	380	3,873.23	10.19 **
Error	924	5,426.99	5.87

*, ** Significant at the 0.05 and 0.01 probability levels, respectively

Trial mean: 3,940 kg ha⁻¹; coefficient of variation (%): 19.4

Table 4. AMMI partition of GE interaction for grain yield $(kg ha^{-1})$ of 21 genotypes grown at 22 sites in 1987

Source of variation	df	Sum of squares $(\times 10^5)$	Mean squares $(\times 10^5)$
Genotypes (G)	20	204.33	10.22 **
Environments (E)	21	37,819.56	1,800.93**
GE	420	4,316.84	10.28 **
IPCA1	40	1,669.74	41.74**
IPCA 2	38	639.55	16.83**
IPCA 3	36	384.42	10.67 **
IPCA4	34	343.12	10.09**
IPCA 5	32	279.82	8.74*
IPCA 6	30	212.65	7.09
IPCA7	28	203.96	7.28
Residual	182	583.57	3.20
Error	924	5,426.99	5.87

*, ** Significant at the 0.05 and 0.01 probability levels, respectively

Trial mean: $3,940 \text{ kg ha}^{-1}$; coefficient of variation (%): 19.4

Various AMMI models using zero to five IPCA can be compared in terms of their predictive success by observing RMS PD (Gauch and Zobel 1988; Gauch and Zobel 1989). The smallest RMS PD value is related to the best predictive AMMI model. After its selection, the best AMMI model is used to analyze the data, including all replications. Six models were fitted to the data (Table 5): the first was the additive model (AMMI0), which estimated the additive main effect (genotypes and environments) and has n equal to zero; i.e., it retains none of the IPCA axes and does not considers the GE interaction. Consequently, the genotype ranking of the AMMI0 model is the same at each site. The second model is AMMI1, which combines the additive main effect from AMMI0 with the GE interaction effect from the first principal component axis (IPCA1) and relegates the rest to the residual (Crossa et al. 1990). The third model, AMMI2, considers main effects plus two IPCA, AMMI3 to AMMI5 models include, sequentially, one more IPCA each.

The yield estimates from the full model (AMMIF) are identical to the mean of the two replications selected at random for model fitting (Gauch 1990).

The approximate number of replications (r_{AMMI1}) needed for the AMMIF model to equal the performance of AMMI1 was estimated as follows (Table 6): [RMS FE/RMS PE]². The approximate gain factor (GF) from the AMMI model used is calculated by dividing the number of replications (r_{AMMI1}) by the number of the replications used in the fit model (r_{fm}) . Additional replications benefit (RB) from using AMMI1 is $(r_{AMMI1} - r_{fm})$ and additional observation benefit (AO) is (RB × G × E).

Results and discussion

Comparison between linear regression and AMMI model

The analysis of variance showed that the mean squares of environments, genotypes, and GE interaction were highly significant (Tables 3 and 4) and accounted for 89.3%, 0.5%, and 10.2% of the treatment combinations SS, respectively. The GE interaction was analyzed (Tables 3 and 4) using two methods: the linear regression technique and the AMMI model. The regression technique partitioned the SS of GE interaction into joint, genotypic, and environmental regressions (Table 3), whereas the AMMI model partitioned the SS of GE interaction into seven interaction principal components axes (IPCA), of which the first five IPCA were significant (Table 4).

The SS of all three regressions accounted for 10.3% of the GE interactions SS (1.0% for the joint regression, 4.1% for the genotypic regression, and 5.2% for the environmental regression), and the remaining 89.7% was accounted for by the SS of the regression residual. As for the AMMI model, 76.8% was accounted for by the five significant IPCA axes and 23.2% by the IPCA residual. Of the five significant IPCA axes, IPCA1 accounted for 38.7% of the GE interaction SS in 9.5% of the interaction df, and IPCA2 14.8% in 9.0% of the df (Table 5). IPCA 3, 4, and 5 captured from the GE interaction SS 8.9%, 7.9%, and 6.5%, respectively, and from the interaction df 8.6%, 8.1%, and 7.6%, respectively.

The SS of the first five significant IPCA axes (IPCA1 – IPCA 5) and the SS of IPCA1 were higher than the combined SS of all three regressions by 7.5 and 3.8 fold, respectively. These results demonstrate the effectiveness of the AMMI model in capturing and partitioning the SS of GE interaction in comparison to the linear regression technique.

Postdictive and predictive assessments

The AMMI1 patterns (Table 6) related to the treatments accounted for 93.6% of the treatments SS, with 81 df (20 for genotypes, 1 for environments, and 40 for IPCA1), and 6.4% of the non-predictive random variation SS (noise), with 380 df. The AMMI model discards the non-interpretable random variation (noise) and uses then

Table 5. Average RMS PD for seven AMMI models based on yield (kg ha^{-1})

Model	RMS PD
AMMI0	859.9
AMMI1	830.5 ^b
AMMI2	884.6
AMMI3	910.3
AMMI4	920.1
AMMI 5	925.1
AMMIF ^a	941.1

^a Full model based on all genotype-environment combinations ^b Selected AMMI model based on predictive assessment

Table 6. Estimates for parameters of AMMI predictive assessment for grain yield (kg ha⁻¹) of 21 genotypes grown at 22 sites in 1987

Parameters	Estimate
Pattern and noise	
Pattern	93.6%
Random variation	6.4%
RMS of discarded residual (RMS DR)	442.0 kg ha ⁻¹
RMS DR relative to grand mean	11.2%
Model assessment	
Postdictive model	5
Postdictive df	221
Number of validation runs	25
Predictive model	AMMI1
Predictive df	81
Parsimony	2.7
Prediction	
Fitting model observations	924
Validation observations	462
RMS of predictive difference (RMS PD)	830.5 kg ha ⁻¹
RMS of fitting model error (RMS FE)	766.4 kg ha ⁻¹
RMS of prediction error (RMS PE)	320.1 kg ha ⁻¹
RMS PE relative to grand mean	8.1%
AMMI gain	
rammi	5.7
Replications benefit (RB)	3.7
Additional observations (AO)	1,725
Gain factor (GF)	2.9

Table 7. Percentage for rank differences (%) between AMMI 1 model and unadjusted yield means for grain yield (kg ha⁻¹) of 21 genotypes grown at 22 sites in 1987

Number of rank difference	Percentage of rank difference	
0	8.2	
1	14.7	
2	13.9	
3	13.2	
4	6.7	
5	7.1	
Remaining	36.2	

information from all test genotypes and environments to identify the trial functional patterns. It also adjusts the genotypic estimates within a site. The estimates of AMMI consist of interpretable and predictable inherent patterns, while the treatments means consist of both predictable patterns and non-predictable random variation. Therefore, AMMI estimates are more predictive than treatment means (Gauch and Zobel 1988).

The criterion of postdictive success for the AMMI model identified the first five IPCA axes in the model (Table 4), whereas the predictive assessment, measured by the RMS PD procedure (Table 5), selected the AMMI1 model (genotypic and environmental main effects plus IPCA1). In general, the model chosen by predictive criterion consists of fewer interaction principal components and uses fewer df than the model chosen by postdictive criteria. The lowest deviation (RMS PD) from the validation data for the AMMI1 model (Table 5) was 830.5 kg ha^{-1} . The mean square of the prediction error (MS PE) expressed in terms of its square root was 320.1 kg ha⁻¹ (Table 6). This represents an error of 8.1% relative to the yield grand mean for RDYT-MR (4,002 kg ha^{-1}). The estimate of predictive criterion (AMMI1) used 81 df, while the postdictive criterion (equals AMMI 5) used 221 df. Thus, the AMMI1 model is 2.7 times as parsimonious as AMMI5 (Table 6).

The approximate number (r_{AMMI1}) of replications needed for the AMMIF model to equal the performance of AMMI1 was 5.7. Therefore, AMMI1 based on 2 replications is as precise as the full model (AMMIF) based on 5.3 replications. AMMI1 had a theoretical gain factor (GF) in precision of 2.9. The replication benefit from the use of the AMMI1 model was 3.7 additional replications, or 1,725 additional observations' (plots) benefit (Table 6).

The ranking of genotypes in each environment in the AMMI1 model was different from that of the AMMIF model (Table 7). Similar results have been found in soybean (Gauch and Zobel 1989), maize (Crossa et al. 1990), and bread wheat (Crossa et al. 1991). Since precise yield estimates are imperative to make successful selections, the use of AMMI1 rankings merits serious consideration (Gauch and Zobel 1989). The ranking difference (Table 7) between actual genotypes' means and the AMMI1 model were similar in 8.2% of the total genotype × environments combinations, different by one rank in 14.7%, by two ranks in 13.9%, by three ranks in 13.2%, by four ranks in 6.7%, and by five ranks in 7.1%. The remaining differential rankings (six and above) represented 36.2% of the total genotype × environments.

The results of the RDYT-MR in the Mediterranean multilocational testing show that the postdictive AMMI models are superior to the linear regression techniques in accounting for and partitioning GE interaction. In addition, the predictive assessment demonstrated its usefulness as a statistical tool in estimating precise yield to make accurate and therefore successful selection.

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