Investigating the Nature of GxE Interaction under Different Management Systems and Yield Levels using Linear-Bilinear Models: The Case of CIMMYT Maize Hybrids Trials in Eastern Africa

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Abstract

The International Center for Maize and Wheat Improvement(CIMMYT) conducts selection of stress-tolerant genotypes under managed stress conditions. Data sets for this study were from Intermediate to Late Hybrid Trials (ILHT) conducted in five Eastern and Central Africa (ECA) countries from 2008 to 2011. Several trials, which were categorized into four management systems and two yield levels were used for this study. Variance Components, broad sense heritability (H), Site Regression (SREG), Genotypic Regression (GREG) and Factor Analytic (FA) models were fitted. We argue that it is preferable to first fit the fixed effect models before proceeding to the mixed effect model, as the former shows the level of complexity of the GE component and the number of axes required to explain it. The fixed effect model, SREG2, is preferable for trials targeting comparison of hybrids with checks. From the GGE biplots it was noted that the first two principale components (PC) did not account for sufficient percentage of variation for all years. Nevertheless, since PC1 accounted for large percentage of variation than PC2, the plot gives some idea of which hybrids won where. Most importantly, location of genotypes along PC1 can serve for judging yielding potential of the genotypes to guide in selection decision. Equivalence between Finlay - Wilkinson and GREG was established. The few environmental covariables obtained for 2009 were used to fit Partial Least Square (PLS) regression. The result indicated complexity in the GE component, as PLS latent factors accounted for small percentage of variation. It was recommended to use information from SREG2, GREG2 and FA(1) models in order to identify stable genotypes.

Introduction

Maize grain yield is reported as being considerably reduced under drought and low-N conditions (Bänziger et al., 2006). Effective development of hybrids requires a genotype testing network that covers the target region adequately, achieves a high level of precision and repeatability in estimating genotypic means. National programs with support of CIMMYT lines serve a large number of farmers over a wide area, but they are exposed to both technical and financial constraints. It is thus important to stick to appropriate subdivision of a breeding target regionand to setup strategy for selection of lines for such situations. CIMMYT Global Maize Program conducts selection of stress-tolerant genotypes indirectly under managed stress conditions. However, the selection efficiency of this approach is not known and provision of additional information will help to understand the scenario better. CIMMYT trials in Africa are conducted in two sub-regions, Eastern and Southern Africa. Within each sub-region the trials are conducted in different countries,at different locations and over years. However, in large and heterogeneous target regions such as Africa genotypes are expected to respond differently to variation in environmental factors such as temperature, soil fertility, and precipitation. Africa is divided into various agro-ecologies and is highly exposed to both optimal and stress conditions. The presence of GE in plant breeding experiments can be expressed in the form of inconsistent responses of some genotypes to such environments due to genotypic rank change or in the absolute differences among the genotypes without rank change.In certain situations, genotypic rank changes can be observed which may even lead to what is known as Cross over Interaction (COI) (Baker, R.J., 1996; Cornelius et al, 1992; Crossa et al, 1995; Frankham et al., 2007; Lynch and Walsh, 1998, Cooper et al., 1996). This phenomenon, referred to as COI, introduces a degree of uncertainty into the measurement of overall genotype performance and thus complicates selection for broad adaptation (Basford and Cooper, 1998). A common strategy to reduce or avoid GE interactions is to explore local adaptation by subdividing the plant breeding program into more homogenous sub-regions, but, this may not always be the solution. It is rather important to understand the cause of GE interaction in plant breeding and work towards disaggregating it and adjusting parameters for its occurrence as subdivision of a target region will not always increase selection efficiency(Atlin et al., 2001, and Baker, R.J, 1988).

Several models are commonly used for describing the mean response of genotypes over environments and for studyingand interpreting GE in agricultural experiments: linear models, bilinear models, and linear-bilinear models.The objectives of this study were, therefore,1) to apply these models to understand the pattern of variability and GE interaction under various management systems and yield levels, 2) to identify links between models that are used to disaggregate and interpret the GE interaction component using CIMMYT maize hybrids trials in Eastern Africa.

Materials and Methods

Setup of the trial

The number of trial sites used for the study varied from year to year (Table 1). The number of locations and trials in a given year may not always match, because more than one trial was planted at the same location. Five Eastern and Central African countries: Ethiopia, Kenya, Tanzania, DR Congo and Uganda were included in the Regional Trial Set. Locations were also associated with the different types of stress management systems. For example, Kenyan sites, Chirendzi (in 2009) and Kiboko (in 2008 and 2010) were considered 'Managed Drought'(MD), characterized by low yield. Similarly, Asfsf-Arusha (2008) in Tanzania and Bako (throughout) in Ethiopia were used as 'Managed Low N' (MLN). The rest of the locations were, however considered 'Optimal'.

Trials were set into four management systems:managed-drought, random stress, managed low N and optimal conditions. Managed drought and managed low N were set as managed stress (Table 1). Managed drought was situation where less than normal water was supplied. Some observations made on the pattern of occurrence of management type and trials were:1) Maseno (trial 6), and Busia (trial 17) in Kenya were the only sites that were used as sole 'Random Drought' sites in 2008 and Maseno was never repeated in subsequent years; 2) Elgon Downs (trial 3) were considered 'Random Drought' in 2009, but the same locations were considered 'Optimal' in 2010 (trial 18) and 2011 (trial 15); 3) Kakamega (trial 14) and Muguge (trial 16), both in Kenya are, considered 'Random Drought' in 2009, but the former was considered 'Optimal' in subsequent years (trial 32 in 2009; trials 22, 26 and 34 in 2010; and trial 31 in 2011). In general, two trials for 2008,three in 2009, and one trial in 2011 were the only trials considered 'Random Drought'. There was no trial site for 'Random Drought' in 2010. Therefore, estimated parameters such as Least Square Means (LSM), Variance Components and H may not be precise for these management types due to low number of observations. All trials were set as alpha lattice design with two replications. Data collected from plots were measured in gram but was converted to q/h for analysis.

Data analysis and model fitting

A trial mean was computed within a year and trials were classified as being 'high' or 'low' yielder based on yield cut-off point of 3t/h. Atlin et al. (2001) proposed this classification to serve as a basis for selection of target environments in breeding. Trial codes were consistent across locations within a given year, but varied from year to year. About 51% of trials in 2008 were classified as low yielders, which was high compared to other years. Proportions of trials classified as high yielding were 67%, 66% and 60% for the years 2009, 2010 and 2011, respectively. Thus, there were sufficient number of trials to fit a model for yield level by year (Table1).

Table 1. Number of trials for a combination of year, management type and yield level. Note that trials are given different codes per year. Therefore trial codes from two or more years may or may not coincide

	Year			
	2008	2009	2010	2011
Trials by Management Types				
Managed Drought	3	3	3	2
Managed Low N	2	1	2	1
Optimal	18	11	24	21
Random drought	2	3	-	1
Trials with H < 0.15	**4**	**2**	**4**	**6**
Trials by yield group				
Low yield (< 3 t/ha)	12	6	10	10
High Yield (> 3 t/ha)	13	12	19	15
Total number of trials	**25**	**18**	**29**	**25**

Models which accounted for variations in trials, years, genotypes, and their interactions were fitted as:

$$YLD = \mu + Y + L(Y) + R(LY) + B(RLY) + G + GY + GL(Y) + \varepsilon$$

Where, YLD is for yield, Y=year, L=location, R=replication, B=incomplete block, G=genotype, μ = grand mean and ε = random error

Different trials may have been given the same code in different years, therefore trials were considered as nested within years in the specification of the models. This model fitted to all data provides overall variance components for Trial, Year, Genotype, their interactions and the error term. It thus shows the overall pattern of occurrence of variability, before trials were split into groups (by management type and yield level).

The second approach was fitting the above model for Yield Levels (P) and Management Types (M). Yield was categorized as 'high' or 'low' based on threshold value adopted by CIMMYT. It is understood that trials under different management conditions depict different characteristics and estimating variance components, H and Best Linear Unbaised Predictor (BLUPs)by management type is commonly practiced among breeders. The yield level and management types would not be incorporated in the same model simultaneously since it over-fit the data.

However, in models (1) and (2),'Management Type' and 'Yield Level', respectively were included to estimate overall contributions of each of them. This helps to determine whether there is sufficient variability among the management types (and yield levels) in order to consider them as legitimate groups where breeders may have to consider them as separate selection environments.

$$YLD = \mu + M + Y(M) + L(YM) + R(LYM) + B(RLYM) + G + GM + GY(M) + GL(YM) + \varepsilon .....(1)$$
$$YLD = \mu + P + Y(P) + L(YP) + R(LYP) + B(RLYP) + G + GP + GY(P) + GL(YP) + \varepsilon ....(.2)$$

Where M=Management type, Y=year, L=location, R=replication, B=block, P=yield level

Because of changes in the coverage of management type and yield level each year, interaction of year with these terms does not make sense. Therefore, year was considered to be nested within management type or within yield level. Similarly, since locations fall under the different management types, or yield level, location is considered to be nested under a combination of Y and M or Y and P. Nevertheless, these models may be over-parameterized since they are additional factors imposed on the already designed experiment. The number of locations that fall under drought or low N conditions is very few compared to the optimal situation and this might introduce some bias in their comparison. Breeders are thus advised to plan setting experiments under this management situation to generate more replications. In the fixed model scenario, however, contrast can be set to test differences between these groups. Therefore, it is advisable to use model (1) and (2) and fit for each management type and yield level.

Normally, about 20-30% of the lines are expected to be carried over from one year to the next to form a basis for evaluation of new entries in a given year. However, 16 lines were included in the trials for three consecutive years (2008-2010). Nevertheless, no line appeared consistently over the four year period (2008-2011). In addition, among lines tested in 2010, only four were repeated in 2011.

Several statistical models and methods of analysis were developed for analysis of Multi-Environment Trials (MET) data over the years and a good review is presented in Smith et al. (2005). Crossa et al. (2009) described both fixed and mixed versions of most of these models and presented examples on their use. These models were originated from principles of Williams (1952) which were later extended by Gollob (1968) and Mandel (1969, 1971) and they are all interrelated. Crossa et al. (2002) called these models families of linear-bilinear models and showed how families of these models are related.

The General Linear-Bilinear Model (Yan et al., 2007 and Burgueno et al., 2008) in matrix have the following form:

$$Y = \sum_{h=1}^{m} \beta_h X h_{ij} + \sum_{k=1}^{t} \lambda_k \alpha_{ik} \gamma_{jk} + \varepsilon_{ij},$$

$$(3)$$

Where, X is known constant, β_h is the vector of regression coefficients for the linear term.

One form of fixed linear-bilinear models, a special case of (3), for non-replicated data may be stated as:

$$Y = \mu + E + G + \sum_{k=1}^{t} \lambda k \, \alpha ik \, \gamma jk + \varepsilon ij$$
(4)

where E is environmental and G varietal main effects, λ is the singular value of the kth multiplicative component, αik are kth left singular vector for ith genotype representing genotype sensitivity to hypothetical environmental factors represented by the kth right singular vector with elements of γjk. According to Gauch (1988), Gauch et al (2001) and Gauch et al (2008), this model is known as Additive Main and Multiplication Interaction (AMMI.) Girma et al (2000), Vargas (1999) and Yan et al (2000) used this models to explore GxE interaction.

Three important variants of model (3) were also discussed in literature. They are i) Site Regression (SREG), also known as GGE biplot, where Site main effect is separately estimated but Genotype main effect and GE interaction is combined; ii) Genotype Regression (GREG), where genotype main effect is separately estimated and environment main effect and GE is combined; iii) Completely Multiplicative Model (COMM), where no main effect is estimated separately. Cornelius and Seyedsadr (1997) expressed the above models in matrix form. Each of these models may be fitted as a fixed effect or mixed effects. Burgueno et al. (2008) discussed and described the two possibilities with their advantage and disadvantages.

In the SREG model, the bilinear term fits the main effects of genotypes (G) plus the GE interaction, a composition of which is subjected to singular value decomposition and is different from what is being fitted in the AMMI (Crossa et al, 2009). In addition, SREG2 can be perceived as consisting of a set of multiple regression equations for each environment on genotypic regressor variables.

A mixed-model analogue of AMMI and/or SREG has been developed using the Factor Analytic (FA) model for approximating the variance-covariance GE structure (Piepho 1998; Smith et al. 2002, 2005; Piepho and Mohring 2005; Cornelius et a, 1999). Crossa et al. (2006) and Burgueñ o et al. (2008) described implementation of these models. Burgueno et al. (2008) described the equivalence between SREG2 and FA(2) for finding subsets of genotypes and environments without crossover interaction (COI).We envisage that similar development can also lead to the equivalence of GREG1 and Finlay-Wilkinson models with FA(1). Since Finlay and Wilkinson (1963) regression is equivalent to SREG1 with the role of genotype and environment interchanged (Yanand Tinker, 2005, 2006), it is straight forward to establish the fact that the fixed effect model GREG1 is equivalent to stability analysis models of the Finlay-Wilkinson (1963) and the Eberhart - Russell(1966), with some re-parameterization. Following Burgueñ o et al. (2008), in this re-parameterization, the first multiplicative term, $\alpha i1 \, \gamma j1$ is considered as the genotype regressions with coefficients $\alpha i1$ on environmental indices $\gamma j1$. The λk parameter can be absorbed

into α_{i1} or γ_{j1},such that $\alpha*_{i1} = \lambda[f]k\alpha_{i1}$ and $\gamma*_{j1} = \lambda(1-f)k\gamma_{j1}$., where f lies between 0 and 1. Although the Mixed model approach (FA models) are flexible and have several benefits, often a maximum of FA(2) is fitted and the Eigen values are absorbed in the random variables. But the fixed effect approach provides a measure of how much each component contributed to the variation in the GE (or GGE) and helps decide how far the GE (or GGE) component is complex. We therefore argue that the fixed effect models are first fitted and observations made before proceeding to the FA models.

Furthermore,Burguen~ o et al. (2008) showed the equivalence between the FA(2) and SREG2 as a set of multiple regressions. They also argued that the interpretation of the loadings and scores of theFA(2) is the same as that obtained by theSREG2. Under factor rotation of the FA(2) to a principal component solution,Burguen~ o et al. (2008)showed that the directions and projections of the vectors of FA(2) andSREG2 in the biplot are the same. Therefore, the same principle can be used to justify equivalence of GREG1 and FA(1), which is easier to demonstrate as we are dealing with one component only. In a situation where FA(1) is applied to 'E+GE', the score of the first factor measures genotypic sensitivity to latent environmental variable. The difference between the fixed and mixed model approach is therefore that, the former is based on observed environmental variable, which is average of all genotypes per site, while the later uses latent (unobservable) environmental variable. Proportion of variation GREG1 is accounted for is an indicator of how much of the 'E+GE' variation can be explained by a linear term. It is therefore important to first fit GREG1 and observe PC1 before proceeding to fit the FA(1) model for stability analysis.

Incorporating external environmental covariables helps to explain genotype by environmental interaction (GE). Multivariate Partial Least Square (PLS) Regression model is one such useful type of models (Vargas et al., 1999).It generalizes and combines features from principal component analysis (PCA) and multiple regression. Following Crossa et al. 2009, when genotypic response over environment (Y) is modeled using environmental covariables, the $j \times h$ matrix Z of H (h=1, 2 ,3…., H) environmental covariables can be stated in bilinear form as follows:

$$Z = t_1 p'_1 + t_2 p'_2 + \cdots . + t_m p'_m + E_m = TP' + E \quad \text{……………………………..(5)}$$

where the T matrix contains the t_j $j \times 1$vectors which are latent environmental covariables (known as Z-score, indexed by environments), and the P matrix contains the $p_1....p_h$ $h \times 1$ Z-loading vectors (indexed by environmental covariables) and Ehas the residual. Similarly, the response variable matrix Y in bilinearof the form:

$$Y = t_1 q'_1 + t_2 q'_2 + \cdots . + t_m q'_m + F_m = TQ' + F \quad \text{……………………………..(6)}$$

Where the Q matrix contains the $q_1....q_h$ $l \times 1$ vector called Y-loading (indexed by genotype) and F has residual. The relationship between Z and Y is transmitted

through the latent variable T. The PLS performs simultaneous but separate principal component analysis of Z and Y.

$$H = \frac{\sigma_G^2}{\sigma_G^2 + \dfrac{\sigma_{GT}^2}{t} + \dfrac{\sigma_{GY(T)}^2}{yt} + \dfrac{\sigma_{GL(YT)}^2}{lyt} + \dfrac{\sigma_\varepsilon^2}{lyter}}$$

--------------------------------(7)

where σ_G^2 σ_{GT}^2, $\sigma_{GY(T)}^2$, $\sigma_{GL(YT)}^2$, and σ_ε^2 are genotypic, genotype-by-managemnt, genotype-by-year nested in managemnt, genotype-by-location nested in year and managemnt, and residual variance components, respectively. Equation 7 was modified when compoting H for yield level.

Interpretation of AMMI2 and SREG2 are similar. The interpretation is based on genotypic and environmental vectors drawn from the origin (0, 0) to the end points of the location of scores (Gower and Hand, 1996). They explained that an angle of less than 90° or larger than 270° between the two vectors is an indicator of positive genotype response at that environment, a negative response if the angle is between 90° and 270°. Phenotypic correlation of environments or genotypes can also be approximated using cosine of the angle between the two, an angle of zero, 90° (or –90°) and 180° indicating a correlation of +1, 0, and –1, respectively.

In this paper, we fit models 1-6 stated above and explore their relationship in the analysis and interpretation of MET data. Practical importance of some of the models emphasized and selectively fitted to the data. Statistical Analysis Software (SAS) version 9.2 was used for the analysis of the data.

Results and Discussion

Variance components after excluding local checks and locations for which (heritablity) H<=0.15 were obtained for the various classifications (Tables2-6). Different checks were used in different sites, and are known locally only and cannot be included in the model. The Variance Component (VC) and H are generated for two time periods, 2008-2010 and 2008-2011 (Tables3-5). That is because 16 entries appeared in all the three years and thought that it would be reasonable to compare the two timeperiods. In addition, the VC and H are estimated for management and yield level. Management and yield level were also combined to produce categories with reasonably large number of sites so that convergence is attained during model fitting using REML.

Table 2: Variance Components and H of Grain yield for a model that includes management type or Yield level, for 2008-2010 Eastern and Central Africa ILHT regional trials. Keys are: T=management or yield level, Y=year, L=location, R=replication, B=block, G=genotype, H=broad sense heritability. In the source of variation column, T stands for either management type or yield level factors. For example, variance component (T) for management type is 1.38, while for Yield level it is 5.54.

Source of variation	Management Type	Yield level
T	1.38	5.54
Y(T)	0.17	0.06
L(YT)	3.38	1.64
R(TYL)	0.18	0.18
B(TYLR)	0.13	0.13
G	0.10	0.11
GT	0.00	0.01
GY(T)	0.08	0.08
GL(YT)	0.21	0.20
Residual	0.81	0.81
Heritability (H)	**0.72**	**0.75**

It was found that 48%, 50%, 34% and 44% of the trials in 2008, 2009, 2010 and 2011,respectively recorded H > 0.50. Trials in 2009 generally recorded better performance as 78% of them had H>0.40, compared to the remaining years where this percentage was 45 for 2010 and 48 for 2008 and 2011. Trials in 2010 recorded relatively low H probably due to their large size (as number of trials is the maximum in 2010). Five sites in 2008 (15, 24, 25, 34 and 40), three in 2009 (9, 12, 35) and two sites in 2010 (22, 26) has recorded highest H (> 0.70). All these sites were optimal sites.

Except for 'MLN, >3 t/ha' and 'RD, >3 t/ha' trial categories, GxE variance component (L*G(Y)) was higher than Genotypic Variance in all other categories, indicating the fact that genetic variability is masked by higher GxE interaction. From Statistical marginality condition, interpretation of the main effects may not be feasible if the interaction term is significant. Therefore, it is important to account for GxE term when estimating parameters. Most of these categories are associated with low yield situation and indicates potential for selection under stressed circumstances.

Variance Component for Management types (Tables3 &4) was high indicating presence of considerable variation in this category which provides an opportunity of breeding for the different management systems. The details of parameter estimates are given in Table 3 for 2008-2010 and in Table 4 for 2008-2011 data sets.

Table3: Variance Components, after excluding local checks and locations with H<=0.15, by management for Grain Yield, 2008-2010 Eastern and Central Africa ILHT regional Trial.

	Optimal	Managed low N	Managed Drought	Random Drought
Y	0.20	0.00	0.4133	2.5768
L(Y)	3.93	1.00	1.0967	0.3763
R(YL)	0.14	0.29	0.3870	0.1059
B(YLR)	0.09	0.14	0.2926	0.3141
G	0.11	0.00	0.1146	0.0274
YG	0.13	0.08	0.0435	0.00
GL(Y)	0.23	0.13	0.0786	0.2028
Residual	0.93	0.27	0.5127	0.4872
H	**0.70**	**0.0**	**0.841**	**0.812**

Table 4: Variance Components, after excluding local checks and locations with H<=0.15, by management for Grain Yield, 2008-2011 Eastern and Central Africa Regional variety trial.

Source Drought	Optimal	Managed L N	Managed Drought	Random
Y	0.03	0.00	0.00	0.86
L(Y)	3.52	0.78	0.41	0.61
R(YL)	0.12	0.23	0.28	0.10
B(YLR)	0.12	0.17	0.26	0.30
G	0.15	0.00	0.11	0.02
YG	0.13	0.12	0.004	0.00
GL(Y)	0.28	0.10	0.10	0.17
Residual	0.86	0.39	0.46	0.45
Trial	36	6	7	6
H	**0.80**	**0.00**	**0.90**	**0.47**

For combined analysis of 2008-2010 and 2008-2011 data, H for 'Managed Drought' remained high indicating possibility of selection for stressed environment (Tables 3 & 4). For the 2008-2011 data H for 'Random Drought' is reduced to 0.47. There is only one such trial in 2011 and may have contributed in reversing the result. On the other hand, H for 'Optimal' and 'Managed Drought' has substantially increased. This may be due to the fact that majority of the hybrids in the 2011 trial were new entries and exhibited better heritability (Table 4). For Yield level categories, there was considerable improvement in H for the data of 2008-2011 over that of 2008-2010. Particularly, H for 'Low yield' category increased from 0.53 to 0.72 (Table 5).

From analysis of the 2008-2010 data by management and year combination, H showed considerable reduction for all categories. 'Managed Drought' in 2010 has the lowest H (0.02) which indicates that the previous high H for analysis of all years must have been contributed from 2008 and 2009 data sets.

To avoid low number of sites for 'Managed Drought' management types were re-categorized with yield level as 'Managed Drought + MLN', 'Random Drought', 'Optimal > 3t/ha' and 'Optimal < 3t/ha'. 'Managed Drought' and 'Low N' are merged to increase replications. Variance components and H for these categories are given in Table 6. It is now evident that high yielding trials in the 'Optimal' category are repeatable, as those in low yielding category registered H of about 0.08. The 'Managed Drought + MLN' category, although slightly reduced, still have high H but this is purely attributed to 'Managed Drought' trials alone. Therefore, it is better to isolate 'Random Drought' and 'Managed Low N' in future analysis as they are not repeatable possibly for reasons of low number of trials.

Table 5: Variance Components and H for High and Low yield levels after locations with H<=0.15 are removed (Grain Yield), for Eastern and Central Africa ILHT regional variety trial for two time periods, 2008 – 2010, and 2008-2011.

Source of variation	2008 - 2010		2008 - 2011	
	High	Low	High	Low
Y	0.11	0.04	0.02	0.06
L(Y)	2.50	0.25	2.16	0.32
R(YL)	0.20	0.14	0.16	0.12
B(YLR)	0.10	0.18	0.13	0.19
G	0.17	0.02	0.22	0.03
GY	0.14	0.04	0.15	0.03
GL(Y)	0.24	0.13	0.29	0.13
Residual	1.11	0.36	1.00	0.35
H	**0.76**	**0.53**	**0.84**	**0.72**

Results from phenotypic and genotypic correlations (data not shown) show that 'Managed Low N' in 2009 was relatively poorly associated with all other categories. Particularly, it had the lowest correlation (r=0.43) with 'Optimal' in 2008. In contrary, 'Managed Low N' in 2008 has relatively stronger association with the other categories. There was very strong correlation between 'Optimal' and 'Managed Drought' regardless of year of experiment. 'Managed Low N' in 2008 has strong correlation with 'Managed Drought' regardless of trial year showing validity of combining the two to overcome shortage of replication. 'Random Drought' seems to correlate better with 'Managed Drought' than 'optimal'. The genetic correlation identified the relatively low correlation between 'Managed Low N' and 'Optimal' in 2010 only.
BLUPs for 2008-2011 trial data by Yield level were computed (but not presented). The result shows that predicted yield for 'high' category was in the order of 5 to 6 t/ha.

But two hybrids from 2011 trial, HYTECH11 and HYTECH20, recorded the lowest predicted mean. Predicted mean in the 'Low' yield category was in the order of 2 t/ha, but few hybrids such as CKH08008, CKH08002, and CKH08053 had the lowest predicted mean and may not have sufficient potential for future candidacy.

As indicated earlier, this data has come from regional variety trials where hybrids are compared with checks and breeding gains are evaluated, therefore we felt that the fixed version of SREG is more appropriate (since we are not interested in prediction) to fit (Gauch 2006; Yang et al. 2009) despite current controversies as to whether Factor Analytic model or Fixed SREG is more appropriate.

Examination of ANOVA table shows that percentage contribution of environmental variation,out of overall variability in the yield,was generally large.This ranged from 40% in 2009 to 69% in 2008. These values were 57% and 67% in 2010 and 2011, respectively. Contribution of Genotype component of variation was 2%, 2%, 3% and 3.7% in 2008, 2009, 2010 and 2011,respectively. Proportion of GE (out of all variability in yield) was 8%, 7%, 10% and 14% for 2008, 2009, 2010 and 2011 respectively.Yan, et al. (2001), by analyzing Ontario Winter wheat found similar results, except that in their case genotype contribution ranged from 1.8% to 28.5%. in the present study, about 48% of variation in yield in 2009 was designated as random error, while this value was only 12% in 2011. This shows that there was some systematic variation operating in the data which could not be accounted for in 2009 but the trials were well managed in 2011.

Table 6. Variance Components, after excluding local checks and locations with H<=0.15, by a combination of Management Type and Yield Level for Grain Yield, 2008-2011 Eastern Africa Regional variety trial.   The columns are 'Optimal' management and yield > 3 t/ha, 'Optimal' management and yield < 3 t/ha, 'MD+LN' stands for a combination of Managed drought and managed Low N.

	Optimal *> 3 t/ha*	*Optimal* *< 3 t/ha*	MD + LN	Random Drought
Y	0.00	0.07	0.00	0.86
L(Y)	2.15	0.12	0.51	0.61
R(YL)	0.14	0.03	0.26	0.10
B(YLR)	0.13	0.08	0.22	0.30
G	0.21	0.00	0.06	0.02
YG	0.15	0.06	0.00	0.00
GL(Y)	0.30	0.11	0.16	0.17
Residual	1.01	0.25	0.44	0.45
NumberofTrials	32	10	13	6
H	**0.83**	**0.08**	**0.89**	**0.47**

We argue that fitting SREG, (sometimes including GREG or COMM) is more important and statistically meaningful than AMMI. This is because in statistical marginality theory of effects, main effects cannot be interpreted independently if the interaction term is significant. In the analysis of MET data, the GE term is often highly

significant with GE sum of squares being much higher than that of G. Therefore, combining the G and GE effects and subjecting to SVD or FA model is appropriate. However, in a situation where the significance probability for the main effects (E and G) is much smaller than that for GE, then AMMI model might be more appropriate to fit. Consequently, the result shows that proportion of variation accountable by GGE (out of the total, E+G+GE, variation) increased from 12.7% in 2008 to 21% in 2011, 2009 and 2010 being about 8.9 % each (Figures 1-2). In other words, in 2008, 3.6% of the total variability (E+G+GE) was accounted for by PCA1 (and about 5.5% accounted for by the first two PCAs). In 2011 PCA1accounted for about 9.9% (about 45% of G+GE variation) of the total variation, while 12.2% of the total variation was accounted for by the first two PCAs.Therefore, more component of the G+GE variation was explained by the new axis in 2011 than in 2008, hence the biplot was more informative for 2011 data. Based on arguments set out by Yang et al.(2001), the G+GE component in all the three years was important (as all contributed > 10% of E+G+GE variation), but the first two PCA did not account sufficiently for the G+GE variation in all years, the total contribution being 58% in 2011 followed by 50% in 2010 and 2009. The contribution of the first two PCA was low in 2008 (< 50%) and may not be important in selection or delineation of mega-environments. To be able to obtain > 65% contribution, one may have to consider up to 5 PCA axes, which is not useful for valid interpretation. But, a peculiar phenomenon in 2010 and 2011 was that the first PCA alone accounted for > 40% of variation in the G+GE, which may be useful to measure potential of the genotypes in these years. When this result was compared with AMMI2 model, the contribution of the axes considerably decreased, particularly, the 2010 data set showed huge reduction. This shows that the GE component is indeed complex and cannot easily be disaggregated and interpreted. However, since the first PCA was highly loaded for 2010 and 2011, some general remarks may be made. First it would be good to see consistency of the plot over the years.

It is apparent that the environment has mostly positive on the first PCA, apart from changing position of the locations from year to year. By drawing an imaginary polygon that connects corner genotypes so that all other genotypes fall inside the polygon, and then drawing straight line from the origin of the biplot to each side of the polygon, it is possible to identify 'what - wins –where'(Yan et al, 2000, 2001). Results for 2009 and 2011 are presented in Figures1 and 2, respectively. Consequently, in 2009, the vertex genotypes particularly located on positive side of PCA1 were wining genotypes in a given environment. Genotype g10 was the wining genotype at Kakamega. Genotype g11 won at Embu, which was close to its side of the line. Genotype g18 without a site in its sector had never been the highest yielding genotype in any of the environments. Genotype g25 was a winner in Kiboko although this site was not in its sector. Such inconsistencies may have occurred due to the fact that the first two PCAs have not accounted for sufficient proportion of variation in 'G+GE'. Genotype g37, a check known as WH403 has very low PCA1 and is lowest yielder in most sites in this year and seem non-adaptable, while the other two checks (G38-WH505 and G39-H513) are located close to the origin, although may not be adaptable to any of the sites, which contradict the expectation that checks are varieties already

adapted to the sites.g19 hybrid known as CKH08053 is also associated with low PCA1 and is low yielder throughout.This hybrid is located very close to g37 check and may perform similarly. On the other hand, g31 and g40 were low yielders at Kiboko, Asffs and SARI and were less adapted to these areas. But since the first two PCA were accountable for about 51% of the GGE variation, caution should be taken in interpreting the result. Bulinidi and Kakamega, the 'Random Drought' locations in 2008were paired on the biplot and were associated with g10, g16 and g23, which showed that the locations still demonstrated some similarity even in different years.

Biplot for 2010 was different from other years in the sense that genotypes were distributed to the four quadrants proportionally. Genotypes g22, g24, g26, g15 were associated with small PCA1 and were low yielders which may not be adapted. The main interest here was to compare performance of the three checks, g39, g40 and g41, with the hybrids. The plot shows that all of them are located in different quadrants and seem to perform differently. For example, g39 which is low yielders is not well adapted to most of the environments, while g40 seem to be adapted to Elgton.

In 2011, the two checks, g38 and g39, were associated with low PCA1 and were very low yielders throughout.The reason for inclusion of these varieties in the trials should be examined. g37, another check variety was also low yielder and non-adaptable at any of these locations. The other three checks, g34 (H513), g35 (WH403) and g36 (WH505) which appeared in the regional trials consistently from 2008 to 2011, also had relatively small PCA1 here, like in 2009, but were closer to the origin. All of them were also well adapted to the two sites, Muguga and Maseno. The genotypes, g1, g26 and g28, which formed group on the plot, had small PCA1 and were the lowest yielders at Elgton, Shik, Think, and Buli. Among the vertex genotypes, those appeared isolated and stood clear from others, g12 and g40, were associated with sites where they won. Accordingly, g12 won in Shika (and thinka as well), while g40 won at Elgon. There was, however no clear cut for a group of genotypes that appeared together around the vertex. This might be due to the fact that the biplot did not have sufficient information since the variation accounted by GGE was not that large.

To establish equivalence between GREG1, Finlay – Wilkinson regression (1963) and FA(1) models, results were presented from the ILHT data set. Results from GREG2 showed that PCA1 contributed 91%, 84%, 87% and 87% of the 'E+GE' variations in 2008, 2009, 2010 and 2011, respectively. This result was in contrary to those obtained from SREG2, where PCA1 contributed in the range of 30% to 45%. Such differences might have occurred due to the fact that in GREG,'E+GE', variation is highly dominated by variations in 'E', unlike variations in 'G' which is small. Therefore, PCA1 mainly captured variations in 'E' as the 'GE' component was relatively small. This indicates that the Finlay – Wilkinson regression type would explain stability of these hybrids. We, however, chose to fit Eberhart and Russell (1966) stability model within the mixed effect model framework to obtain the stability parameters using Factor Analytic model (Piepho et al, 1997, 1998a). Eberhart and Russell (1966) in their fixed effect approach advocated that a genotype with regression slope approaching

unity and deviation variance approaching zero is more stable. The Factor Analytic model computes genotypic sensitivity parameter to the latent environmental index. In the traditional Eberhart and Russell approach, genotype means are regressed on environmental means to obtain stability parameters. This approach has, however been criticized since environmental means are calculated from genotype performance and do not provide an independent information for judging stability of genotypes.

For stability study, only 'Optimal' trials were included in the analysis since sites dedicated to ' Managed Drought', 'Random Drought' and 'Low N' trials were very few and that these stressed environments would be under represented and the results were biased. Sites categorized as 'Optimal' were 20, 15 and 24 for 2008, 2009 and 2010, respectively. Often, about 20% to 30% of the genotypes were carried over to the following year, but all genotypes included in a given year appeared in all sites. Therefore, stability was computed on yearly basis for those genotypes included in a given year, but overall stability was obtained for genotypes includedduring 2008-2010 (Table7). Heterogonous error variance approach was used in FA model so that each genotype would have an associated deviation from the fitted model.

Results showed that mostly different genotypes were stable in different years, except g44 (CKH08072), g40 (CKH08066), and g3 (CKH08004), which were stable in 2009 and 2010. Genotype, g31(CKH08051), which was among the first five high yielding genotypes in 2008 and 2010 was stable in 2008 but not in other years. Genotype CKH08017 was the top yielder and stable genotype (intermediate stability in 2009) in 2010, the required quality from genotype performance.The check variety, WH403,was high yielding in 2008 but unstable; it was stable in 2009 but exceptionally low yielder (very small PCA1 of SREG2). It had intermediate performance both in stability and yield in 2010.This shows that it is not possible to provide a clear-cut approach of selecting stable genotype; breeders must consider several criteria to select genotypes of interest based on their objectives. In general, to judge the relative stability of genotypes, it is better to look at 'Stability Coefficients', 'Stability Variance' or 'unexplained variation' and the genotype's relative position on the biplot of SREG2 for yield potential. For a genotype to stable it therefore needs to have small stability coefficient, small unexplained variation and high or intermediate SREG2 PCA1 value (an indicator of high or intermediate yield level).

Table 7. Stability Parameters for ILHT2008-2010 Eastern Africa Regional Trial Data set. This analysis is only for 16 Genotypes those were repeated over all the three years period.

Genotype Code	Stability coefficients	Unexplained variation	Least Square means	STD Error of the mean
CKH08004	1.507	0.297	3.577	0.253
CKH08017	1.373	0.434	3.881	0.241
CKH08036	1.850	0.497	4.048	0.313
CKH08039	1.877	0.400	4.592	0.313
CKH08041	1.555	0.427	3.724	0.267
CKH08047	1.947	0.510	4.205	0.328
CKH08048	2.115	0.613	4.625	0.357
CKH08049	2.380	0.820	4.508	0.403
CKH08051	2.020	0.827	4.829	0.350
CKH08066	1.469	0.316	3.757	0.249
CKH08072	1.372	0.674	3.809	0.253
CKH08073	1.794	0.407	4.027	0.301
CKH08075	1.516	0.295	3.886	0.255
CKH08078	1.471	0.430	3.815	0.255
CKH08079	1.645	0.360	3.804	0.277
H513	1.703	0.314	3.733	0.283
WH403	1.657	0.908	3.745	0.303
WH505	1.808	0.217	4.188	0.295

PLS model was fitted for ILHT 2009 data only due to lack of availability of environmental covariables for other years. Very few environmental covariables were obtained for 2009, but analysis conducted to show the possible benefitthat PLS biplot may provide and contrast that can be made with other biplots when sufficient number of environmental covariables exist. Results from PLS is shown using Figure 3. Three latent vectors of PLS may be obtained (as the covariables were only 3). The three latent vectors can explain only about 28% of variations in the GE component. The two latent vectors explained about 98% of the variation in the environmental covariable but explained about 18% of variation in the GE interaction component only, which was even smaller than what was explained by the SREG showing complexity of the GE component. This is related to the fact that very few environmental covariables were used here, two of which were minimum and maximum temperature which were also highly related.But the good indication for importance of the method is that such very few environmental covariables could explain considerable portion of variation in the response variable.The result also showed that the minimum and maximum temperature values were highly associated as expected as they were very close in the plot (Fig. 3). This indicates that the minimum and maximum temperatures affect the genotype performance in the same way. The biplot did not completely manage to separate high and low yielding genotypes due to low percentage accountability of the

latent factors.But, the biplot seemed to somehow agree with SREG plot in commonly identifying some high and low yielding genotypes. For example, both plots highlighted genotypes g23, g16 and g22 as high yielding and genotypes g37 and g8 as low yielding. As the rainfall covariable was located in the top right quadrant, it was associated with high yielding genotypes (Fig. 3). More environmental covariables might be required to provide a better interpretation of the GE component as it is complex and could not be effectively disaggregated.
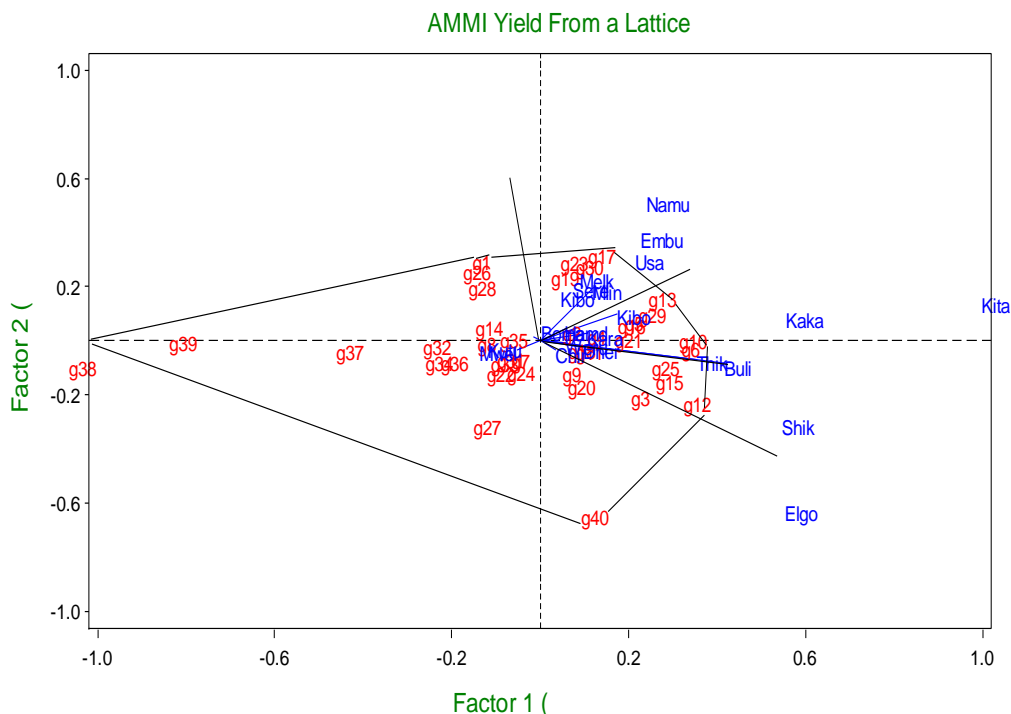

Figure 1. Site Regression (SREG2) biplot of the first two PCA for ILHT Eastern Africa regional trial 2009 data. A polygon is imposed on the biplot by joining the outer genotypes (vertex genotypes) and drawing straight line from the origin perpendicular to the lines.

Figure 2: Site Regression (SREG2) biplot of the first two PCA for ILHT Eastern Africa regional trial 2011 data. A polygon is imposed on the biplot by joining the outer genotypes (vertex genotypes) and drawing straight line from the origin perpendicular to the lines.
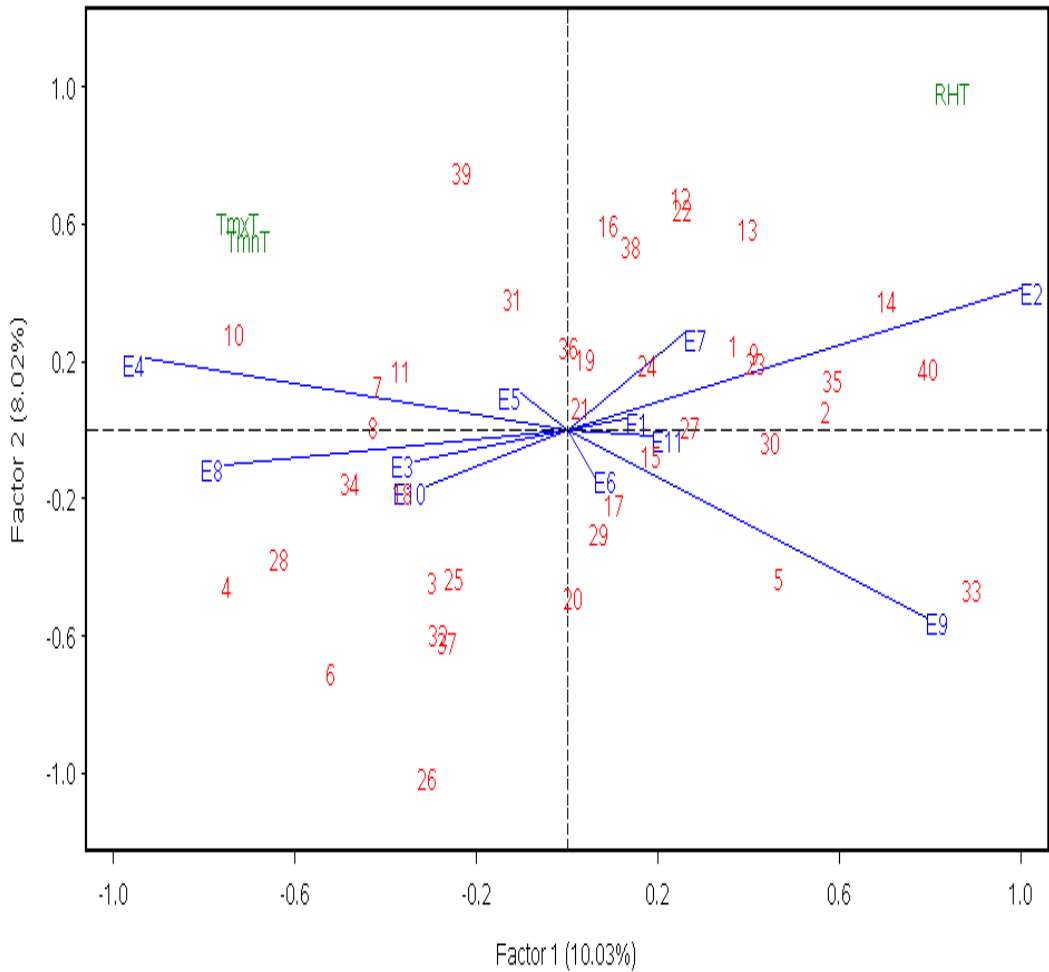
Fig.3: Biplot of the first and second PLS factors representing 11 locations(indexed as E1 to E11, locations in eastern and central Africa region where CIMMYT conduct trials in collaboration with national programs) as Z-Score, 40 genotypes (indexed by 1 to 40) as Y-loading supported by 3 environmental covariables (TmxT=maximum Temperature, TmnT=minimum temperature, RHT=average annual rainfall)as Z-Loading. Measurements for the environmental covariable are that of 2009.

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