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Cell Mean Versus Best Linear Unbiased Predictors in Biplot Analysis of Genotype × Environment Interaction in Barley

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Abstract

In multi-environment trials, accurate estimation of yields in individual environments and astute choice of models to extract and display agronomically relevant signals enhance genotype evaluation and accelerate breeding progress. The objective of this study is to (i) compare patterns of genotype × environment interaction (GE) using additive main effect and multiplicative interaction (AMMI) biplots arising from cell means versus best linear unbiased predictors (BLUPs), and (ii) examine some features of the genotype main effect plus GE interaction (GGE) in relation to AMMI in comprehending the GE patterns. A data set generated from 39 barley genotypes grown in 18 environments (three sowing dates and two crop protection treatments over three years) in the central highlands of Ethiopia was used. AMMI analysis of variance based on cell means depicted the first five principal components (PCs) to be significant. However, only the first two PCs were significant when BLUPs were used. Partitioning of the original GE sum of squares into signal and noise confirmed that only the first two AMMI PCs contained signals required to explain the real GE pattern. AMMI PC1 contained 76.5% and AMMI PC2 15.9% of the total GE variance. AMMI biplot based on BLUPs depicted patterns that were more in tandem with agronomic interpretations than biplot based on cell mean data. PC1 of GGE contained 66.9%, PC2 11.2% and PC3 14.5% of the total GE variance. AMMI2 explained as much GE variance as PC1, PC2 and PC3 of GGE put together. AMMI2 biplot depicted a GE pattern that was not obvious from GGE2. AMMI2 biplot was more similar to GGE PC1 versus PC3 biplot than GGE2 biplot. AMMI2 was more efficient than GGE2 for displaying patterns of GE interaction in this data set. However, GGE2 was quite elegant and simple for presenting G and GE combined in a biplot graph including the which-won-where pattern. BLUPs might improve yield estimation and pattern recognition, and that attempting both AMMI and GGE analysis might provide important insights on genotype performance and GE.

Introduction

Crop yield is a product of the interaction between a crop's genetic potential and the biophysical environment. In crop trials, genotypes or treatments are compared in multiple of environments such as locations, management levels and years. Yield data obtained from multi-environment trials often display a complex genotype-by-environment interaction (GE). Estimation of GE pattern is, therefore, a major challenge in multi-environment trials. Biplots have been used to visualize patterns in such large and complex G × E data sets (Gabriel, 1971; Kempton, 1984; Zobel et al., 1988). Recognition of real patterns in GE biplots is as good as the extent to which the G × E cell means represent 'true' means of each genotype in individual environments.

However, GE variance is known to contain noise, in fact much more noise than genotype or environment variance, because of large GE degrees of freedom (Gauch and Zobel, 1997). Failure to minimize noise before subjecting GE attribute matrix residuals to singular value decomposition may result in capture of spurious patterns by one or two of the first PCs. Employing statistical approaches that give better estimates or predictions of true mean yields in individual environments may increase the accuracy of genotype mean yields in those environments and thereby visualization of real patterns in ensuing graphics.

When the required assumptions are satisfied, a mixed model approach is often more preferable to a fixed effect model and is applied in breeding experiments. One of the advantages of such models is that the parameter estimates are unbiased and more efficient compared to mean yield obtained from fixed effect model. That is why parameters from mixed or random models are known as shrinkage estimators. Thus mixed model based best linear unbiased predictiors (BLUPs) may give more reliable environment-specific genotype trait predictors using information from the entire trait data structure than would be possible with measured means in individual environments (Piepho, 1994; Littell et al., 1996). Despite this, in many studies, cell means are used instead of BLUPs. Ma et al. (2004) reported BLUPs in place of cell means in their GGE and AMMI biplot analysis of GE for wheat yield in Canada. They did, however, not elaborate whether their use of BLUPs instead of cell means improved visualization of agronomically interpretable treatment × E interaction patterns contained in their data set.

AMMI and GGE are two contemporary GE analysis tools that make use of biplots (Zobel et al., 1988; Yan et al., 2000; Gauch, 2006; Yan et al., 2007). AMMI analysis has been a popular statistical approach for comprehending the nature of GE in yield trials for over two decades now. However, GGE biplot analysis has gained currency since its wider reporting some nine years ago. Recently, proponents of AMMI and GGE have made strong arguments on the merits of their model vis-à-vis the other (Ma et al., 2004; Gauch, 2006; Yan et al., 2007; Gauch et al., 2008). Given the existent controversy and the proponents' arguments, it may be important to explore features of both models in the analysis and visualization of GE patterns for individual data sets.

Broadly, barley exhibits GE particularly in stress-prone environments (van Oosterom et al., 1993; Ceccarelli, 1994). Ethiopian barleys display specific adaptation to variable stresses such as low nitrogen and drought (Gróny, 2001; Woldeyesus Sinebo, 2002) owing to the large genetic and agroecological diversity in the country. The importance of GE arising from differential performance of genotypes across environments has been recognized in barley breeding works in Ethiopia. As a result, variety screening takes place across a range of test sites, years and management levels. However, few reports are available on the patterns of GE in barleys grown in the variable and increasingly unpredictable environment in Ethiopia. The first objective of this report is to compare AMMI biplots arising from singular value decomposition (SVD) of residuals of cell means versus SVD of BLUP residuals in interpreting GE in a data set. The second objective is to examine some features of the GGE in relation to AMMI in comprehending the GE patterns in this particular data set.

Materials and Methods

Data were obtained from 39 barley genotypes tested in a factorial combination of three sowing dates and two crop protection treatments for three years (2002 - 2004) on a Eutric Nitosol at Holetta Agricultural Research Center (9°03'N, 38°31'E, elevation 2400 m), Ethiopia. The three sowings were done at fortnightly intervals starting from about mid-June (Woldeyesus et. al., 2010). The two crop protection treatments were either a no pesticide control or insecticidal seed treatment with Gaucho (Imidacloprid) 70% WS at a rate of 1 g product kg^{-1} seed followed by foliar application of the fungicide Propiconazole at a rate of 125 g a.i. ha^{-1}. The genotypes included 13 improved released varieties, nine landrace cultivars grown in different parts of the country, four experimental lines developed from local crosses, three introduced experimental lines, and 10 experimental lines developed from landrace populations. The experiment was planted in a split-plot arrangement with a factorial combination of sowing dates and crop protection treatments in the main plots and the genotypes in the sub-plots in three replications.

The SAS statistical package version 8.12 (SAS Institute INC, Cary, NC) was used for data analyses. Analysis of variance was done assuming a simple two-way G × E data whereby 39 genotypes were tested in eighteen environments. Following this, detailed analysis of variance was carried out with PROC GLM and PROC MIXED using the following model:

$$T_{ijklm} = \mu + Y_l + S_m + C_k + G_i + R(Y)_{jl} + YS_{lm} + YC_{lk} + SC_{mk} + YSC_{lmk} + SCR(Y)_{mkjl} + GY_{il} + GS_{im} + GC_{ik} + GYS_{ilm} + GYC_{ilk} + GSC_{imk} + GYSC_{ilmk} + e_{ijklm},$$

where T is the observation of the i^{th} variety G in the l^{th} year Y of the m^{th} sowing date S and k^{th} crop protection treatment C in the j^{th} replication R within year l; μ is the general mean, e is the variation due to random error or the residual, and YS, YC, CS, YSC, GY, GS, GC, GYS, GYC, GSC, $GYSC$, and $SCR(Y)$ are the interactions. In the analysis, Y, S, C, and all possible interactions among these three factors were considered fixed, and all the remaining effects were considered random. Genotypes were considered as a random sample of germplasm handled by the breeding program at Holetta in order to be able to draw broad inferences on the patterns of response of the barley materials in the breeding program with respect to the management levels and the years tested. Incidentally, the test years were contrasting manifesting features apparent in short and long season barley growing ecologies of the country. As a result, years were considered fixed representing short cycle and long cycle barley growing locations of the country. Sowing date is often specific to a particular location over the years and, therefore, considered fixed. Likewise, crop protection treatments were assumed to be individual elements about which conclusions are made, hence fixed. PROC MIXED was used to determine statistical significance of variances for the fixed effects and to obtain genotype × year × sowing date × crop protection treatment BLUPs (Littell et al., 1996; Woldeyesus Sinebo, 2002). PROC GLM was used to obtain genotype means in individual environments and to determine significance of variances for the random effects (Littell et al., 1996).

AMMI analysis of GE pattern was done using both cell means and BLUPs. GGE biplot analysis was done with the BLUPs when BLUPs improved pattern visualization meaningfully in the AMMI analysis. In the AMMI analysis (Kempton, 1984; Gauch, 1988) data were doubly centered by removing both genotype and environment main effects as:

$y_{ij} - \hat{y}_{i\cdot} - \hat{y}_{\cdot j} + \hat{y}_{\cdot\cdot}$, for the genotype i and environment j cell. In the GGE biplot, environment centered residuals were obtained as:

$y_{ij} - \hat{y}_{\cdot j}$, for the genotype i and environment j cell.

The G × E grain yield residuals were subjected to singular value decomposition using the PROC IML in SAS. The resulting singular values for the first, second and third (for GGE biplot only) principal components were partitioned to the respective genotype and environment eigenvectors using a factor of 0.5 as:

$g_{il} = \lambda_l^{0.5}\xi_{il}$ and $e_{jl} = \lambda_l^{0.5}\eta_{jl}$

where g_{il} and e_{jl} are PC l scores (l = 1, 2 or 3) for genotype i and environment j, respectively. The resulting genotype and environment PC scores were plotted using Microsoft® Excel 2000 Software (Microsoft Corporation). In the GGE analysis, variances due to each of G and GE contained in the first three PCs were extracted in order to compare the level of explanation of GE by each PC using AMMI and GGE.

Results

G and GE variances using cell means and BLUPs

Environment, genotype and GE effects were highly significant for grain yield of barley (Table 1). Environment contributed to 65%, GE to 26.6% and G to 8.4% of the G + E + GE sum of squares (SS) (Table 1). Hence, GE was more important than G and analysis of GE was appropriate to understand patterns of genotype response to environments in this data set. Mean grain yields in individual environments ranged from 178 g m^{-2} to 555 g m^{-2} and mean genotype grain yield ranged from 323 g m^{-2} to 517 g m^{-2} (Table 2). Effects of the components of environment (year, sowing date, crop protection treatment and their interaction) shall not be presented here. Instead G and GE shall be focused on. Of the GE components, only genotype × year (GY) and G × crop protection (GC) were significant ($P < 0.05$; Table 1). GY interaction was the single largest source of GE accounting for 14.1% of the total SS and 53% of the GE SS (Table 1). Genotype × management interaction [G × sowing date (GS) plus G × crop protection (GC) plus GSC interactions] accounted for 5.5% and G × management × year interaction (GMY) for 7.1% of the total SS. Separate analysis for each year (data not shown) indicated significant GS in the year 2002 (year of high season-end moisture stress) only.

Table 1. Significance of variances of the components of G × E based on cell means, sum of squares recovered from BLUPs for each source, the contribution of the components of G × E to the total G × E variance, and the magnitude of variances based on BLUPs relative to cell means for grain yield in barley tested under 18 environments (a combination of 3 sowing dates, two crop protection treatments and three years) at Holetta, Ethiopia.

Source	Based on cell means					Based on BLUPs				BLUPs SS as percent of cell mean SS
	df	SS	MS	% of G+ E+GE	% of GE	SS	MS	% of G + E + GE	% of GE	
E	17	31790107	1870006***	65.0	-	-	-	-	-	-
G	38	4100105	107898***	8.4	-	3487351	91772	8.4	-	85.1
G × E	646	13040448	20186***	26.6	-	6247933	9672	15.0	-	47.9
G × Y	76	6915386	90992***	14.1	53.0	5699103	74988	13.7	91.2	82.4
G × S	76	1020186	13424	2.1	7.8	143536	1889	0.3	2.3	14.1
G × C	38	863844	22733*	1.8	6.6	343949	9051	0.8	5.5	39.8
G × Y × S	152	1406239	9252	2.9	10.8	12242	81	0.0	0.2	0.9
G × Y × C	76	784769	10326	1.6	6.0	27627	364	0.1	0.4	3.5
G × S × C	76	765536	10073	1.6	5.9	21406	282	0.1	0.3	2.8
G × Y × S × C	152	1284489	8451	2.6	9.9	69	0	0.0	0.0	0.0

* and *** indicate significance at $P \leq 0.05$ and $P \leq 0.001$, respectively.

Sum of squares were calculated for G and GE using BLUPs. The use of BLUPs reduced G SS by 15% and GE SS by 52% (Table 1). As a result, the relative contribution of G and GE to G+GE was altered. The contribution of G and GE to the G+GE sum of squares was 23.9 and 76.1%, respectively using cell means and 35.8 and 64.2%, respectively using BLUPs (Table 1). GY made up 53% of GE SS using cell means but 91.2% of GE SS using BLUPs. On the other hand, G × management interaction (GM) made up 20.3% of GE using cell means and 8.1% using BLUPs. The contribution of GMY to GE declined from 26.7% using cell means to 0.6% using BLUPs. BLUP SS recovered 82% of cell mean SS for GY, 40% for GC and 14% for GS, with the remaining interactions recovering trivial amounts. BLUPs SS retained only 19.2% of the cell mean SS (mainly contributed by GC followed by GS) for GM and 1.2% for GMY (Table 1). The large reduction in GE SS when BLUPs were used implies that a large proportion of the cells mean SS for GE in general and GM and GYM in particular was simply noise.

Table 2. Genotype grain yield expressed as best linear unbiased predictors for 39 barley genotypes grown in 18 environments (a combination of 3 sowing dates, two crop protection treatments and three years) at Holetta, Ethiopia.

Genotype	EN2†	EY2	NN2	NY2	LN2	LY2	EN3	EY3	NN3	NY3	LN3	LY3	EN4	EY4	NN4	NY4	LN4	LY4	Mean
gin	113	254	157	222	54	176	275	486	212	496	260	476	310	449	400	546	388	535	323
fer	260	339	333	349	244	299	303	449	259	494	332	480	173	263	295	407	309	400	333
ehil	261	366	327	340	227	313	282	461	233	468	284	468	197	319	308	420	308	437	334
3371	309	377	365	349	266	326	314	451	244	446	314	466	189	276	284	370	291	394	335
em13	231	298	322	306	230	278	321	443	300	487	376	502	222	282	361	421	362	429	343
bal	183	262	260	244	163	212	318	456	268	458	336	467	312	384	437	498	437	505	344
sem	201	310	257	262	166	245	309	455	242	433	310	450	321	404	421	483	431	509	345
bh2	201	251	270	236	174	220	337	432	284	443	349	465	339	352	454	463	458	492	346
bh1	207	292	275	278	179	246	326	465	280	486	342	487	301	373	421	493	428	506	355
1829	253	315	318	304	228	279	306	427	247	442	324	459	314	372	416	481	433	506	357
em44	194	293	264	290	167	251	339	506	291	534	355	531	268	378	393	513	379	500	358
2038	207	285	283	276	203	257	301	448	260	473	344	493	323	392	437	504	471	541	361
ts8b7	186	272	261	269	166	241	359	485	318	516	379	518	313	385	430	506	428	514	364
sho	261	350	337	353	241	312	338	505	287	532	357	532	232	325	358	462	373	473	368
eh65	205	289	270	273	179	243	341	481	295	500	370	513	329	412	435	519	448	536	369
bbti	171	294	239	268	163	248	310	500	253	497	348	522	328	467	442	569	473	598	372
aby	247	333	319	332	224	309	367	512	313	537	380	549	250	342	359	463	370	486	372
cha	191	275	251	261	168	241	356	489	296	505	380	526	342	420	448	537	468	561	373
eh07	172	247	230	215	135	192	451	584	389	579	468	605	330	403	433	496	430	509	381
ahr	79	147	145	136	53	98	510	637	456	652	521	648	359	439	473	560	462	544	384
hb52	148	216	208	202	123	188	442	561	380	572	467	606	374	427	488	550	497	574	390
eh82	135	222	225	229	134	216	423	561	401	604	469	626	317	411	461	553	461	576	390
ard	191	291	248	259	152	246	386	552	324	549	384	570	361	460	457	551	463	583	390
hkr	135	246	199	215	122	199	425	590	368	587	454	607	355	467	467	567	478	581	392
hb42	114	194	186	194	108	186	418	555	361	577	444	604	387	472	506	604	530	639	393
th2	216	338	265	305	183	278	375	574	303	567	392	587	322	452	402	532	440	568	394
ts1	156	318	206	269	126	251	341	571	270	550	345	562	389	559	483	636	497	655	399
sas	286	398	358	391	270	346	338	517	290	539	365	532	291	410	406	530	421	527	401
bka	167	243	206	205	138	201	482	608	396	594	504	641	391	466	470	551	504	592	409
em42	176	267	251	268	184	246	423	563	384	599	491	624	344	441	469	576	497	592	411
mis	267	391	351	398	236	342	369	556	331	591	381	574	287	431	421	573	416	567	416
hb33	200	250	260	238	151	201	503	590	432	597	490	601	407	455	510	570	497	572	418

shg	153	226	233	208	152	199	456	572	406	574	493	606	416	492	541	600	562	637	418
3381	269	368	334	349	249	324	369	535	302	531	386	551	367	469	477	579	507	612	421
hb20	166	222	223	208	145	183	483	573	409	577	502	597	447	504	547	615	573	636	423
iar	201	270	242	236	156	230	484	632	407	629	481	658	448	495	529	586	542	622	436
3304	320	382	382	361	271	317	441	581	374	581	434	584	388	440	489	544	488	550	440
dim	258	378	309	318	229	323	440	636	359	592	450	643	522	647	616	711	635	758	490
eh42	208	302	269	273	174	229	568	717	508	715	579	711	566	657	671	752	662	737	517
Mean	202	292	268	274	178	248	383	531	326	541	401	555	337	425	447	536	457	553	386

† In EN2, the first letter represents sowing date (E = early sowing, N = normal sowing and L = late sowing) and the second letter absence (N = no) or presence (Yes = Y) of crop protection treatment and the number refers to year (2 = 2002, 3 = 2003 and 4 = 2004).

Table 3. Analysis of variance for grain yield of 39 barley genotypes tested at three sowing dates and two crop protection treatments for three years (2002 - 2004) at Holetta, Ethiopia.

Source	df	SS	MS	*F*	*P*	% of G + E + GE
	AMMI analysis of G × E based on cell means					*% of GE*
G × E	646	13040448	20186	2.41	< 0.0001	100
PC1	54	6200511	114824	13.69	0.00000	76.5
PC2	52	1765139	33945	4.05	0.00000	15.9
PC3	50	1056432	21129	2.52	0.00000	5.0
PC4	48	830272	17297	2.06	0.00003	1.3
PC5	46	679918.3	14781	1.76	0.00140	0.7
Deviations	396	2508645	6335	0.76	0.99963	0.7
	AMMI analysis of G × E based on BLUPs					*% of GE*
G × E	646	6248401	9672	1.15	0.01640	100
PC1	54	4780352	88525	10.55	0.00000	76.5
PC2	52	993118	19098	2.28	0.00000	15.9
Deviations	540	474931	879	0.10	1.00000	7.6

AMMI analysis: cell means versus BLUPs

AMMI analysis of variance using cell means indicated the first five interaction components to be significant (Table 3). PC1 and PC2 accounted for 76.5% and 15.9%, respectively together making up for 92% of the GE sum of squares. AMMI analysis based on BLUPs showed only the first two PCs to be significant with the same level of explanation as for the cell mean analysis above (Table 3). The partitioning of the 13040449 GE SS contained in the cell means (Table 1) into signal and noise (equals residual mean square multiplied by the GE degrees of freedom; Gauch and Zobel, 1997; Gauch, 2006) resulted in 7621551 for the signal and 5418898 for the noise. The first PC with a SS of only 6200511 is likely to under fit the real patterns of GE apparent in the data. However, the combined PC1 and PC2 SS of 7965650 is closer to the signal SS of 7621551 than PC1 SS alone. Hence, the nearest interaction PCs SS that approximates the signal SS is those SS accounted for by the first two PCs. Hence the appropriateness of AMMI2 model to explain patterns of GE contained in this data set was confirmed by both AMMI ANOVA using BLUPs and by the attempt to separate noise from signal using cell means.

Figures 1 and 2 give AMMI2 biplots based on cell means and BLUPs, respectively. The first AMMI axis identified environments largely based on the years rather than based on management factors (sowing date and crop protection treatments) (Figures 1 and 2). There were two major groups of environments, namely those distinguished by the year 2002 and those identified together by the years 2003 and 2004 environments. The year 2002 was the most stressful year with early cessation of rainfall. The second PC distinguished most of the year 2003 environments from the year 2004 environments (Figure 1). However, it is important to note differences between AMMI2 biplot based on cell means (Figure 1) and AMMI2 biplot based on BLUPs (Figure 2). Sowing dates and crop protection treatments within each year clustered together totally when BLUPs were used instead of cell means. For instance, early sowing plus crop protection treatment in the year 2003 (EY3) identified itself more with environments in the year 2004 than the other treatments in the year 2003 when cell means were used than when BLUPs were used (Figures 1 and 2). Given that GY interaction was an overriding component of GE interaction, closer aggregation of environments based on years using BLUPs than using cell means is appropriate. Hence, AMMI2 biplot pattern obtained using BLUPs was agronomically more meaningful than that obtained using cell means.

Description and interpretation of patterns in the AMMI biplot

Genotypes projecting to the direction of the year 2002 environments were all early maturing (Figure 2). Of these, genotypes *3371*, *ehil* and *fer* projected the most towards the year 2002 environments. *Ahr* projected the most in the direction of the year 2003 environments and *dim* and *ts1* towards EY4 environment indicating proportionally greater response of these genotypes in these respective environments. Of all the genotypes, *ahr* is the latest in both heading and maturity (data not shown). Those that projected towards the year 2003 and year 2004 environments were all late maturing full season high yielding varieties (Figure 2). *Eh42* while had low PC2 score projected the most to the direction of these high yielding environments indicating its high

yielding ability and relative stability in average to high yielding environments. *Eh42* had the highest mean grain yield, the lowest lodging score (4%), the most number of spikes per unit area and was one of the highest in kernel weight (data not shown). Within each year, crop protection treatments identified themselves from no crop protection treatments always occupying the upper side in the biplot.

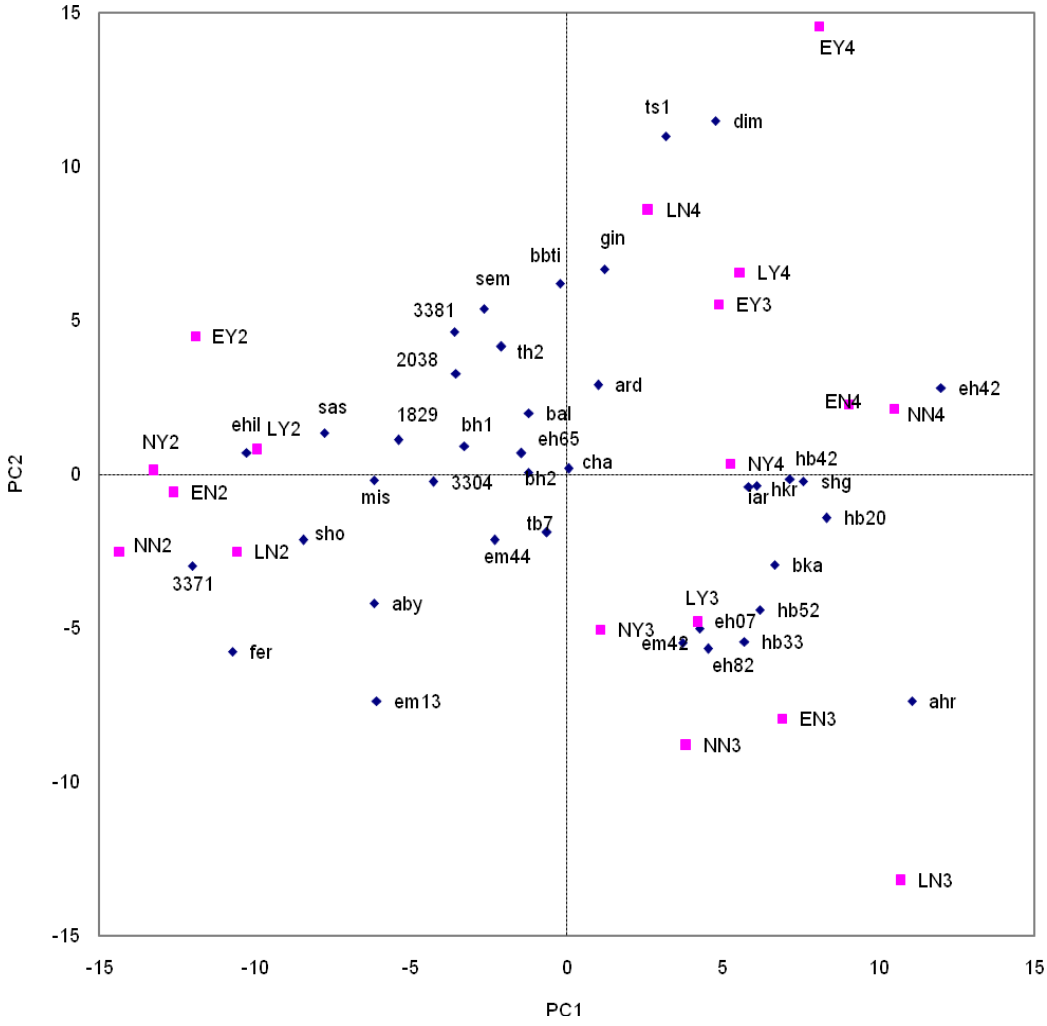

Figure 1. AMMI biplot of the first and the second principal components resulting from singular value decomposition of doubly centered mean grain yields of 39 genotypes grown in 18 environments at Holetta, Ethiopia

AMMI biplot of the genotype main effect against the first PC is given in Figure 3. In AMMI1 biplot, it is clear that *ahr* and *eh42* contrast with genotypes such as *3371*, *fer* and *ehil* for PC1. Generally, from this figure most of the late maturing genotypes had positive interaction with the first principal component axis while most of the early maturing genotypes had opposite and large negative scores with the first PC axis. *Dim* appears to have associated itself with the high yielding environments in which crop protection treatments were applied more than any other high yielding genotype, which indicates its relative high yield potential but also greater disease susceptibility than other high yielding full cycle improved genotypes.

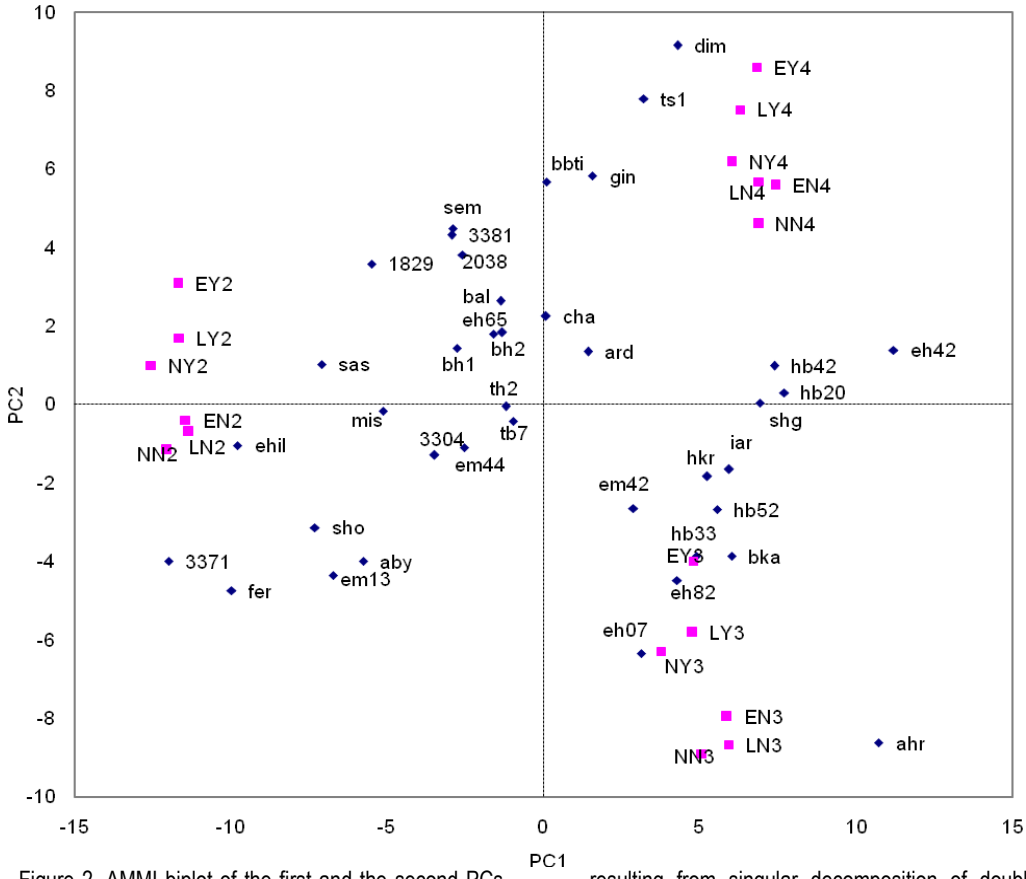

Figure 2. AMMI biplot of the first and the second PCs resulting from singular decomposition of doubly centered genotype × year × sowing date × crop protection treatment BLUPs for grain yield of 39 genotypes grown in 18 environments at Holetta, Ethiopia

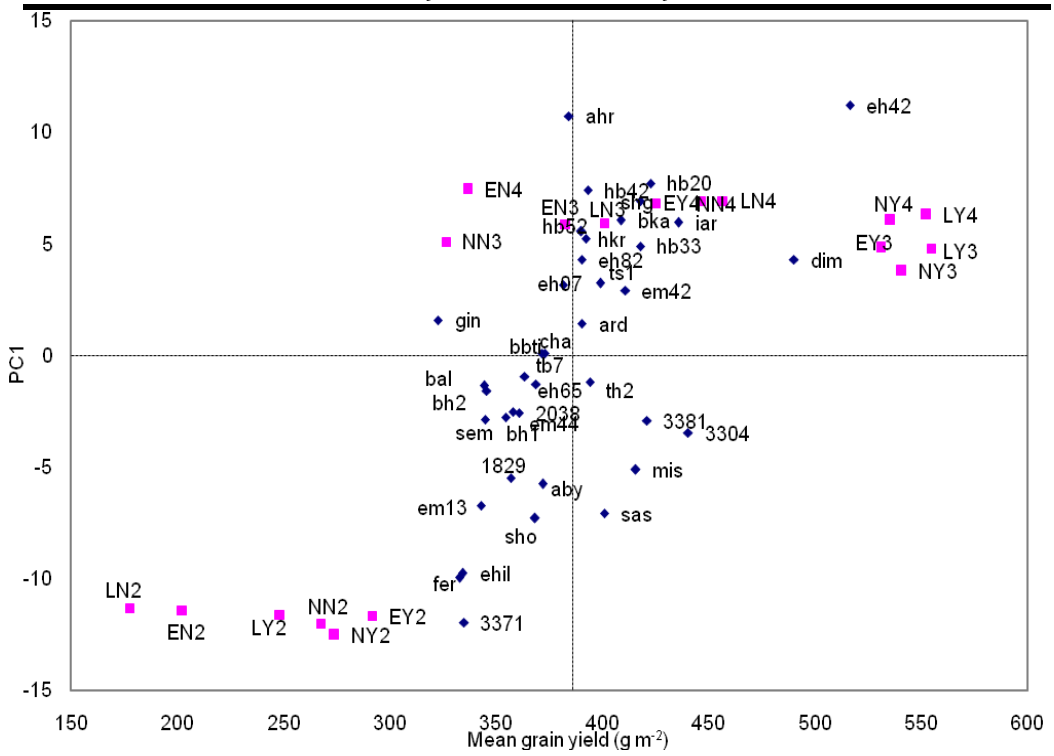

Figure 3. AMMI biplot of genotype main effect and the first PC resulting from singular decomposition of doubly centered genotype × year × sowing date × crop protection treatment BLUPs for grain yield of 39 genotypes grown in 18 environments at Holetta, Ethiopia

AMMI versus some features of the GGE

Table 4 gives G, GE and G+GE sum of squares recovered from each of the first three PCs in the GGE analysis. PC1 recovered 71% and PC2 27.8% of the genotypic SS making up for a total of 98.8%. PC1 recovered 66.9%, PC2 11.2% and PC3 14.5% of the GE SS. AMMI required only the first two PCs to recover 92.5% of the GE variance (Table 3) whereas GGE needed the first three PCs to recover the same magnitude of GE variance (Table 4). If GE is to be described by a biplot using GGE analysis, it is a biplot of PC1 against PC3 that explained most of the variation (81.4%) contained in a GE matrix than the usual PC1 vs PC2 biplot of the GGE (explained 78% of the variation). Note the considerable similarity between the AMMI2 biplot (explained 92.5% of the variation; Figure 2) and the GGE biplot of PC1 vs. PC3 with the PC3 axis reversed (reversing the sign does not change interpretation) (Figure 5). Both AMMI2 and GGE PC1 versus PC3 biplots (Figures 2 and 5) clearly separated the year 2003 and 2004 environments a feature that was not clear from GGE2 biplot (Figure 4). Hence, to explain the GE patterns for this data set using the GGE, one should go up to GGE3.

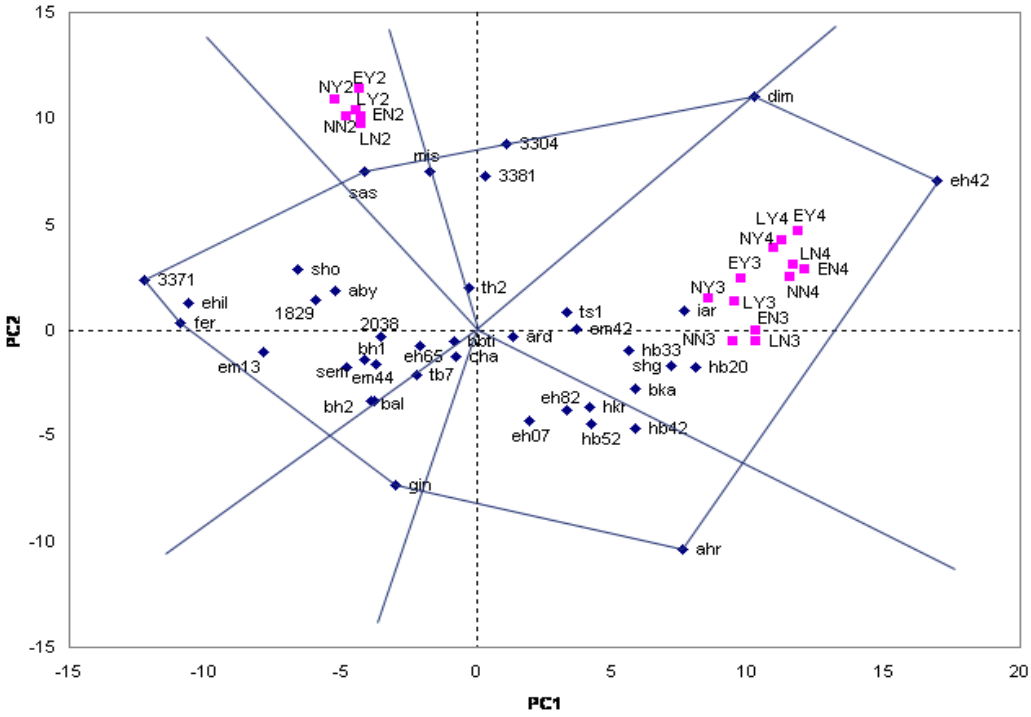

Figure 4. GGE biplot of the first and the second principal components resulting from singular value decomposition of environment centered genotype × year × sowing date × crop protection treatment BLUPs for grain yield of 39 genotypes grown in 18 environments at Holetta, Ethiopia.

Table 4. Partitioning into G and GE sum of squares of the variances contained in the first three principal components of the GGE analysis for grain yield (expressed as best linear unbiased predictors) obtained from 39 barley genotypes tested under three sowing dates and two crop protection treatments in 2002, 2003 and 2004 at Holetta, Ethiopia.

Source	PC1	PC2	PC3	GGE2 (PC1+PC2)	Full model SS
G	2476461 (71.0†)	968573 (27.8)	41826 (1.2)	3445034 (98.8)	3487351 (35.8)
GE	4176860 (66.9)	699181 (11.2)	903329 (14.5)	4876040 (78.0)	6247939 (64.2)
G+GE	6653320 (68.3)	1667754 (17.1)	945154 (9.7)	8321074 (85.5)	9735290 (100)

† Figures in brackets indicate percentages relative to full model sum of squares.

Discussion

In multi-environment testing, cell mean is the commonest estimate of genotype yield in individual environments (Piepho, 1994). However, cell means contain noise associated with large GE degrees of freedom (Gauch and Zobel, 1997). Singular value

decomposition of cell mean based G × E, therefore, result in interaction PCs that contain both structural variance from real GE and noise from error variance (Moreno-González, et al., 2003). Gain in estimates of cell means can be achieved ex-ante by employing appropriate field plot techniques and by increasing the number of replications. Accuracy can also be improved ex-poste by using statistical analysis tools that enable better yield predictions. In our study, both BLUP based analysis and partitioning of cell mean based GE into signal and noise depicted much of the GE variance to be noise, which is in agreement with reports elsewhere (Piepho, 1994; Gauch and Zobel, 1997; Moreno-González, et al., 2003). Importantly, the use of BLUPs improved pattern visualization in graphical biplots of our GE yield data.

G and GE can be combined in a biplot using AMMI1 or GGE2 model. However, the choice depends on the proportion of the G and GE variance captured by either model. In the present study, GE variance captured by AMMI1 (76.5%) and the GGE2 (78%) were comparable (Tables 3 and 4). Also, GGE2 capturing 98.8% of the G is nearly similar to the 100% G contained in the AMMI1. Hence AMMI1 and GGE2 were comparable in explaining G+GE for this data set. However, perusal of GGE2 (Figure 4) and AMMI1 (Figure 2) biplots indicates the attraction of the GGE's which-won-where pattern (perhaps even without the diagonals and perpendiculars required in the polygon view of the GGE biplot).

According to Gauch (2006) when G and GE is mixed as in the GGE analysis, it is not clear from a biplot whether a given PC captured G, GE or both. Moreover, such a mixing may relegate important GE signals to higher order PCs lowering the utility of the most important first two PCs for displaying GE interaction in a two dimensional graphic biplot (Gauch, 2006). Also the manner in which GGE PCs capture GE is haphazard at times with higher order PCs capturing more of the GE variation than lower order PCs (Gauch, 2006). In the present study, the GE variation contained in PC3 was more than the GE variation contained in PC2. Our findings using a relatively simple data set, therefore, support Gauch's argument that some of the GE signals might not be captured and described parsimoniously using the first two PCs independent of the nature of a data set. Thus, AMMI is more effective in describing GE than GGE. Nonetheless, Yan et al. (2007) argued that combining G and GE is important for genotype evaluation and mega-environment analysis. Because of this and by design, GGE extracts as much as possible of G + GE variation combined in a monotonic way without regard to how the PCs captured G or GE individually.

In conclusion, although AMMI2 was more efficient than GGE2 for displaying patterns of GE interaction in this data set, GGE2 was quite elegant and simple for presenting G and GE combined in a biplot graph, including the which-won-where pattern. BLUPs might improve yield estimation and pattern recognition, and that attempting both AMMI and GGE analysis might provide important insights on genotype performance and GE.

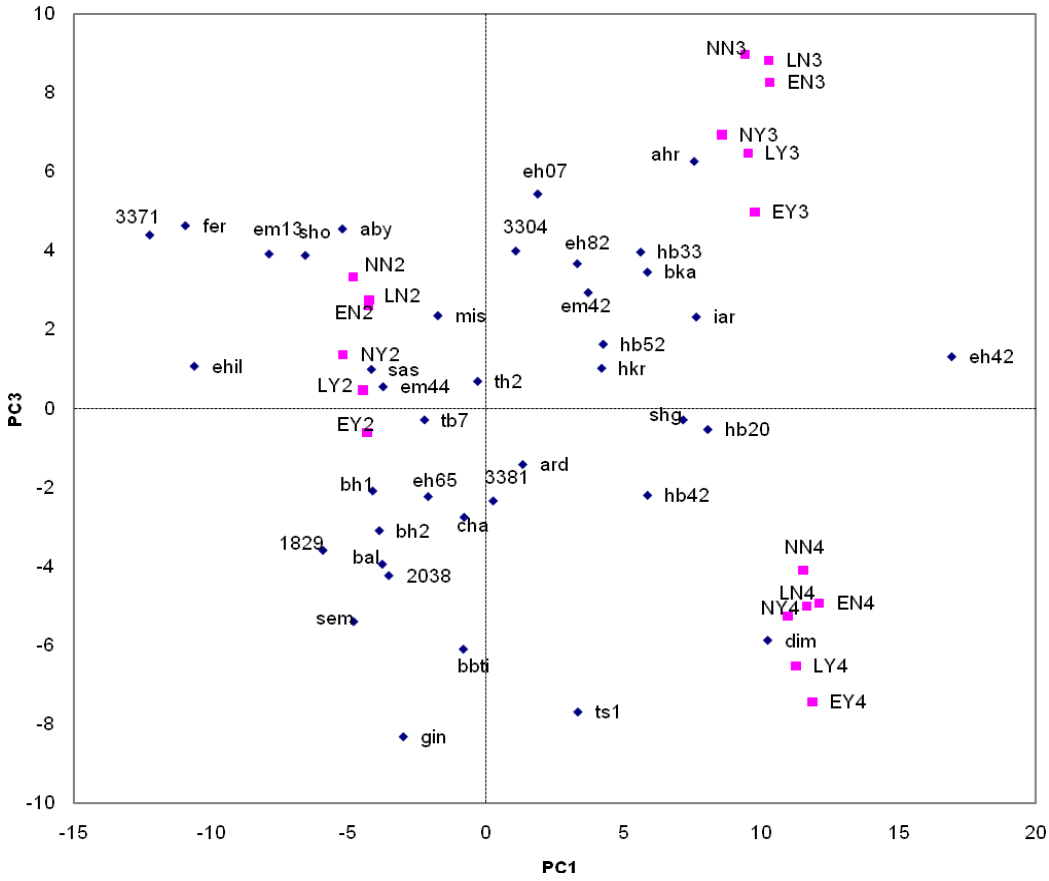

Figure 5. GGE biplot of the first and the third principal components resulting from singular value decomposition of environment centered genotype × year × sowing date × crop protection treatment BLUPs for grain yield of 39 genotypes grown in 18 environments at Holetta, Ethiopia.

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