GGE Biplot vs. AMMI Analysis of Genotype–by–Environment Data

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ABSTRACT

The use of genotype main effect (G) plus genotype-by-environment (GE) interaction (G+GE) biplot analysis by plant breeders and other agricultural researchers has increased dramatically during the past 5 yr for analyzing multi-environment trial (MET) data. Recently, however, its legitimacy was questioned by a proponent of Additive Main Effect and Multiplicative Interaction (AMMI) analysis. The objectives of this review are: (i) to compare GGE biplot analysis and AMMI analysis on three aspects of genotype-by-environment data (GED) analysis, namely mega-environment analysis, genotype evaluation, and test-environment evaluation; (ii) to discuss whether G and GE should be combined or separated in these three aspects of GED analysis; and (iii) to discuss the role and importance of model diagnosis in biplot analysis of GED. Our main conclusions are: (i) both GGE biplot analysis and AMMI analysis combine rather than separate G and GE in mega-environment analysis and genotype evaluation, (ii) the GGE biplot is superior to the AMMI1 graph in mega-environment analysis and genotype evaluation because it explains more G+GE and has the inner-product property of the biplot, (iii) the discriminating power vs. representativeness view of the GGE biplot is effective in evaluating test environments, which is not possible in AMMI analysis, and (iv) model diagnosis for each dataset is useful, but accuracy gain from model diagnosis should not be overstated.

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Abbreviations: AEC, average environment coordination; AMMI, Additive Main Effect and Multiplicative Interaction; G, genotype main effect; GE, genotype-by-environment interaction; GED, genotype-by-environment data (for a single trait); GGE, genotype main effect plus genotype-by-environment interaction; IPC, interaction principal component; MET, multi-environment trials; NID, normally and independently distributed; PC, principal component; SREG, Sites (Environments) Regression model; SVD, singular value decomposition; SVP, singular value partitioning.

Plant breeders and geneticists, as well as statisticians, have a long-standing interest in investigating and integrating G and GE in selecting superior genotypes in crop performance trials (Barah et al., 1981; Kang, 1988, 1993; Eskridge, 1990; Kang and Pham, 1991; Hühn, 1996; Yan et al., 2000). Many statistical methods have been developed for GED analysis, including AMMI analysis (Gauch 1992) and GGE biplot analysis (Yan and Kang, 2003; Yan and Tinker, 2006).

The biplot (Gabriel, 1971) has become a popular data visualization tool in many scientific research areas, including psychology, medicine, business, sociology, ecology, and agricultural sciences. Earlier uses of biplots in GED analyses include Bradu and Gabriel (1978), Kempton (1984), and Cooper and DeLacy (1994). The biplot tool has become increasingly popular among plant breeders and agricultural researchers since its use in cultivar evaluation and mega–environment investigation (Yan et al.,

2000). Yan et al. (2000) referred to biplots based on singular value decomposition (SVD) of environment-centered or within-environment standardized GED as "GGE biplots," because these biplots display both G and GE, which are the two sources of variation that are relevant to cultivar evaluation (Kang, 1988, 1993; Gauch and Zobel, 1996; Yan and Kang, 2003).

The commonly used GGE biplot is based on the Sites Regression (SREG) linear-bilinear (multiplicative) model (Cornelius et al., 1996), which can be written as

$$\overline{y}_{ij} - \mu_j = \sum_{k=1}^{t} \lambda_k \alpha_{ik} \gamma_{jk} + \overline{\varepsilon}_{ij} \quad [1]$$

where $\overline{y}_{ij}$ is the cell mean of genotype i in environment j; μ_j is the mean value in environment j; $i = 1, \cdots g; j = 1, \cdots e$, g and e being the numbers of cultivars and environments, respectively; and t is the number of principal components (PC) used or retained in the model, with $t \leq \min(e, g - 1)$. The model is subject to the constraint $\lambda_1 \geq \lambda_2 \geq \cdots \lambda_t \geq 0$ and to orthonormality constraints on the α_{ik} scores, that is, $\sum_{i=1}^{g} \alpha_{ik}\alpha_{ik'} = 1$ if $k = k'$ and $\sum_{i=1}^{g} \alpha_{ik}\alpha_{ik'} = 0$ if $k \neq k'$, with similar constraints on the γ_{jk} scores [defined by replacing symbols (i,g,α) with (j,e,γ)]. The $\overline{e}_{\mathbf{ij}}$ are assumed $\mathrm{NID}(0, \sigma^2/r)$, where r is the number of replications within an environment.

Least squares solution for μ_j is the empirical mean $(\overline{y}_{.j})$ for the jth environment, and the least squares solutions for parameters in the term $\lambda_k \alpha_{ik} \gamma_{jk}$ (for $i = 1, \cdots, g; j = 1,\ldots,e$) are obtained from the kth PC of the SVD of the matrix $\mathbf{Z} = [z_{ij}]$, where $z_{ij} = \overline{y}_{ij} - \overline{y}_{.j}$. The maximum number of PCs available for estimating the model parameters is $p = \mathrm{Rank}(\mathbf{Z})$. In general, $p \leq \min(e, g - 1)$, with equality holding in most cases. For k = 1, 2, 3, $\cdots$, α_{ik} and γ_{jk} have also been characterized as primary, secondary, tertiary, etc., multiplicative effects of the ith cultivar and jth environment (for first usage of such terminology in a multiplicative model context, see Seyedsadr and Cornelius, 1992). Thus, Eq. [1] may be described as modeling the deviations of the cell means from the environment means as a sum of PCs, each of which is the product of a cultivar score (α_{ik}), an environment score (γ_{jk}), and a scale factor (the singular value, λ_k).

The GGE biplot is constructed from the first two PCs from the SVD of $\mathbf{Z}$ with "markers," one for each cultivar, plotted with $\hat{\lambda}_1^f \hat{\alpha}_{i1}$ as abscissa and $\hat{\lambda}_2^f \hat{\alpha}_{i2}$ as ordinate. Similarly, markers for environments are plotted with $\hat{\lambda}_1^{1-f} \hat{\gamma}_{j1}$ as abscissa and $\hat{\lambda}_2^{1-f} \hat{\gamma}_{j2}$ as ordinate. The exponent f, with $0 \leq f \leq 1$, is used to rescale the cultivar and environment scores to enhance visual interpretation of the biplot for a particular purpose. Specifically, singular values are allocated entirely to cultivar scores if $f = 1$ [this is "cultivar-focused" scaling (Yan, 2002)], or entirely to environment scores if $f = 0$ ("environment-focused" scaling); and $f = 0.5$ will allocate the square roots of the $\hat{\lambda}_k$ values to cultivar scores and also to environment scores ("symmetric" scaling). Mathematically, a GGE biplot is a graphical representation of the rank 2 least squares approximation of the rank p matrix $\mathbf{Z}$. This representation is unique except for possible simultaneous sign changes on all $\hat{\alpha}_{i1}$ and $\hat{\gamma}_{j1}$ and/or all $\hat{\alpha}_{i2}$ and $\hat{\gamma}_{j2}$. An important property of the biplot is that the rank 2 approximation of any entry in the original matrix $\mathbf{Z}$ can be computed by taking the inner product of the corresponding genotype and environment vectors, i.e., $\left(\hat{\lambda}_1^f \hat{\alpha}_{i1}, \hat{\lambda}_2^f \hat{\alpha}_{i2}\right)\left(\hat{\lambda}_1^{1-f} \hat{\gamma}_{j1}, \hat{\lambda}_2^{1-f} \hat{\gamma}_{j2}\right)' = \hat{\lambda}_1 \hat{\alpha}_{i1} \hat{\gamma}_{j1} + \hat{\lambda}_2 \hat{\alpha}_{i2} \hat{\gamma}_{j2}$.

This is known as the inner-product property of the biplot.

The GGE biplot methodology (Yan et al., 2000; Yan, 2001, 2002; Yan and Kang, 2003; Yan and Tinker, 2006) consists of a set of biplot interpretation methods, whereby important questions regarding genotype evaluation and test-environment evaluation can be visually addressed. Increasingly, plant breeders and other agronomists have found GGE biplots useful in mega-environment analysis (Yan and Rajcan, 2002; Casanoves et al., 2005; Samonte et al., 2005; Yan and Tinker, 2005b; Dardanellia et al., 2006), genotype evaluation (Bhan et al., 2005; Malvar et al., 2005; Voltas et al., 2005; Kang et al., 2006), test-environment evaluation (Yan and Rajcan, 2002; Blanche and Myers, 2006; Thomason and Phillips, 2006), trait-association and trait-profile analyses (Yan and Rajcan, 2002; Morris et al., 2004; Ober et al., 2005), and heterotic pattern analysis (Yan and Hunt, 2002; Narro et al., 2003; Andio et al., 2004; Bertoia et al., 2006). The legitimacy of GGE biplot analysis was, however, recently questioned by Gauch (2006), who concluded that, for GED analyses, AMMI analysis was either superior or equal to GGE biplot analysis.

The objectives of this review and interpretation paper are: (i) to compare GGE biplot analysis and AMMI analysis on three aspects of GED analysis, namely, mega-environment analysis, genotype evaluation, and test-environment evaluation; (ii) to discuss whether G and GE should be combined or separated in GED analysis; and (iii) to discuss the importance of model diagnosis in SVD-based analysis of GED. This discussion should enhance agricultural researchers' understanding of biplot analysis of GED.

THREE ASPECTS OF GED ANALYSIS USING GGE BIPLOTS

The analysis of GED (i.e., MET data for a single trait) should include three major aspects: (i) mega-environment analysis; (ii) test-environment evaluation, and (iii) genotype evaluation (Yan and Kang, 2003). We use the yield data of 18 winter wheat (*Triticum aestivum* L.) genotypes (G1 to G18) tested at nine Ontario locations (E1 to E9) (Table 1) as an example to illustrate the three aspects of biplot analysis. The same dataset was used extensively in Yan and Kang (2003) and Yan and Tinker (2006). When

supplemental information (e.g., data on environmental or genotypic covariates) is available, a fourth aspect, which is to understand the causes of G and GE, can be included (Yan and Hunt, 2001; Yan and Kang, 2003; Yan and Tinker, 2005b, 2006).

Mega-environment Analysis

A GGE biplot is constructed by plotting the first principal component (PC1) scores of the genotypes and the environments against their respective scores for the second principal component (PC2) that result from SVD of environment-centered or environment-standardized GED. The "which-won-where" view of the GGE biplot (Yan et al., 2000) is an effective visual tool in mega-environment analysis. It consists of an irregular polygon and a set of lines drawn from the biplot origin and intersecting each of the sides at right angles. The vertices of the polygon are the genotype markers located farthest away from the biplot origin in various directions, such that all genotype markers are contained within the resulting polygon. A line that starts from the biplot origin and perpendicularly intersects a polygon side represents the set of hypothetical environments in which the two cultivars defining that side perform equally; the relative ranking of the two cultivars would be reversed in environments on opposite sides of the line (the so-called "crossover GE"). Therefore, the perpendicular lines to the polygon sides divide the biplot into sectors, each having its own winning cultivar. The winning cultivar *for* a sector is the vertex cultivar at the intersection of the two polygon sides whose perpendicular lines form the boundary of that sector; it is positioned usually, but not necessarily, *within* its winning sector (see Yan, 2002 for a detailed example).

If all environment markers fall into a single sector, this indicates that, to a rank-two approximation, a single cultivar had the highest yield in all environments. If environment markers fall into different sectors, this indicates that different cultivars won in different sectors. Revealing the which-won-where pattern of a GED set is an intrinsic property of the GGE biplot rendered by the inner-product property of the biplot (Yan and Kang, 2003). Once a GGE biplot is constructed, the polygon and the lines that divide the biplot into sectors can be drawn by hand without further calculation. In the which-won-where view of the GGE biplot (Fig. 1) based on the data in Table 1, the nine environments fell into two sectors with different winning cultivars. Specifically, G18 was the highest yielding cultivar in E5 and E7 (but only slightly higher than several other cultivars with markers in close proximity to G18), and G8 was the highest yielding cultivar in the other environments. This crossover GE suggests that the target environments may be divided into different mega-environments.

Since a mega-environment is defined as a group of locations that consistently share the best set of genotypes

or cultivars across years (Yan and Rajcan, 2002), data from multiple years are essential to decide whether or not the target region can be divided into different mega-environments. Furthermore, a definitive conclusion must be based on data in which the *same* (sub-)set of genotypes is tested at the *same* (sub-)set of test locations across multiple years. Repeatable environment grouping is necessary, but not sufficient, for declaring different mega-environments. For example, even if the target environments can be subdivided into Group 1 and Group 2 repeatedly across years, the target environment still may not be meaningfully divided if cultivar A and B win in Groups 1 and 2, respectively, in 1 yr, but the which-won-where pattern is reversed in another year. The necessary and sufficient condition for mega-environment division is a repeatable which-won-where pattern rather than merely a repeatable environment-grouping pattern (Yan and Rajcan, 2002; Yan and Kang, 2003).

If the which-won-where or crossover patterns are repeatable across years and, hence, the target environment can be divided into subregions or mega-environments, as in the barley example given in Yan and Tinker (2005b), the GE that causes the crossovers among winning genotypes can be exploited by selecting in and for each mega-environment. If the crossover GE patterns are not repeatable across years, the GE cannot be exploited. Rather, it must be avoided by selecting high yielding and stable genotypes across target environments.

Appropriate mega-environment analysis should classify the target environment into one of three possible

Table 1. Mean yield (Mg ha⁻¹) of 18 winter wheat cultivars (G1 to G18) tested at nine Ontario locations (E1 to E9) in 1993.

Geno-types	Test Environments									
	E1	E2	E3	E4	E5	E6	E7	E8	E9	Mean
G1	4.46	4.15	2.85	3.08	5.94	4.45	4.35	4.04	2.67	4.00
G2	4.42	4.77	2.91	3.51	5.70	5.15	4.96	4.39	2.94	4.31
G3	4.67	4.58	3.10	3.46	6.07	5.03	4.73	3.90	2.62	4.24
G4	4.73	4.75	3.38	3.90	6.22	5.34	4.23	4.89	3.45	4.54
G5	4.39	4.60	3.51	3.85	5.77	5.42	5.15	4.10	2.83	4.40
G6	5.18	4.48	2.99	3.77	6.58	5.05	3.99	4.27	2.78	4.34
G7	3.38	4.18	2.74	3.16	5.34	4.27	4.16	4.06	2.03	3.70
G8	4.85	4.66	4.43	3.95	5.54	5.83	4.17	5.06	3.57	4.67
G9	5.04	4.74	3.51	3.44	5.96	4.86	4.98	4.51	2.86	4.43
G10	5.20	4.66	3.60	3.76	5.94	5.35	3.90	4.45	3.30	4.46
G11	4.29	4.53	2.76	3.42	6.14	5.25	4.86	4.14	3.15	4.28
G12	3.15	3.04	2.39	2.35	4.23	4.26	3.38	4.07	2.10	3.22
G13	4.10	3.88	2.30	3.72	4.56	5.15	2.60	4.96	2.89	3.80
G14	3.34	3.85	2.42	2.78	4.63	5.09	3.28	3.92	2.56	3.54
G15	4.38	4.70	3.66	3.59	6.19	5.14	3.93	4.21	2.93	4.30
G16	4.94	4.70	2.95	3.90	6.06	5.33	4.30	4.30	3.03	4.39
G17	3.79	4.97	3.38	3.35	4.77	5.30	4.32	4.86	3.38	4.24
G18	4.24	4.65	3.61	3.91	6.64	4.83	5.01	4.36	3.11	4.48
Mean	4.36	4.44	3.14	3.49	5.68	5.06	4.24	4.36	2.90	4.19

PC1 = 58.9%, PC2 = 19.1%, Sum = 78%
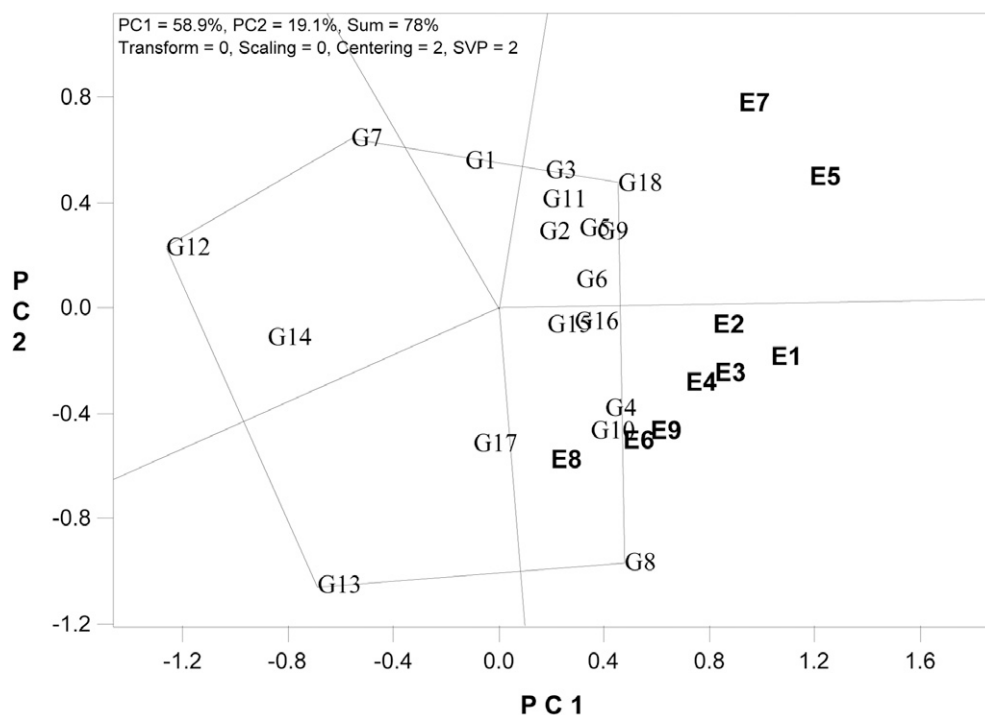Transform = 0, Scaling = 0, Centering = 2, SVP = 2

Figure 1. The "which-won-where" view of the GGE biplot based on the G × E data in Table 1. The data were not transformed ("Transform = 0"), not scaled ("Scaling = 0"), and were environment-centered ("Centering = 2"). The biplot was based on environment-focused singular value partitioning ("SVP = 2") and therefore is appropriate for visualizing the relationships among environments. It explained 78% of the total G+GE. The genotypes are labeled as G1 to G18 and the environments are labeled as E1 to E9.

1. This AEC view is based on genotype-focused singular value partitioning (SVP), that is, the singular values are entirely partitioned into the genotype scores (GGE biplot option "SVP = 1") (Yan, 2002). This AEC view with SVP = 1 is also referred to as the "Mean vs. Stability" view because it facilitates genotype comparisons based on mean performance and stability across environments within a mega-environment. The axis of the AEC abscissa, or "average environment axis," is the single-arrowed line that passes through the biplot origin and the "average environment," which is at the center of the small circle with coordinates $(\bar{\hat{\gamma}}_{.1}, \bar{\hat{\gamma}}_{.2})$, i.e., means of environment PC1 and PC2 scores. The axis of the AEC ordinate is the double-arrowed line that passes through the biplot origin and is perpendicular to the AEC abscissa. Because of the inner-product property of the biplot, the projections of the genotype markers on the "average environment axis" are proportional to the rank-two approximation of the genotype means and represent the main effects of the genotypes, G. The arrow shown on the axis of the AEC abscissa points in the direction of higher mean performance of the genotypes and, consequently ranks the genotypes with respect to mean performance. Unless G is too small to be meaningful, the ranking of the genotypes on the AEC abscissa is always perfectly or highly correlated with G, the correlation being 1.0 for the current example. Thus, the genotypes are ranked according to G as follows: G8 > G4 = G10 > G5 = G9 = G15 = G16 = G17 = G18 > G6 > G2 > Mean = G11 > G3 > G13 > G1 > G14 > G7 > G12.

Since GGE represents G+GE and since the AEC abscissa approximates the genotypes' contributions to G, the AEC ordinate must approximate the genotypes' contributions to GE, which is a measure of their stability or instability. Thus, G4 was the most stable genotype, as it was located almost on the AEC abscissa and had a near-zero projection onto the AEC ordinate. This indicates that its rank was highly consistent across environments within this mega-environment. In contrast, G17 and G6 were two of the least stable genotypes with above average mean performance.

Yan (2001) defined an "ideal" genotype on the basis of both mean performance and stability, and the geno-

types (Table 2). Type 1 is the easiest target environment one can hope for, but it is usually an overoptimistic expectation. Type 2 suggests opportunities for exploiting some of the GE. Such opportunities should not be overlooked if they exist, which is the whole point of mega-environment analysis and GE analysis. Type 3 is the most challenging target environment and, unfortunately, also the most common one.

Genotype evaluation and test-environment evaluation become meaningful only after the mega-environment issue is addressed. Within a single mega-environment, cultivars should be evaluated for their mean performance and stability across environments (Fig. 2); and the test environments should be evaluated for being, or not being, representative of the target environment and for their power to discriminate among genotypes (Fig. 3).

Genotype Evaluation

Genotype evaluation is meaningful only for a specific mega-environment, and an ideal genotype should have both high mean performance and high stability within a mega-environment. Assuming that the mega-environment differentiation in Fig. 1 is repeatable across years, genotype evaluation should be conducted for each mega-environment. Figure 2 is the "Average Environment Coordination" (AEC) view (Yan, 2001) of the GGE biplot involving the seven environments in the G8 niche identified in Fig.

types can be ranked based on their bip-lot distance from the ideal genotype. Dimitrios Baxevanos (personal communication, 2006) found this GGE distance to be more repeatable across years than either mean performance or a stability index.

Test Environment Evaluation

The purpose of test-environment evaluation is to identify test environments that effectively identify superior genotypes for a mega-environment. An "ideal" test environment should be both discriminating of the genotypes and representative of the mega-environment. Figure 3 is the same GGE biplot as Fig. 2 except that it is based on environment-focused scaling (Yan, 2002), that is, the singular values were entirely partitioned into the environment scores ("SVP = 2") so that it is appropriate for studying the relationships among test environments. This type of AEC can be referred to as the "Discriminating power vs. Representativeness" view of the GGE biplot. It can be helpful in evaluating each of the test environments with respect to the following questions:

1. Is the test environment capable of discriminating among the genotypes, i.e., does it provide much information about the differences among genotypes?
2. Is it representative of the mega-environment?
3. Does it provide unique information about the genotypes?

When the data are not scaled (or standardized) ("Scaling = 0"), the length of an environment vector is proportional to the standard deviation of cultivar means in the environment, which is a measure of the discriminating power of the environment, assuming that the experimental errors of the test environments are comparable. Test environments with longer vectors (like E1 in our example) are more discriminating of the genotypes. If a test environment marker falls close to the biplot origin, that is, if the test environment has a very short vector, it means that all genotypes performed similarly in it and therefore it provided little or no information about the genotype differences. A short vector could also mean that the environment is not well represented by PC1 and PC2 if the biplot does not explain most of the GGE of the data.

A second usage of Fig. 3 is to indicate the test-environments' representativeness of the mega-environment. Since the AEC abscissa is the "average-environment axis," test
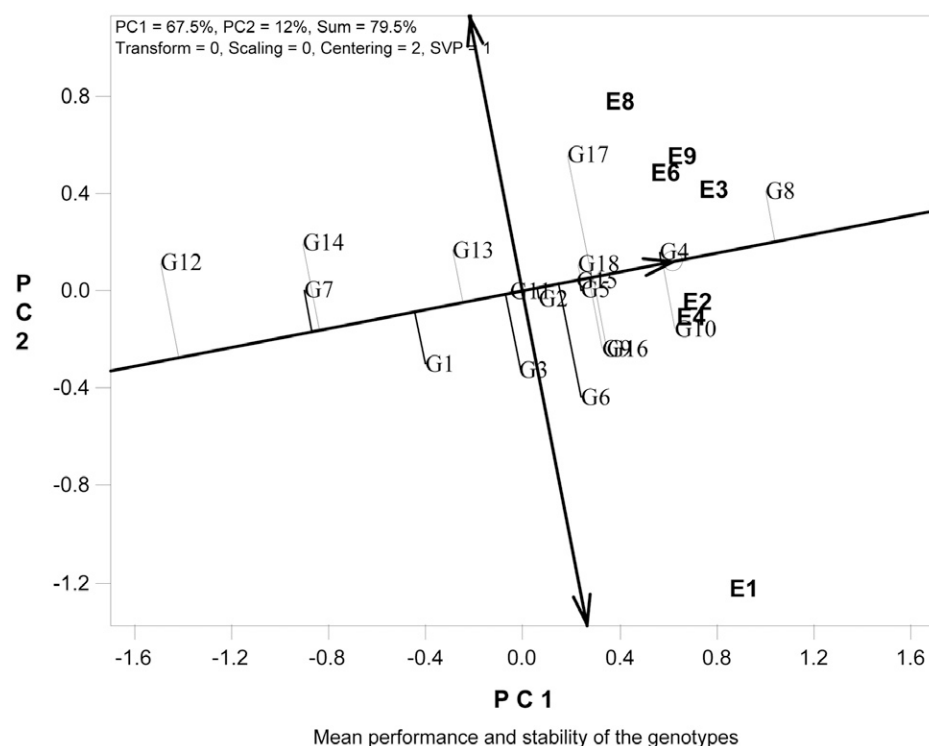

Figure 2. The "mean vs. stability" view of the GGE biplot based on a subset of the G × E data in Table 1. The data were not transformed ("Transform = 0"), not scaled ("Scaling = 0"), and were environment-centered ("Centering = 2"). The biplot was based on genotype-focused singular value partitioning ("SVP = 1") and therefore is appropriate for visualizing the similarities among genotypes. It explained 79.5% of the total G+GE for the subset.

Table 2. Three types of target environment based on mega-environment analysis.

	With Crossover GE	No Crossover GE
Repeatable across years	Type 2: target environment consisting of multiple mega-environments. Strategy: select specifically adapted genotypes for each mega-environment. A single year multilocation trial may be sufficient.	Type 1: target environment consisting of a single, simple mega-environment. Strategy: test at a single test location in a single year suffices to select for a single best cultivar.
Not repeatable across years	Type 3: target environment consisting of a single but complex mega-environment. Strategy: select a set of cultivars for the whole region based on both mean performance and stability based on data from multiyear and multilocation tests	

environments that have small angles with it (e.g., E2, E3, E4, E6, and E9 are more representative of the mega-environment than those that have larger angles with it, e.g., E1 and E8). This follows from the fact that when SVP = 2, the cosine of the angle between any environment vector and the "average environment axis" approximates the correlation coefficient between the genotype values in that environment and the genotype means across the environments.

Based on Fig. 3, a test environment may be classified into one of three types (Table 3). Type 1 environments have short vectors and provide little or no information
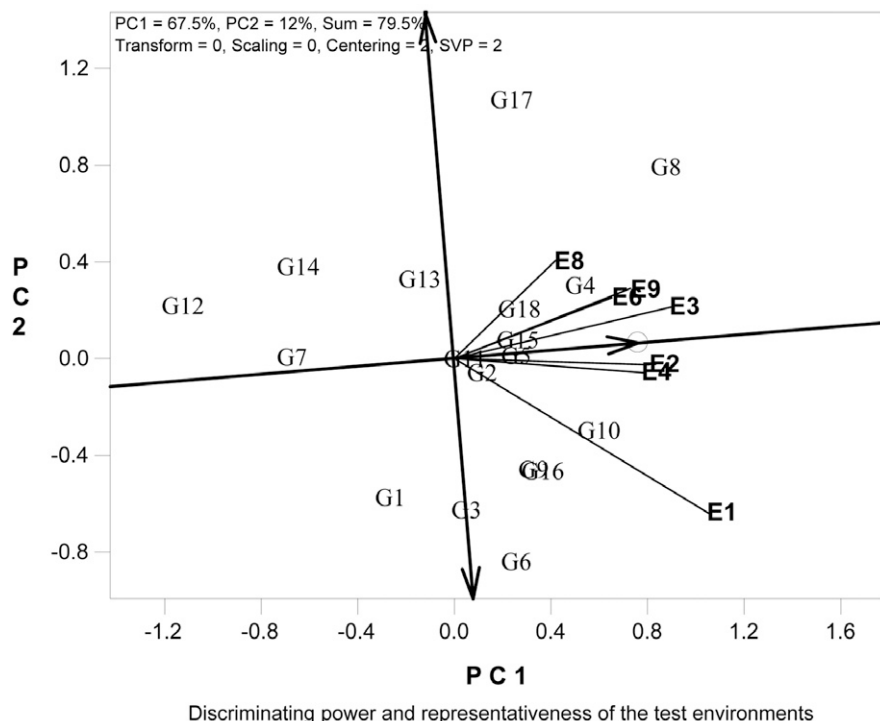
Figure 3. The "discriminating power vs. representativeness" view of the GGE biplot based on a subset of the G × E data in Table 1. The data were not transformed ("Transform = 0"), not scaled ("Scaling = 0"), and were environment-centered ("Centering = 2"). The biplot was based on genotype-focused singular value partitioning ("SVP = 2") and therefore is appropriate for visualizing the relationships among environments. It explained 79.5% of the total G+GE for the subset.

about the genotypes and, therefore, should not be used as test environments. Type 2 environments have long vectors and small angles with the AEC abscissa and are ideal for selecting superior genotypes. If budgetary constraints allow only a few test environments, Type 2 test environments are the first choice. Type 3 environments have long vectors and large angles with the AEC abscissa (e.g., E1); they cannot be used in selecting superior genotypes, but are useful in culling unstable genotypes.

Useful test environments should be further examined for their uniqueness. Some environments may never provide unique information, as they are always similar to some other environment(s) in separating and ranking the genotypes. Some (not all) of these environments can be dropped without losing much information about the genotypes. Testing cost can be reduced and efficiency improved by using a minimum set of test environments. Identification and removal of noninformative and redundant test locations (not environments) must be based on multiyear data. In Fig. 3, five environments (E2, E3, E4, E6, and E9) were highly correlated in their ranking of the genotypes, indicating that these environments produced similar information about the genotypes. If this pattern repeats across years, then it can be concluded that some of them are redundant and can be dropped. In analyzing a multiyear Ontario soybean performance trial dataset, Yan

and Rajcan (2002) reported one test location that was always highly correlated with one of the other three locations in ranking genotypes and was regarded as a redundant test location.

Yan (2001) defined an "ideal" test environment, which is a virtual environment that has the longest vector of all test environments (most discriminating) and is located on the AEC abscissa (most representative). Test environments can be visually ranked for their usefulness in identifying superior genotypes based on the distances on the GGE biplot between their markers and the marker of the ideal test environment. Blanche and Myers (2006) used this idea creatively in their study of cotton test locations. Test-environment evaluation should be an important aspect of GED analysis. Analysis of historical MET data can lead to the identification of a minimum set of test environments (locations) for cultivar evaluation. For example, E3 may be regarded as an ideal test location and E1, E3, and E8 may constitute a minimum set of test locations if the pattern shown in Fig. 3 is repeatable across years. For quantitative trait loci (QTL) mapping studies, the identification of a few discriminating and representative test environments (locations) is even more crucial because it is usually not feasible to test a large number of genotypes in many environments (Anna McClung, personal communication, 2006).

THREE ASPECTS OF GED ANALYSIS USING AMMI GRAPHS
Mega-Environment Analysis

The AMMI1 graph, first proposed in Gauch and Zobel (1997), was designed to address the which–won–where pattern. In this graph, the abscissa represents the environment scores for the first interaction principal component (IPC1) and the ordinate represents the "nominal yield" based on genotype mean yield (G) and IPC1. Each genotype is represented by a straight line defined by that genotype's mean yield and IPC1 score (i.e., regression on the environment IPC1 score). Ebdon and Gauch (2002b) claimed that mega-environment classification based on this method should be virtually the same as that based on a GGE biplot like Fig. 1. This may be true in some cases, but, even then, the GGE biplot is more advantageous in several aspects. First, the GGE biplot always explains more G+GE than the AMMI1 graph and is, therefore, a more accurate presentation of the GGE of the data. For exam-

ple, for a rice dataset, the GGE bip-
lot and the AMMI1 graph explained
77.3 and 64.6% of the total G+GE,
respectively (Samonte et al., 2005).
Second, the which–won–where pat-
terns are not always easy to visualize

Table 3. Three types of test environments based on test environment evaluation.

	Discriminating	Nondiscriminating
Representative	Type 2: Ideal for selecting superior genotypes.	Type 1: Useless
Not representative	Type 3: Useful for culling inferior genotypes.	

in the AMMI1 graph, particularly when many geno-
types and test environments are involved, as shown in
Fig. 2 of Ebdon and Gauch (2002b). This is because, in
the AMMI1 graph, the environments can be labeled only
along the abscissa rather than across the graph, and the
genotypes are represented by straight lines rather than by
dots. Moreover, whereas the which–won–where view of
a GGE biplot is an intrinsic property of the GGE biplot,
the AMMI1 graph is a completely different graph than the
AMMI1 biplot. Therefore, the AMMI1 graph is better
viewed as a tool for presenting conclusions rather than as a
tool for discovering which–won–where patterns.

The GGE biplot was criticized by Ebdon and Gauch
(2002b) and Gauch (2006) for not being able to reveal
which–won–where patterns if more than two PCs are
required to approximate the data. This problem, however,
is easily solved by generating GGE biplots for each group
of environments, as exemplified in Fig. 2 vs. Fig. 1. In
contrast, such remains a challenge in AMMI analysis if
more than one IPC is required. Although Gauch (1992)
proposed an AMMI2 graph for mega-environment analy-
sis when two IPCs are needed to approximate the data,
its usefulness has not been demonstrated thus far. This
graph is a plot of test environments defined by their IPC1
and IPC2 scores; the test environments are grouped by
the IPC1 and IPC2 scores, and the winning genotypes
for each group are identified from the genotype by envi-
ronment table of "predicted" yield based on the AMMI2
model and superimposed on the graph. Because one must
go to the predicted yield table to identify the winning
genotypes, this graph is better understood as a conclu-
sion-presentation tool rather than a pattern-discovery
tool, while pattern discovery is the primary interest of
GED analysis. Gauch (1992) envisioned this graph as a
3D plot with G being a third dimension perpendicular
to the IPC1 vs. IPC2 plane. Even so, it is still not capable
of identifying the which–won–where patterns, because
G and the IPC scores are not in the same units, just as
the two axes of the AMMI1 biplot are not in the same
units (more discussion on this later). Moreover, neither
AMMI1 nor AMMI2 graph has the inner-product prop-
erty of a true biplot, which is the underpinning of bip-
lot analysis. Gauch (1992) hypothesized that the universal
winners would be located near the origin of the IPC1
vs. IPC2 graph. This may be true in some cases; how-
ever, the universal losers would also be located exactly in
the same area. The usefulness of this AMMI2 graph has
never been demonstrated, even in the work of the AMMI

advocates where AMMI2 (AMMI with two IPCs) and
AMMI7 (AMMI with seven IPCs) were identified as the
best models (Ebdon and Gauch, 2002b).

Genotype Evaluation

The AMMI1 biplot (Zobel et al., 1988) is the most well-
known and appealing component of AMMI analysis. Its
abscissa represents the main effects (G and E) and its ordi-
nate represents the IPC1 scores. Therefore, it provides a
means of visualizing the mean performance (G) and the
stability (IPC1) of the genotypes simultaneously. However,
although regarded as a biplot, the AMMI1 biplot does not
have the most important property of a true biplot, namely
the inner-product property. As a result, the performance
of a given genotype in a given environment cannot be
accurately visualized even if it fully displays the data. This
is why a different AMMI1 graph (Gauch and Zobel, 1997)
is needed for visualizing the which–won–where pattern
as discussed above. There are two other reasons why the
AMMI1 biplot is less useful to breeders than the GGE bip-
lot. First, it always explains less G+GE than the GGE bip-
lot. Second, its shape is completely subjective because the
axes are in different units (original unit for the abscissa and
square root of the original unit for the ordinate). Unlike
the GGE biplot, the AMMI1 biplot also presents the envi-
ronment main effects of the test environments or E, which
is irrelevant to cultivar and test-environment evaluation
(Yan and Kang, 2003).

Test Environment Evaluation

Although identifying test environments for effective
genotype evaluation is an important component of GED
analysis, which has a great impact in plant breeding, it has
not been a research topic in AMMI analysis. The AMMI1
biplot (Zobel et al., 1988) displays the test environments
by their main effects E and IPC1 scores, but it provides no
information on the environment's ability in identifying
superior cultivars.

G AND GE: JOINTLY OR SEPARATELY?

Gauch (2006) criticized GGE biplot analysis for not
explicitly separating G from GE and concluded that
AMMI analysis was "always superior" over GGE biplot
analysis for its clear separation of G from GE. However,
it is neither in the interests of plant breeders, nor in the
interests of growers, to base selection of cultivars either
solely on G or on GE (Kang, 1993). We believe that GGE
biplot analysis achieves much more than AMMI analysis

relative to the three objectives of GED analysis, namely mega-environment analysis, test-environment evaluation, and genotype evaluation. In this section, we will examine from a more theoretical point of view whether G and GE should be separated.

G and GE Must Be Considered Simultaneously in Genotype Evaluation

There is no disagreement among AMMI users and GGE biplot users on this issue; all agree that G and GE must be considered simultaneously in genotype evaluation. The GGE biplot was designed to include both G and GE. The AMMI1 graph for mega-environment analysis and the AMMI1 biplot for genotype evaluation also contain both G and GE; they might as well be called "GGE graphs." They differ from the GGE biplot only in that they contain less G+GE and have less functionality than the GGE biplot. The AMMI analysis separates G from GE first and then puts them together again, whereas GGE biplot analysis deals with G+GE directly. Therefore, explicit separation of G from GE in AMMI analysis does not lead to the conclusion that it is superior to GGE biplot analysis.

G and GE Are Mathematical Definitions

Gauch (2006) argued that AMMI analysis was superior to other methods because it clearly separated G and GE and that G and GE have different agricultural implications, with G representing wide adaptation and GE representing specific adaptation. Indeed, if wide adaptation is high performance across environments, it is fair to say that G represents wide adaptation, but only within the confines of the test environments. If specific adaptation is high performance in specific environments, however, it is determined by G+GE, not by GE alone. The GE is a component of specific adaptation; it alone has no defined agricultural implications, because a genotype interacting positively with an environment can have the lowest yield in that environment.

It should also be recognized that G and GE are fundamentally mathematical partitioning of the total variation of a GED set. Their correspondence to biological and agricultural implications is not automatic. The G and GE can be regarded as representing different biological interpretations only if it is shown that G and GE are under the control of distinct genes or genetic interactions. There is much evidence that the expression of genes and their effects on crop productivity are affected by the environment, and the same gene can exert different effects on crop productivity in different regions (vernalization genes and photoperiodism genes are the most notable examples), but there is little evidence for the existence of genes whose expression is completely independent of the environment, particularly for those that control agronomically important traits. The QTL studies involving multiple environments often reveal that major QTL are responsible for both G and GE (e.g., Romagosa et al., 1996; Tinker et al., 1996; de Koeyer et al., 2004). An AMMI analysis often reveals strong correlations between G and genotypic scores for GE (e.g., see figures in Ebdon and Gauch, 2002a), suggesting common genetic controls for both G and GE. Therefore, the stance that G and GE must be treated as distinct entities in GED analysis is neither plausible nor supported by agricultural and biological evidence.

The G and GE Are Interchangeable

There is no clear biological boundary between G and GE; G and GE are interchangeable. It is understood that G, the genotype main effect, is always specific to the environments in which it is estimated. It has no meaning when separated from its environmental context. The G estimated from a small range of environments can be GE if put into a wider scope of environments. Conversely, GE estimated in a wider range of environments can become G if the environments are subdivided. In other words, G and GE can be interpreted only in the context of the actual set of cultivars evaluated in the actual set of environments. Recognition of the interchangeability between G and GE is the sole justification for mega-environment analysis, as discussed earlier. The GE becomes G if the scope of the environments is narrowed; G becomes GE when the scope of environments is widened. The gist of mega-environment analysis is to seek opportunities to subdivide the target environment into subregions (mega-environments) so that some repeatable GE can be converted into G.

In summary, G and GE must be considered simultaneously in mega-environment analysis, genotype evaluation, and test-environment evaluation; separation of G from GE is primarily a mathematical manipulation that is not always supported by biological evidence. Combining G and GE in GGE biplot analysis is essential for addressing plant breeding and agricultural problems. It is an intention rather than a mistake, a strength rather than a weakness.

The Utility of the AEC Is Beyond Reseparation of G from GE

The AEC view of the GGE biplot (Fig. 2 and 3) does reseparate G from GE whenever G is sizable, as pointed out by Gauch (2006); however, as discussed in the previous sections, it partitions GGE in a way that genotype evaluation and test-environment evaluation can be visually addressed in terms familiar to researchers without sacrificing the inner-product property of the biplot. That is, the AEC allows genotypes to be evaluated by their mean performance and stability, and test environments evaluated by their discriminating power and representativeness. Such functionality has not been shown for any other GED analysis methodology.

In a GGE biplot, the vector length of a genotype, which is the distance from the biplot origin to the position of the genotype marker, approximates the genotype's contribution to GGE. When all environments are on the same side of the AEC ordinate (i.e., when G is large enough to be meaningful), the Mean vs. Stability view of the GGE biplot (Fig. 2) partitions this GGE into the genotype's contribution to G (projection onto the AEC abscissa) and its contribution to GE (projection onto the AEC ordinate). This property allows identification of "ideal" genotypes (a large and positive contribution to G and a small contribution to GE) for a given mega-environment. Many breeders have found this application of GGE biplots to be useful. However, as illustrated in earlier sections, the AEC view of the GGE biplot is used only for genotype evaluation for a single mega-environment, where the GE is either small (a simple mega-environment) or not exploitable (a complex mega-environment).

The length of an environment vector in the GGE biplot approximates the environment's discriminating power. When all environments are on the same side of the AEC ordinate (i.e., when the G in the data is large enough to be meaningful), the "Discriminating power vs. Representativeness" view of the GGE biplot (Fig. 3) partitions this discriminating power into two components: discrimination on G (projection to the AEC abscissa) and discrimination on GE (projection to the AEC ordinate), whereby test environments ideal for selecting high-yielding and stable genotypes can be identified. Gauch (2006) considered E as an essential component for environment evaluation. Although E is essential for environment evaluation for nonbreeding purposes, it is irrelevant for identifying test environments that are superior for genotype evaluation.

MODEL DIAGNOSIS AND ACCURACY GAIN
Model Diagnosis Is Useful

We agree with Gauch (2006) that model diagnosis for each dataset is useful. Many methods have been proposed to determine how many PCs are required to fully approximate a two-way table of data, which can be used to determine whether a biplot under-fits or over-fits the data. Currently, we (Yan, Ma, and Cornelius) are investigating alternative methods for addressing two questions: (i) how does one know if the biplot is adequate in approximating the two-way table that is under investigation, and, (ii) what should one do if the biplot is inadequate. Briefly, whenever the biplot is judged as inadequate, attempts should be made to divide the data into subsets based on environmental and/or genotypic groups revealed in the biplot, as demonstrated in the above example. Data subdivision should stop when the biplot is judged as sufficient in displaying the patterns of the subset or when there are

no clear patterns (environmental or genotypic groupings) in the biplot.

Accuracy Gain from Model Diagnosis Should Not Be Overstated

Great accuracy gain and many "free observations" are claimed for model diagnosis and identification of "predictively accurate" models in AMMI analysis. For example, Ebdon and Gauch (2002b) reported for a perennial ryegrass (*Lolium perenne* L.)performance dataset that a statistical efficiency of 5.6 was achieved by using the AMMI2 model (AMMI with two IPCs), which was converted to 101 844 "free observations" or a saving of $1,000,000 (Gauch, 2006). However, this claim can be justified only if all of the following conditions are met: (1) the accuracy that was achieved by the "best model" is absolutely necessary; (2) the cultivar recommendations are made exactly as suggested by the "best model"; and (3) future performances are exactly the same as expected from the current data. However, Condition 1 is met only if adopting the best model leads to different cultivar recommendations, bearing in mind that, in practice, multiple cultivars rather than a single one are recommended for each mega-environment. Condition 2 is often false due to practical considerations. For example, AMMI1 was used in mega-environment analysis and cultivar recommendation, even though AMMI2 and AMMI7 were identified as the best models for two turfgrass datasets (Ebdon and Gauch, 2002b), which renders the model diagnosis completely irrelevant. Condition 3 is almost always false because genotype × year and genotype × location × year interactions are inevitable. Pertaining to Condition 3, the term "predictive success" used in AMMI analysis must be interpreted properly. There is a fundamental difference between predicting future performance and "predicting" past performance (cross-validation). It is the former that is important and it remains a question whether the best model identified through cross-validation is truly more predictive of future performance (Sneller and Dombek, 1995). Therefore, model diagnosis is useful, but accuracy gain from model diagnosis must not be overstated.

As Gauch (2006) pointed out, GED analysis is first of all an agricultural issue rather than a statistical one. Therefore, it is important to understand how cultivars are selected and recommended in the real world to have a realistic assessment about gains from model diagnosis. Breeders do not select cultivars on the basis of only a single trait (e.g., yield), because superior cultivars must meet requirements for multiple breeding objectives. Breeders do not select just one genotype with respect to a trait, because breeding objectives are often negatively associated, and it is rare to find a genotype that is best for everything (Yan and Wallace, 1995). For the same reason, agronomists always recommend a set of cultivars, rather than a single cultivar,

to the growers for any given region. Consequently, the choice among similar models may not affect cultivar selection and recommendations, and the argument of Gauch (2006) that using a suboptimal statistical model in GED analysis is like "turning the clock back on plant breeding" is an overstatement. In practice, it suffices to classify the genotypes into a few categories based on each breeding objective (trait), e.g., excellent, acceptable, and unacceptable, and to select those that are excellent or at least acceptable for all of the breeding objectives. Therefore, understanding the patterns in a GED set is more important than getting some "accurate" estimates, and GGE biplot is an effective tool for this purpose.

The Penalty for Not Conducting Model Diagnosis

It is important to have realistic understanding of the penalty when the GGE biplot under-fits or over-fits the G+GE of the data. When the data are over-fitted, some of the patterns in the biplot can be spurious. This can be easily prevented if formal statistical tests are conducted before any serious decisions are made. Furthermore, this situation happens only when the dataset is small and, thus, it is normally not a problem. When under-fitting is suspected, it is important to understand that the GGE biplot still presents the most important patterns of the GGE in the GED. These patterns are not only directly meaningful; they also serve as guide for data subdivision so that additional patterns can be explored. Continued data subdivision without a stopping criterion may eventually lead to data over-fitting. This can be prevented by conducting a formal statistical test or by imposing some practical considerations so that subdivision terminates when a feasible number of mega-environments (or groups of environments) is defined (Ebdon and Gauch, 2002b). By definition, the GGE biplot always displays the most important patterns of the G+GE in the GED. Therefore, if no pattern is seen from the biplot, it means that there is no clear pattern in the data; the question about the adequacy of the biplot becomes irrelevant and the search for patterns should stop. Yan and Tinker (2005b) presented an example of environment subdivision based on the GGE biplot patterns.

Essential Information about a Biplot

Since biplot analysis has been increasingly used in GED analysis and multivariate data analysis, this section discusses specifications of a biplot that are essential for its correct interpretation. Although the focus of this paper is on GGE biplot analysis, it is important to be aware that many different types of biplots can be constructed based on a single two-way dataset. All types of biplots are useful depending on the research objectives (Yan and Tinker, 2005b). The GGE biplots presented in this paper were generated using the "GGEbiplot" software first reported in Yan (2001) and

later detailed in Yan and Kang (2003), and more recently summarized in Yan and Tinker (2006). One feature of the GGEbiplot software that has not been described previously is that it provides information on the methods of data transformation, centering, scaling, and singular-value partitioning associated with the biplot, along with its goodness of fit (see top-left corner in Fig. 1–3), which is essential for correct interpretation of the biplot.

"Transform = 0" indicates that the data were not transformed before biplot analysis. Other transformation options in GGEbiplot include: (i) transformation to natural logarithm; (ii) transformation to base 10 logarithm; and (iii) square-root transformation. The purpose of transformation is to normalize or stabilize the data and thereby to linearize the relationships among variables. For example, log transformation is usually desirable for biplot analysis of gene expression data (Pittelkow and Wilson, 2003).

"Scaling = 0" means that the data were not rescaled (i.e., not divided by anything). Other data scaling options in GGEbiplot include: 1, rescaled by the within–environment standard deviation; 2, rescaled by the within–environment standard errors; 3, rescaled by the environmental means. The purpose of scaling is to put the variables (environments) in comparable ranges (i.e., max- min). Scaling is optional for GED, but it is necessary if the variables are of different units. For the GED of a given trait, which are expressed in the same unit of measure in all environments, use of "Scaling = 0" will retain the information of differential standard deviations in different environments, which may be used as a measure of the discriminating ability of the environments. Use of "Scaling = 1" will remove this information and assume all environments to be equally important. Use of "Scaling = 2" can remove any heterogeneity among environments with regard to their experimental errors while retaining the information about the environments' discriminating ability. Replicated data are required for using this option. Use of "Scaling = 3" removes the differences in unit and data range among variables while retaining the discriminating ability of the environments. Therefore, this option may have some advantage over "Scaling = 1." The choice of a transformation method and of a scaling method is dataset and research purpose specific.

"Centering = 2" indicates that the data were environment centered (i.e., the main effect E was removed from the data and the biplot displays only G+GE). Other centering options in GGEbiplot include: 0, no centering; 1, grand mean centered, useful when both row main effects and column main effects are of interest; and 3, double-centered. The choice of a centering method is also research purpose specific. Use of "Centering = 0" is useful for visualizing the original data and is effective for datasets whose grand mean is close to 0. "Centering = 0" was used in studying QTL-by-environment interactions (Yan and

Tinker, 2005a) and genotypic covariate-by-environment interactions (Yan and Tinker, 2005b). Use of "Centering = 3" is desirable if GE is of sole interest; it is also desirable for studying gene expression data where it is the relative change of gene expression levels, as opposed to the absolute levels of the genes or of the treatments, that is the research focus (Pittelkow and Wilson, 2003). Centering by a "shift parameter" is more suitable than centering by the grand-mean ("Centering = 1") for studying crossover interactions (Seyedsadr and Cornelius, 1992).

"Sum = 78%" indicates that the GGE biplot explained 78% of the G+GE variation. Generally speaking, the greater this value, the more confidence the researcher would have in the interpretations based on the biplot. However, if a smaller portion of the total variation is explained, it does not necessarily mean that the biplot is useless. See more discussion of this issue in the model diagnosis section.

"SVP = 2" indicates that the singular values are partitioned entirely into the environment scores before the construction of the biplot to enhance the suitability of the biplot for visualizing the relationships among the environments (e.g., Fig. 1 and 3). Conversely, "SVP = 1" indicates that the singular values are partitioned entirely into the row or genotype scores to enhance the suitability of the biplot for comparing the genotypes (e.g., Fig. 2). These two SVP options are equally useful for visualizing the responses of the genotypes to the environments (e.g., the which-won-where patterns) (Yan, 2002).

Clearly, for a single two-way dataset, numerous unique biplots can be generated, depending on data transformation, data scaling, data centering, and SVP. Specifying these pieces of information for a biplot is essential for its correct interpretation. So far, biplots generated by other statistical packages and biplots published in most scientific journals do not contain such information. Such information should be standard in biplot analysis.

SUMMARY AND CONCLUSIONS

The discussion of issues in this review leads to the 10 conclusions listed below. While points 3 to 5 are comparisons between GGE biplot and AMMI analysis of GED, other points are summaries of our general understanding on GED analysis and biplot analysis.

1. The GED analysis must address these three important aspects: mega-environment analysis, genotype evaluation, and test-environment evaluation. Understanding the target environment is a prerequisite for meaningful genotype and test-environment evaluations because superior genotypes and superior test environments are mega-environment-specific.

2. The G and GE are the two sources of variation that are relevant to mega-environment analysis, genotype evaluation, and test-environment evaluation; they must be considered simultaneously for these purposes. Both GGE biplot analysis and AMMI analysis combine rather than separate G and GE in mega-environment analysis and genotype evaluation; AMMI graphs for these purposes are also "GGE" graphs.

3. The which-won-where view of the GGE biplot is superior to the AMMI1 graph for mega-environment analysis in that it explains more G+GE, it is easier to construct, and it is easier to visualize the which-won-where patterns, especially for large GED sets.

4. The mean vs. stability view of the GGE biplot is superior to the AMMI1 biplot for genotype evaluation because it explains more G+GE, it has the same units on both axes, and it has an objective shape that inherently results from the data and the SVP method (if the axes are drawn to scale as required for correct biplot interpretation), whereby it shows the relative importance of G vs. GE in the data. Furthermore, the GGE biplot has the inner-product property of a biplot; it shows not only the mean performance and stability of each genotype, but also the relative performance of each genotype in each environment.

5. The discriminating power vs. representativeness view of the GGE biplot is an effective tool for test-environment evaluation, which can lead to the identification of a minimum set of discriminating and representative test environments. Test-environment evaluation has not been a research topic in AMMI analysis.

6. The G and GE are first of all mathematical definitions, and moreover, there is little evidence that G and GE are controlled by distinct genes and thereby can be subjected to selection separately.

7. The G and GE are specific to the environments in which they are estimated, and G and GE are interchangeable, depending on the scope of the environments. This understanding is the basis and justification for mega-environment analysis and GE analysis.

8. While G can be regarded as representing wide adaptation, it is only as wide as the range of the test environments allows; specific adaptation is determined by both G and GE rather than by GE alone.

9. Model diagnosis for each dataset is useful, but accuracy gain from model diagnosis should not be overstated.

10. A biplot should be companioned with the following specifications for its correct interpretation: (i) how the data are transformed, centered, and scaled (standardized), (ii) what is the goodness of fit of the biplot, and (iii) how the singular values are partitioned. In addition, the biplot axes must be drawn to scale for correct interpretation.

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