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GGE biplot analysis of genotype × environment interaction in wheat-barley disomic addition lines

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Abstract

Identification of the genetic architecture of phenotypic stability and management of adaptational genes are prerequisites for improvement of plant adaptation. To locate the genes controlling adaptation in barley, wheat-barley disomic addition lines were used in a randomized complete block design with three replications under rainfed and irrigated conditions for three consecutive cropping seasons (2009-2011). The GGE [genotype main effect (G) and genotype by environment interaction (GE)] biplot graphical tool was applied to analyze multi-environment trials (MET) data. Combined analysis of variance showed that the GE interaction effect accounted for 57.3% of total variation, indicating that the GE interaction is more complex. The first two principal components (PC1 and PC2) were used to display a two-dimensional GGE biplot. Thus, genotypic PC1 scores >0 classified the high yielding genotypes while PC1 scores <0 identified low yielding genotypes. Unlike genotypic PC1, genotypic PC2 scores near zero exhibited stable genotypes whereas large PC2 scores discriminated the unstable ones. The GGE biplot analysis was useful in identifying stable genotypes with high yield performance. Disomic addition line (DAL) H7, was characterized as genotype with the highest mean yield and low stability. In contrast, DAL H2, was identified as the best genotype in integrating mean yield with the highest stability performance. It was concluded that most of the genes controlling yield and yield stability in barley are located on chromosome H2.

Keywords: GGE biplot**,** multi-environment trials, stability, wheat-barley disomic addition lines.
Abbreviations: ANOVA - analysis of variance; ATC- average tester coordinate; CS - chinese spring; DALs - disomic addition lines; EI1- irrigated environment1; EI2- irrigated environment2; EI3- irrigated environment 3; ER1- rainfed environment1; ER2- rainfed environment2; ER3- rainfed environment3; GEI- genotype by environment interaction; GGE-genotype main effect (G) and genotype by environment interaction (GE); MET- multi-environment trials; PC- principal component; TSS- total sum of squares

Introduction

Multi-environment trials (MET) are conducted to evaluate yield stability performance of genetic materials under varying environmental conditions (Delacy et al., 1996; Yan et al., 2000; Yan and Rajcan, 2002). A genotype grown in different environments will frequently show significant fluctuations in yield performance. These changes are influenced by the different environmental conditions and are referred to as genotype-by-environment (GE) interaction (Allard and Bradshow, 1964). However, GE interaction reduces the genetic progress in plant breeding programs through minimizing the association between phenotypic and genotypic values (Comstock and Moll, 1963). Hence, GE interaction must be either exploited by selecting superior genotype for each specific target environment or avoided by selecting widely adapted and stable genotype across wide range of environments (Ceccarelli, 1989). Numerous methods such as regression coefficient (Finlay and Wilkinson, 1963), sum of squared deviations from regression (Eberhart and Russel, 1966), stability variance (Shukla, 1972), coefficient of determination (Pinthus, 1973), coefficient of variability (Francis and Kanneberg, 1978) and additive main effects and multiplicative interaction (AMMI) (Gauch and Zobel, 1988; Zobel et al., 1988; Gauch 1992; 2006) have been commonly used to analyze MET data to reveal patterns of GE interaction. Yan et al. (2000) proposed another methodology known as GGE-biplot for graphical display of GE interaction pattern of MET data with many advantages. GGE biplot analysis considers both genotype (G) and GE interaction effects and graphically displays GE interaction in a two way table (Yan et al., 2000). GGE biplot is an effective method based on principal component analysis (PCA) to fully explore MET data. It allows visual examination of the relationships among the test environments, genotypes and the GE interactions. It is an effective tool for: (i) mega-environment analysis (e.g. "which-won-where" pattern), where by specific genotypes can be recommended to specific mega-environments (Yan and Kang, 2003; Yan and Tinker, 2006), (ii) genotype evaluation (the mean performance and stability), and (iii) environmental evaluation (the power to discriminate among genotypes in target environments) (Ding et al., 2007). It has been proposed that GGE biplot analysis was a useful method for the analysis of GE interactions (Butron et al., 2004; Fan et al., 2007; Laffont et al., 2007; Yan and Kang, 2003; Samonte et al., 2005) and had been exploited in the variety evaluation of wheat (Yan and Hunt 2001; Yan et al., 2000), Maize (Fan et al., 2007) and soybean (Yan and Rajcan, 2002). Irrespective of how a stability

parameter is measured, one of the most critical question is whether it is genetic? If the characteristic measured by the parameter is non- genetic, it is not heritable and thus selection for such a parameter is fruitless (Lin and Binns, 1994; Jalata et al., 2011). Various authors have proved that stability indices are genetic and hence heritable (Lin and Binns, 1988a; Lin and Binns, 1988b; Lin and Binns, 1991; Farshadfar et al., 1999).

If stability is heritable, the next step in the genetic analysis is identification of the chromosomal location of the genes controlling the character (Farshadfar et al., 2011). Therefore to understand the genetics of continuous variation, it is necessary to identify the chromosomal location of the genes controlling quantitative attributes such as yield and yield stability (Eskridge et al., 2000). Various techniques (biometrical, cytogenetic and molecular) have been used to locate the genes monitoring quantitative traits among which cytogenetic methods (monosomic, disomic, substitution and disomic addition analysis) have been widely used. Because of the complex nature of phenotypic stability, very little information is available on the chromosomal location of the genes conditioning adaptation (Morgan, 1991; Koszegi et al., 1996; Farshadfar and Sutka, 2003). Disomic addition lines in which a single pair of chromosomes from related species is added to the full chromosome complement of the recipient, can be used to indentify chromosomes carrying the genes controlling adaptation and phenotypic stability and form the starting point for gene transfer and genetic improvement of genotypic stability (Ellis et al., 2000; Farshadfar et al., 2008). Wheat-barley disomic addition lines have been used to evaluate gene expression and physical mapping of barley (Cho et al., 2006). Using wheat-barley chromosome addition lines, isozymes and DNA markers have been physically mapped to chromosomes and chromosome arms (Islam and Shepherd, 1990; Garvin et al., 1998). Thus, the main objectives of the present investigation were to (i) evaluate the stability performance of seven wheat-barley disomic addition lines (DALs) under different growing conditions using GGE biplot methodology, (ii) evaluate the yield performance of each genotype in relation to ideal genotype and (iii) examine the relationship among test environments in genotype discrimination.

Results and discussion

Combined analysis of variance

The results of combined-ANOVA for grain yield data indicated that the differences among all sources of variation were highly significant (P<0.01) (Table 1). The environment (E) effect was accounted for 21.7 % of total sum of squares (TSS). The GE was accounted for 55.3% of TSS and was greater about four times than the G effect. The large GE interaction, relative to G effect, in this study suggests the possible existence of different mega-environments with different top-yielding genotypes (Yan and Kang, 2003). This result revealed that there was a differential yield performance among disomic addition lines across testing environments due to the presence of GE interaction. The presence of GE interaction complicates the selection process as GE interaction reduces the usefulness of genotypes by confounding their yield performance through minimizing the association between genotypic and phenotypic values (Comstock and Moll, 1963). It is commonly reported that MET data may constitute a mixture of cross over and non-cross over types of GE interaction, the former indicate the change in yield ranking of genotypes across environments and the later term shows constant yield rankings of genotypes across environment (Yan and Hunt, 2001; Matus-Cadiz et al., 2003).

Polygon view of GGE biplot analysis of MET data

The polygon view of a biplot is the best way to visualize the interaction patterns between genotypes and environments (Yan and Kang, 2003) to show the presence or absence of cross over GE interaction which is helpful in estimating the possible existence of different mega environments (Gauch and Zobel, 1997; Yan and Rajcan, 2002; Yan and Tinker, 2006). Visualization of the "which won where" pattern of MET data is necessary for studying the possible existence of different mega environments in the target environment (Gauch and Zobel, 1997; Yan et al., 2000). Fig. 1 represents a polygon view of wheat-barley disomic addition lines MET data in this investigation. In this biplot, a polygon was formed by connecting the vertex genotypes with straight lines and the rest of the genotypes placed within the polygon. The partitioning of GE interaction through GGE biplot analysis showed that PC1 and PC2 accounted for 39.1% and 37.7.9% of GGE sum of squares, respectively, explaining a total of 76.8% variation. The vertex genotypes in this study were H7, H2, H3, H5, H1 and CS. These genotypes were the best or the poorest genotypes in some or all of the environments because they were farthest from the origin of the biplot (Yan and Kang, 2003). From the polygon view of biplot analysis of MET data in three years, the genotypes fell in four sections and the test environments fell in three sections. The first section contains the test environments EI2 (irrigated environment 2), ER2 (rainfed environment 2) and ER3 (rainfed environment 3) which had the genotype H7 as the winner; the second section contains the environments EI1 (irrigated environment 1) and ER1 (rainfed environment 1) with H3 as the best yielder. The test environment EI3 irrigated environment 3) was fallen in a separate section without any yielder. The vertex genotype CS, H1 and H5 were not the top-yielding genotypes in any environment.

Mean yield and stability performance of genotypes

The ranking of seven wheat-barley DALs and the two parents based on their mean yield and stability performance are shown in Fig. 2. The line passing through the biplot origin is called the average tester coordinate (ATC), which is defined by the average PC1 and PC2 scores of all environments (Yan and Kang, 2003). More close to concentric circle indicates higher mean yield. The line which passes through the origin and is perpendicular to the ATC with double arrows represents the stability of genotypes. Either direction away from the biplot origin on this axis indicates greater GE interaction and reduced stability. For selection, the ideal genotypes are those with both high mean yield and high stability. In the biplot, they are close to the origin and have the shortest vector from the ATC. The DALs H2, followed by H4, can be considered as genotypes with both high yield and stability performance. The other genotypes on the right side of the line with double arrows have yield performance greater than mean yield and the genotypes on the left side of this line had yields less than mean yield. The genotypes with highest yielding performance but low stability were H7 and H3, whereas the genotypes with low yield and low stability were the both parents (CS, Betzes). The DALs of H4 (with relatively high yield) and H1 (with lowest yield) were similar in GE interaction. Breeders can also use Fig. 2 for selecting

Table 1. Analysis of variance for grain yield of seven disomic addition lines and two parents across six growing conditions.

Source	Df	MS	SST (%)
Genotype (G)	8	973.37**	15.6
Environment (E)	5	2699.73**	27.1
GE interaction	40	713.06**	57.3

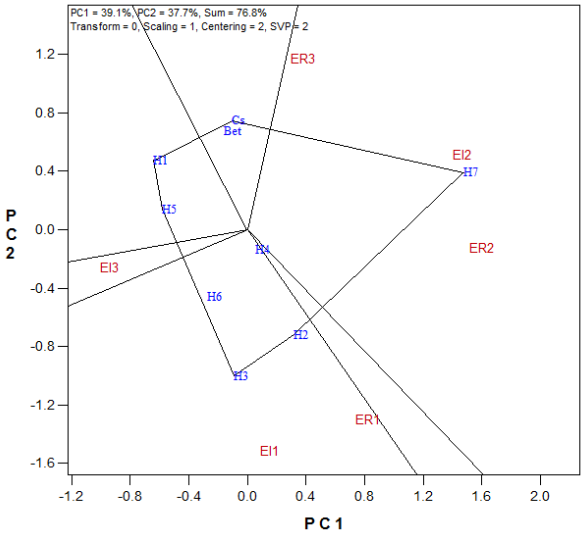

Fig 1. Polygon view of genotype- environment interaction for wheat-barley disomic addition lines over six test environments. The vertex genotype in each sector is the best genotype at environments whose markers fall into the respective sector. Environments within the same sector share the same winning genotype, and environments in different sectors have different winning genotypes. H1-H7 is the codes for the wheat-barley disomic addition lines and CS and Bet are the recipient and donor parents, respectively. ER1, ER2 and ER3 are environmental codes for the environments under rainfed conditions in 2009, 2010 and 2011 cropping seasons, respectively. EI1, EI2 and EI3 are environmental codes for the environments under irrigated conditions in 2009, 2010 and 2011 cropping seasons, respectively.

the genotypes with the best response to particular environments. For instance the DAL H7 had the highest yielding performance in environments EI2 and ER2; and the DALs H2 and H3 well performed in the environments ER1 and EI1, whereas H7 was poor in these two environments and the H2 and H3 had low yield performance in EI2 and ER2.

Evaluation of genotypes relative to an ideal genotype

An ideal genotype should have the highest mean performance and be absolutely stable (Yan and Kang, 2003). Such an ideal genotype is defined by having the greatest vector length of the high-yielding genotypes and with zero GE (or highest stability), as represented by the dot with an arrow pointing to it (Fig. 3). An ideal genotype, which is located at the center of the concentric circles in Fig. 3, is the one that has both high mean yield and high stability. Ideal genotype projection on the ATC x-axis is designed to be equal to the longest vector of all the genotypes. The ideal genotype is stable because its projection on the ATC y-axis is near zero. A genotype is more favorable if it is closer to the ideal genotype. The H2 was near to the ideal genotype. Ranking of other genotypes based on the ideal genotype was H7 > H4 > H3 > H6. In other words, the lower yielding genotypes (H5, H1, CS and Betzes) were unfavorable because they are far from the ideal genotype. The relative contributions of stability and grain yield to the identification of desirable genotype found in this study by the ideal genotype procedure of the GGE biplot are similar to those found in other crop stability studies (Samonte et al., 2005; Fan et al., 2007).

Relationship among test environments

Fig. 4 provides the summary of the interrelationships among the test environments. The lines that connect the biplot origin and the markers for the environments are called environment vectors. The angle between the vectors of two environments is related to the correlation coefficient between them. The cosine of the angle between the vectors of two environments approximates the correlation coefficient between them (Kroonenberg, 1995; Yan, 2002). Acute angles indicate a positive correlation, obtuse angles a negative correlation and right angles no correlation (Yan and Kang, 2003). A short vector may indicate that the test environment is not related to other environments. Based on the angles between environment vectors, the ER1 and EI1 (corresponding to rainfed and irrigated conditions in 2009 cropping season, respectively) tend to separated in a same group. Similarly, the two environments of ER2 and EI2 (corresponding to rainfed and irrigated conditions in 2010 cropping season, respectively) were highly correlated and were differed from the environments belonged to 2009 cropping season in genotype discrimination. The environments ER3 and EI3 which represent for rainfed and irrigated conditions in 2011 cropping seasons, respectively, made an obtuse angle with each other, which indicates a negative correlation between the response of genotypes to rainfed and irrigated conditions in 2011 cropping season. According to Fig. 4, no positive relationship was found between the years which the trials conducted, showing that the response of genotypes in one year either independent from other years or negatively associated.

Ranking of genotypes relative to highest yielding environment

Fig. 5 illustrates the graphic comparison of the relative performance of all genotypes relative to the environment EI1 with the highest yielding production. A line was drawn that passed through the biplot's origin and the EI1 marker to make an EI1-axis, and then a line was perpendicularly drawn from each genotype toward the EI1-axis. This line (EI1-axis) is called the axis for this environment (Yan and Tinker, 2006) and along it is the ranking of genotypes. The genotypes were ranked on the basis of their projections onto the EI1-axis, with rank increasing in the direction toward the positive end (Yan et al.,2000). Thus, Fig. 5 shows ranks of genotypes based on their yield performance in EI1. From the graph, genotypes ranging from H3 to H4 on the right side of the perpendicular line to the axis had higher than the average yield in this environment, while genotype H5 to CS showed lower yield that average yield performance.

Ranking test environments relative to the highest yielding genotype

Fig. 6 shows ranking of test environments in relative to the performance of genotype H7. To study the specific adaptation of a genotype, a line is drawn that passes through the biplot origin and the genotype. On the axis, genotype (H7)

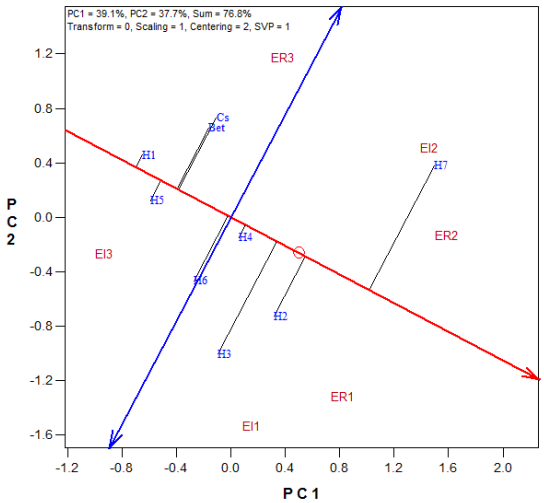

Fig 2. GGE biplot showing the ranking of genotypes for both yield and stability performance over environments. The line passing through the biplot origin is called the average environment coordinate (AEC). More close to concentric circle indicates higher mean yield. The line which passes through the origin and is perpendicular to the AEC with double arrows represents the stability of genotypes. Either direction away from the biplot origin, on this axis, indicates greater GE interaction and reduced stability. H1-H7 is the codes for the wheat-barley disomic addition lines and CS and Bet are the recipient and donor parents, respectively. ER1, ER2 and ER3 are environmental codes for the environments under rainfed conditions in 2009, 2010 and 2011 cropping seasons, respectively. EI1, EI2 and EI3 are environmental codes for the environments under irrigated conditions in 2009, 2010 and 2011 cropping seasons, respectively.

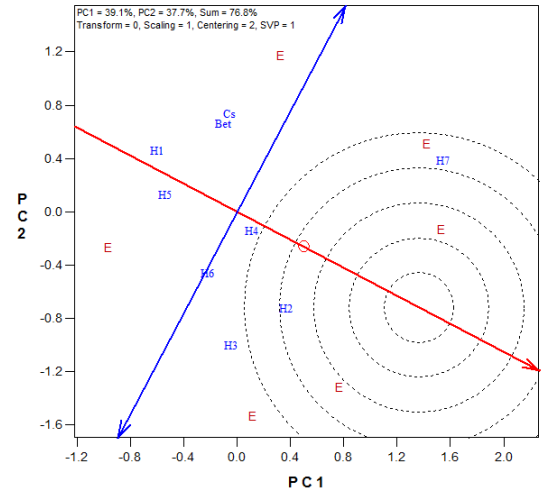

Fig 3. Ranking of genotypes relative to an ideal genotype. The ideal genotype can be used as a reference for genotype evaluation. Thus, using the ideal genotype as the center, concentric circles were drawn to help visualize the distance between each genotype and the ideal genotype. H1-H7 is the codes for the wheat-barley disomic addition lines and CS and Bet are the recipient and donor parents, respectively.

and environments are ranked along it (Yan et al., 2000). Thus, the graph indicates that H7 had higher than the average in four (EI2 followed by ER2, ER3, ER1) out of six environments, but had low yield performance in EI1 and EI3. Among this, it performed best in EI2 and ER2 environments than the other remaining environments.

Materials and methods

Plant genetic materials

In this study, seven wheat-barley disomic addition lines (H1 to H7) along with two parents: a bread wheat cultivar (*Tritium aestivum* cv. Chinese Spring) as recipient and a barley cultivar (*Hordeum vulgar* cv. Betzes) as donor parents were studied during 2009-11 cropping seasons under both rainfed and supplemental irrigation (two irrigations with 30 mm for each irrigation applied at flowering and grain-filling stages) conditions at the experimental farm of college of agriculture, Razi University, Kermanshah, Iran (47°20′ N latitude, 34°20′E longitude and 1351 m altitude). The genotypes were sown in a randomized complete block design with three replications. Each plot consisted of 3 rows with 1 m in length and 20-cm row spacing.

Statistical analysis

The grain yield data were subjected to combined analysis of variance (ANOVA) to determine the effects of environment (E), genotype (G), and their interactions. The data were graphically analyzed for interpreting GE interaction using the GGEbiplot software (Yan, 2001). GGE biplot methodology, which is composed of two concepts, the biplot concept (Gabriel, 1971) and the GGE concept (Yan et al., 2000), was used to visually analyze the wheat-barley disomic addition lines MET data. This methodology uses a biplot to show the factors (G and GE) that are important in genotype evaluation and that are also the sources of variation in GE interaction analysis of MET data (Yan, 2001). The graphs generated based on (i) "which-won-where" pattern, (ii) ranking of genotypes on the basis of yield and stability, (iii) comparison of genotypes to an ideal genotype, (iv) ranking of test environment relative to the highest yielding genotype, (v) ranking of genotypes relative to the test environment with highest yielding performance and (vi) relationships between testing environments based on the angles between the vectors of the environments.

Conclusion

The results indicated that yield performance of wheat-barley DALs were highly influenced by GE interaction effect followed by the environment and genotype with the least effects, showing that the GE interaction pattern is complex. The magnitude of GE interaction effect was about four times than that of genotype effect. The DALs showed crossover GE interactions across environments and among genotypes tested, there were desirable genotypes in terms of high mean yield (i.e, H7). The GGE biplot analysis allowed a meaningful and useful summary of GE interaction data and assisted in examining the natural relationships and variations in genotype performance across test environments. According to GGE biplot, the DAL H7, which carrying the chromosome number 7 of barley, can be characterized as genotype with the highest mean yield production and low in stability.

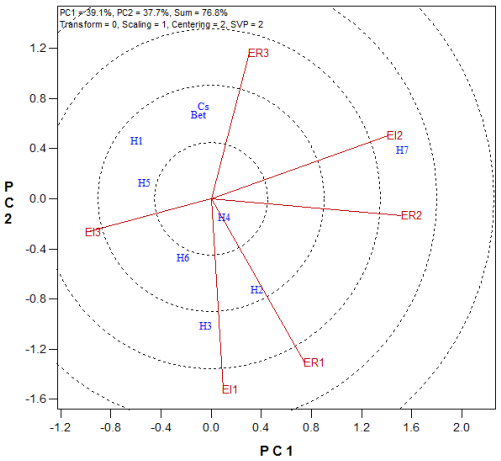

Fig 4. GGE biplot which shows the relationships among test environments. The correlation coefficient between any two environments is approximated by the cosine of the angle between their vectors. Acute angles indicates a positive correlation, obtuse angles a negative correlation and right angles no correlation. H1-H7 is the codes for the wheat-barley disomic addition lines and CS and Bet are the recipient and donor parents, respectively. ER1, ER2 and ER3 are environmental codes for the environments under rainfed conditions in 2009, 2010 and 2011 cropping seasons, respectively. EI1, EI2 and EI3 are environmental codes for the environments under irrigated conditions in 2009, 2010 and 2011 cropping seasons, respectively.

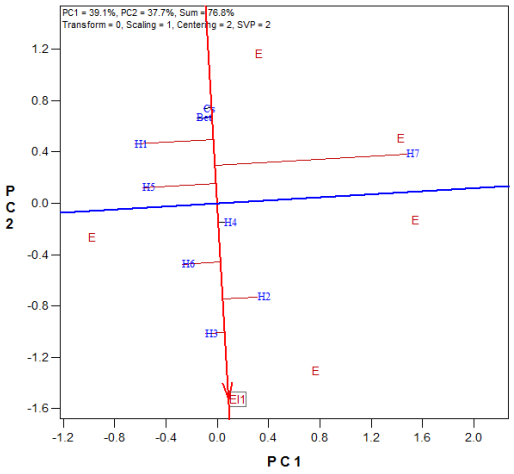

Fig 5. Comparison relative performance of different genotypes in a specific environment (EI1) with the highest yielding performance. A line was drawn that passed through the biplot's origin and the MI7 marker to make a MI7-axis, and then an another line was perpendicularly drawn from each genotype toward the MI7-axis. The genotypes are ranked on the basis of their projections onto the EI1-axis, with rank increasing in the direction toward the positive end. H1-H7 is the codes for the wheat-barley disomic addition lines and CS and Bet are the recipient and donor parents, respectively. ER1, ER2 and ER3 are environmental codes for the environments under rainfed conditions in 2009, 2010 and 2011 cropping seasons, respectively. EI1, EI2 and EI3 are environmental codes for the environments under irrigated conditions in 2009, 2010 and 2011 cropping seasons, respectively.

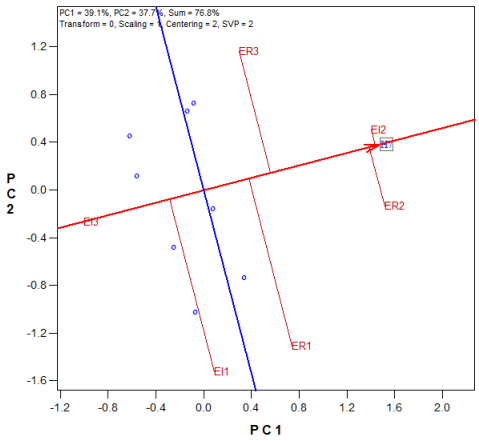

Fig 6. Ranking the test environments relative to the highest yielding genotype (H7). It compares the relative performance of the highest yielding DAL (H7) at different environments. This is done by first drawing a straight line passing the biplot origin and the marker of genotype H7, then drawing perpendiculars to this straight line from the environment. An environment's rank in producing H7 grain yield was based on its projection onto the H7 axis, with rank increasing in the direction toward the H7 marker. ER1, ER2 and ER3 are environmental codes for the environments under rainfed conditions in 2009, 2010 and 2011 cropping seasons, respectively. EI1, EI2 and EI3 are environmental codes for the environments under irrigated conditions in 2009, 2010 and 2011 cropping seasons, respectively.

The DAL H2, which carrying the chromosome number 2 of barley, was the best in integrating mean yield with the highest stability performance. Therefore, most of the genes controlling yield and yield stability are located on chromosomes H7 and H2 in barley, respectively.

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