

Estimation of Combining Ability and Gene Action for Improvement Drought Tolerance in Bread Wheat (*Triticum aestivum* L.) Using GGE Biplot Techniques

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Abstract

Study of combining ability and gene action for drought tolerance in wheat were carried out using Genotype-by-Environment (GGE) biplot techniques. Eight-parental diallel crosses, excluding reciprocals, were grown in a randomized complete block design with three replications under two different water regimes (irrigated and rainfed) in the Agricultural Research Institute of Sararood, Kermanshah, Iran. Significant differences were found for yield potential (Y_p), stress yield (Y_s), stress tolerance index (STI), water use efficiency (WUE) and evapotranspiration efficiency (ETE). GGE biplot analysis showed that the parent A, A, A and B were the best general combiners with two additive genes (A_1 and A_2), for improvement of Y, STI, WUE and ETE under drought conditions, respectively. Parents A and C also exhibited positive GCA for all the studied traits. The crosses (A, D and H) \times (C, E, F and G), (A, C and F) \times (B, E, H and G), (A, C and E) \times (B, G, H and F) and (A, C, G and D) \times (F, B, E and H) for Y, STI, WUE and ETE were identified as heterotic groups with different dominant tolerance genes (D_1 and D_2), respectively. The polygon view of the biplot indicated that combining of A \times G and A \times C produced the best drought tolerance hybrids for all the traits through integrated the four tolerance genes (A_1 , A_2 , D_1 , and D_2).

Keywords: bread wheat, drought tolerance, combining ability, gene action, GGE biplot

1. Introduction

Drought is one of the major environmental challenges in crop productions to worldwide today, and recent global climate change has made this situation more serious. (Blum, 1985; Geravandi et al., 2011). Wheat (*Triticum aestivum* L.) is a staple food for more than 35% of the world population and it is also the first grain crop in Iran (Golestani & Assad, 1998; Farshadfar et al., 2000). Wheat is mainly grown on rainfed land about 35% of the area of developing countries consists of semi-arid environments in which available moisture constitutes a primary constrain on wheat production, so wheat often experiences drought stress conditions during its growth cycle (Farshadfar et al., 2001; Bayoumi et al., 2008). Thus, improvement of wheat production for drought tolerance is a major objective in plant breeding programs for rainfed conditions (Farshadfar et al., 2011a). Wheat breeding programs mostly involve hybridization, evaluation and selection of desirable genotypes. In addition, the assessment of combining ability and determine gene action are elementary tools for selection of ideal genotypes (Jensen, 1970; Blum, 1985). The concept of combining ability was introduced by Sprague and Tatum (1942). Combining ability has a prime importance in plant breeding since it provides information for the selection of parents and also provides information about of involved gene action. The knowledge of genetic structure and mode of inheritance of different characters helps breeder to select suitable breeding methodology for the development of drought tolerance genotypes (Kiani et al., 2007). Plant breeding programs use different mating systems to study combining ability of quantitative traits. Diallel analysis has been often applied in genetic research to evaluate combining ability, gene action and heterotic responses of agronomically more important traits within a set of genotypes (Baker, 1978; Farshadfar et al., 2011b). There are several methods that can be used for diallel analysis. The mostly used one is the Griffing methods (1959), which partitions the total variance to GCA variance of parents and SCA variance of crosses. Yan and Hunt (2002) suggested the application of GGE biplot techniques for graphical analysis and presentation of diallel cross. Although the GGE biplot methodology was developed for multi-environment trial (MET) data analysis (Yan, 2002), but they stated that it

should be applicable to all types of two-way data that assume an entry-by-tester data structure. In MET data, genotypes are entries and environments are testers. In diallel data, each genotype is both an entry and a tester (Yan, 2001). The GGE biplot technique has also been used for combining ability analysis of bread wheat (Bertoia et al., 2006). The objective of this investigation was to estimation of combining ability and gene action for improvement drought tolerance using GGE biplot methods of diallel analysis in bread wheat genotypes.

2. Materials and Methods

2.1 Plant Material and Experimental Conditions

The plant material consisted of eight-parent diallel cross excluding reciprocals, was developed in the Agricultural Research Institute of Sararood, Kermanshah, Iran during year 2004 to 2005 (47° 20' N latitude, 34° 20' E longitude and 1351.6 m altitudes). Climate in this region is classified as semi-arid with mean rainfall of 478 mm. Minimum and maximum temperature in the research station was -27 and 44°C, respectively. The cultivars used were Plainsman (A), Regina (B), Capelle desprez (C), Chinese spring (D), Shakha (E), Saberbeg (F), Karchia (G) and Kobomugi (H). The plant genetic materials (parents and F₁s) were grown in a randomized complete block design with three replications under irrigated and rainfed conditions. Single seeds were sown in 3 m rows and at 3 × 15 cm plant to plant and row to row distances, respectively. Data were recorded from five competitive plants from each replication on the following characters.

2.2 Grain Yield and Stress Tolerance Index (STI)

Grain yield was recorded under normal (Y_p) and stress (Y_s) conditions at physiological maturity stage. The physiological maturity stage was considered when 90% of seed changed color from green to yellowish and stopped photosynthetic activity. Stress tolerance index (STI) was calculated using the formula suggested by Fernandez (1992) as:

$$STI = \frac{(Y_s \times Y_p)}{(\bar{Y}_p)^2}$$

Where, Y_s, Y_p and \bar{Y}_p represent yield under stress condition, yield under non-stress and overall mean of the entries in non-stress condition, respectively.

2.3 Water Use Efficiency (WUE) and Evapotranspiration Efficiency (ETE)

According to total consumed water through wheat life circle, WUE was calculated by referring to Ehdaie and Waines (1993). Three seeds from each line were sown in the greenhouse, two of which were eliminated 10 days after germination. To calculate the amount of evaporation, one empty pot was used in each replication. The pots were irrigated with the measured amount of water. The run-off water in each pot was subtracted from the water applied to each pot. After 39 days, the dry matter (after drying at 70°C for 24 h) and the amount of water applied were used to calculate WUE using the following formula:

$$WUE = \frac{GY}{TWU}$$

$$ETE = \frac{TDM}{TWU}$$

Where, TDM = total dry mater; TWU = total water used and GY= grain yield.

2.4 Statistical and Genetic Analyses

Statistical analysis was performed by SPSS ver. 16 (analysis of variance; ANOVA). The GGE biplot software was used to generate biplot figures for drought tolerance indicators and grain yield (Yan, 2001). Each parent was considered both an entry and a tester. A two-way matrix of entries and testers was generated from the mean values for hybrids, where rows were entries and columns were testers. The biplot model is as follows:

$$\hat{Y}_{ij} - \mu - \beta_j = \lambda_1 \xi_{i1} \eta_{j1} + \lambda_2 \xi_{i2} \eta_{j2} + \varepsilon_{ij}$$

Where \hat{Y}_{ij} is genotypic values of the combination between entry i and tester j; μ is the grand mean; β_j is the mean of all combinations involving tester j; λ_1 and λ_2 are the singular values for PC₁ and PC₂, respectively; ξ_{i1} and ξ_{i2} are the PC₁ and PC₂ eigenvectors, respectively, for entry i; η_{j1} and η_{j2} are the PC₁ and PC₂ eigenvectors, respectively, for tester j; and ε_{ij} is the residual of the model associated with the combination of entry i and tester j. When $i \neq j$, the combination is a hybrid.

3. Results and Discussion

The results of analysis of variance (ANOVA) showed significant differences among parents and hybrids for Y_p , Y_s , STI, WUE and ETE. Presence of genotypic variability and different level of responses of genotypes to water deficit were indicated by the results which could help to identify possible drought tolerant genotypes (Table 1). According to the results suggested that significant heterosis among parents and hybrids (Rastogi et al., 2010). Breeding for drought tolerance by selecting solely for grain yield may not be successful, because the heritability of grain yield under drought conditions is low (Golestani & Assad, 1998; Farshadfar et al., 2008b; Geravandi et al., 2011). Several physiological criteria have been proposed for selecting resistant genotypes. RWC, ETE and WUE were shown as screening techniques for discrimination of drought tolerance genotypes in bread wheat (Eric et al., 2005; Farshadfar et al., 2011c). In fact the development of any plant breeding program is dependent upon the existence of genetic variability, the efficiency of selection and expression of heterosis in the plant population (Jensen, 1970; Malla et al., 2010).

Table 1. Analysis of variance for the characters under investigation

S.O.V	df	Mean squares				
		Y_p	Y_s	STI	ETE	WUE
Replications	2	24.63**	0.47 ^{NS}	0.02 ^{NS}	0.01 ^{NS}	0.01 ^{NS}
Genotypes	35	21.38**	1.86**	0.08**	0.32**	0.03**
Error	70	2.10	0.71	0.02	0.05	0.01
CV %	-	15.2	12.3	12.1	10.31	12.33

*, ** Significant at the 0.05 and 0.01 probability levels, respectively; NS: non-significant.

3.1 Grain Yield

The biplot for grain yield explained 65.3% (38.2 and 27.1% by PC_1 and PC_2 , respectively) of the total variation, which, in conventional analyses (Figure 1). The general combining ability (GCA) and specific combining ability (SCA) effects of the crosses (entries) were examined by drawing an average tester coordinate (ATC) view for entries (Figure 1a). The small circle represents an average tester, which is defined by the average PC_1 and PC_2 values of all testers. The line passing through the biplot origin and the average tester, with an arrow pointing to the average tester, is called the ATC abscissa. The GCA effects of the entries are approximated by their forecasted on to the ATC abscissa (Yan, 2001). As seen in Figure 1a, entries a, c, e and h were on the positive side of the ATC abscissa suggesting that they had positive GCA effects and exhibited higher drought tolerance hybrids while entries b, d, g and f had negative GCA effects. Based on the distance between entry and ATC abscissa, entry a had the highest GCA effects and entries h and b had the lowest GCA effects (Malla et al., 2010). A higher GCA rate indicates that additive gene action was important and parents differed in the level of the tolerance to drought they contributed to the progeny (Butorac et al., 2004). The GCA effects of the entries are in the order of: $a > c \approx e > h > d > f > g \approx b$. According to Yan and Kang (2003), to explain the differences in GCA can be assumed that entries h and d (Group 2) had an additive gene for drought tolerance (A_1) relative to entries f, g and b (Group 1), also entries a, c and e (Group 3) had an additional gene (A_2) relative to Group 2. Baker (1978) reported that, when combining ability ratio approaches unity, GCA alone can predict the performance of the parents. The biplot also displayed the SCA effects of the entries. The SCA effects of the entries were estimated based on the projection of the entries on the ATC ordinate (Yan, 2001). Testers F, H and A, had the highest projected on the ATC ordinate from the biplot origin, so they had large SCA effects compared to other testers (Figure 1a). Based on SCA, testers can be divided in two heterotic groups: testers C, E, F and G as one group and A, D and H as the other. Tester D falls between groups 1 and 2 and has a short vector. If it is assumed heterosis arises from the accumulation of different dominant genes, then two groups must have different dominant drought tolerance genes that are designated as D_1 and D_2 (Farshadfar et al., 2011c). These results clearly indicated heterosis in crosses (A, D and H) \times (C, E, F and G). The heterotic effect might be due to over dominance or epistatic effect of different dominant genes present in these parents (Farshadfar et al., 2008a; Khalil et al., 2010). The biplot (Figure 1b) shows the polygon which provided the best way to demonstrate the interaction patterns between entries and testers (Yan & Hunt, 2002). The biplot was divided into six sectors, with entries a, b, c, d, f and g as the vertex entries, and are referred to as sector a, sector b, sector c, sector d, sector f and sector g, respectively. The biplot indicated that entry a was the best mating partners for F and G. Since the

tester A was not in the sector a, all crosses between genotype A with F and G were heterotic (Rastogi et al., 2010). Entry d and b were the best mating with B and D respectively. Since tester D was not in sector d and tester b was not in the sector b, hybrid D × B exhibited higher tolerance than D × D and B × B (B and D pure lines). The biplot showed entry c produced best hybrids with tester C, A, E and H, since C was in the sector c, all crosses between genotype C with A, E and H were not heterotic. Thus, the combination C × C (Pure line C) is the best among all crosses involving C. The biplot indicated no tester fell in g and f sectors, suggesting that these entries produced the poorest hybrids with some or all of the testers (Bertoia et al., 2006). Therefore, the best combination for improved drought tolerance were: seven hybrids involving C × C, C × A, C × E, C × H, A × F, A × G and D × B. The hybrids between C with A and H were the best hybrids relative to drought tolerance because they each integrated the four tolerance genes (A₁, A₂, D₁, and D₂). Also the crosses C × C and C × E might be have the four drought tolerance genes (A₁, A₂ and D₂). In the Figure 1a, the concentric circles are drawn to identify the best tester for assessing GCA of parents with hypothesized ideal tester at the center (Yan and Kang, 2003). Clearly, tester E was the best tester in this data set, as it was very close to the ideal tester. Whereas, D was the poorest tester, as it is the least representative of all testers.

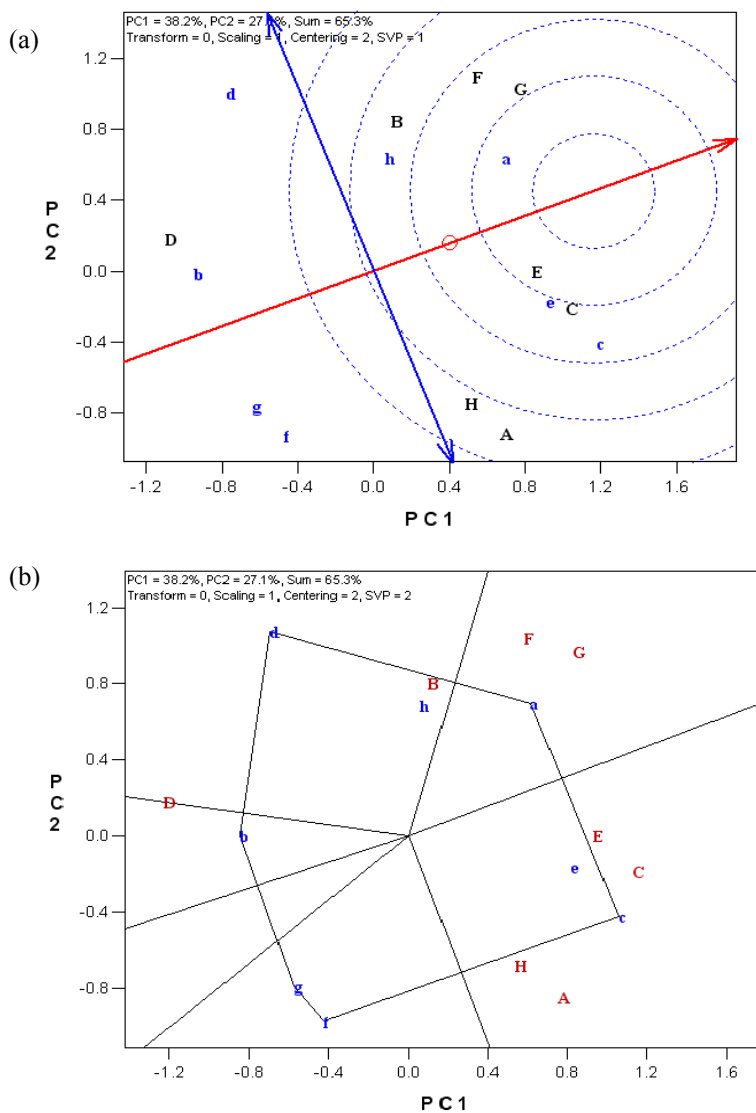
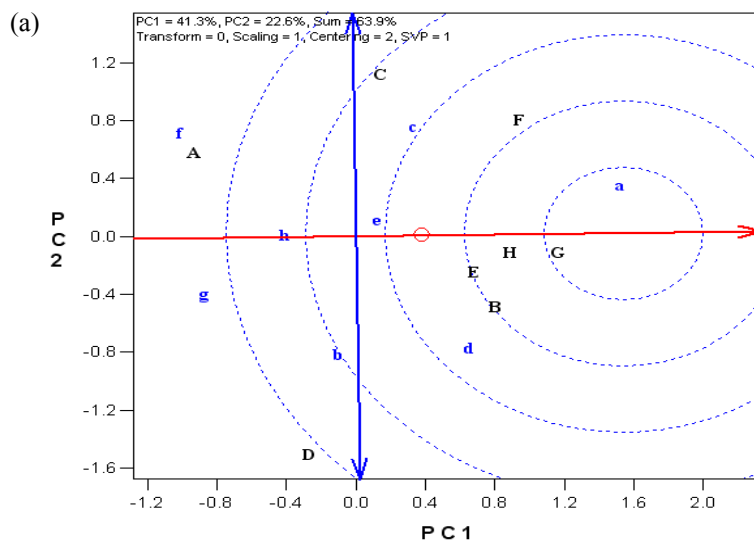


Figure 1. Biplot showing (a) average tester coordinate (ATC) view and (b) polygon view of eight parents for grain yield in rainfed condition. Uppercase letters are testers and lowercase letters are entries of eight parents. Parents are: Plainsman (A), Regina (B), Capelle desprez (C), Chinese spring (D), Shakha (E), Saberbeg (F), Karchia (G) and Kobomugi (H)

3.2 Stress Tolerance Index (STI)

Stress tolerance index (STI) suggested by Fernandez (1992) for identification of genotypes which produce high grain yield under both conditions. Currently, efforts are directed to access new and cheap reliable indices that can help in selection of drought tolerant genotypes (Geravandi et al., 2011). The first two principal components described 63.9% ($PC_1 = 41.3\%$ and $PC_2 = 22.6\%$) of the total variation for STI (Figure 2a). Base on the biplot, entry a has high GCA, b, g, h and f have low GCA and d, e and c have intermediate GCA. The ranking of entries to GCA effects were $a > d > c > e > b > h > g > f$. Farshadfar et al. (2000) reflected that the high GCA ratio and narrow sense heritability emphasizes the importance of additive gene action to drought tolerance. To illustrate differences in GCA can be hypothesized that entries d, c and e (Group 2) had an additive gene (A_1) for drought tolerance relative to entries b, h, g and f (Group 1), also entries a and d (Group 3) had an additional gene (A_2) relative to Group 2 (Figure 2a). The testers D, C, A and F have the greatest distance from the ATC ordinate, so they had large SCA effects compared to other testers (Figure 2a). The large SCA effects indicating the role of dominant gene action in their genetics; hence it may be necessary to resort to heterosis breeding (Butorac et al., 2004). The biplot clearly indicates heterosis in crosses (A, C and F) \times (B, E, H and G) with different dominant tolerance genes (D_1 and D_2) to produced tolerance hybrids. The polygon view of STI content showed six sectors, namely a, b, c, d, g and f (Figure 2b). The biplot indicated no tester fell in the d and g sectors, suggesting that, these entries were not the best mating partners with any of the genotypes (Malla et al., 2010). Moreover, this suggests that entry d and g produced the worst hybrids with some or all of the testers. The testers C, D and A fell in the c, b and f sector, respectively, indicating that entries c, b and f we the best crossing to produced tolerance hybrids with C, D and A. The results indicated the combination C \times C (Pure line C) is the best among all crosses involving C. In finally, entry a was the best mating partners for B, E, F, G and H. In the Figure 2a, tester G was the best tester in all, as it was very close to the ideal tester. Whereas, A was the weakest tester, also it is the least representative of all testers. Thus, the hybrids between A with G was the best hybrids relative to drought tolerance because they have complex the four tolerance genes (A_1 , A_2 , D_1 , and D_2). As well as, the hybrids between A with B, H, E and F have set of the three drought tolerant genes (A_1 , A_2 , and D_1). Since drought tolerance caused by the accumulation of these genes (Khalil et al., 2010), thus the crossing A \times B, A \times E, A \times F, A \times G, A \times H produced the best drought tolerance hybrids. Jensen (1970) reported that the crosses involving high \times low general combiners besides expressing favorable additive effects of high parent showed complementary gene action due to interaction between favorable genes contributed by the relevant parents.



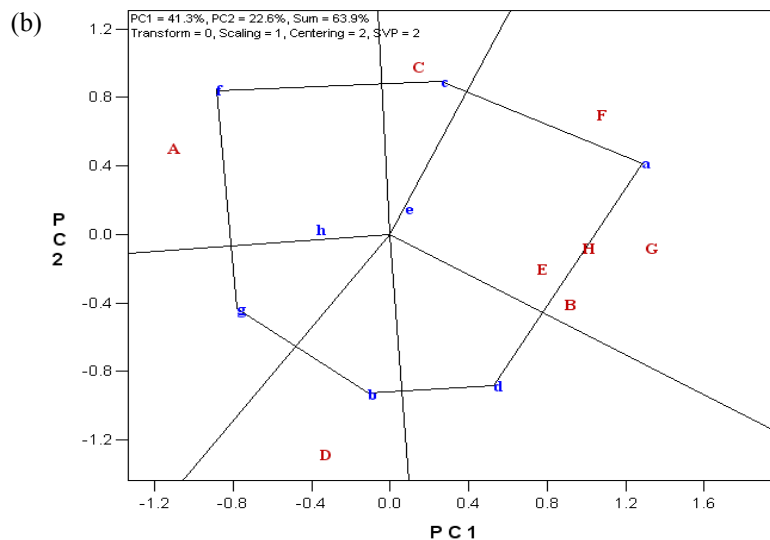


Figure 2. Biplot showing (a) average tester coordinate (ATC) view and (b) polygon view of eight parents for stress tolerance index (STI). Uppercase letters are testers and lowercase letters are entries of eight parents. Parents are: Plainsman (A), Regina (B), Capelle desprez (C), Chinese spring (D), Shakha (E), Saberbeg (F), Karchia (G) and Kobomugi (H)

3.3 Water Use Efficiency (WUE)

Water use efficiency (WUE) is a key factor that determining plant production under limited water supply. Also, it is often equated with drought resistance and the improvement of crop yield under stress (Blum, 1985; Ehdaie & Waines, 1993; Farshadfar & Sutka, 2002). The biplot for WUE explained 62.6% (37.5 and 25.1% by PC₁ and PC₂, respectively) of the total variation (Figure 3). Based on the biplot, entry a, c, e and h has high GCA, b, g and f have low GCA and d have intermediate GCA (Figure 3a). The orders of the entries based on GCA effects were: $a > h \approx c > e > d > b \approx g \approx f$. According to the results can be hypothesized that entry d (Group 2) had an additive gene (A_1) for drought tolerance relative to entries b, g and f (Group 1), also entries a, c, e and h (Group 3) had an additional gene (A_2) relative to Group 2 (Yan and Hunt, 2002). It is clear the success of any hybridization programme chiefly depends on general combining ability of parents used in crossing programme (Khalil et al., 2010). Testers A and F had the highest SCA effects due to their largest projections onto the ATC. Based on PC₂ axis, the tester seems fall into two groups: A, C and E in group 1 and B, G, H and F in group 2. Tester D falls between groups 1 and 2 and has a short vector. Groups 1 and 2 interacted positively to produce heterosis in terms of drought tolerance. They are two heterotic groups with different dominant tolerance genes (D_1 and D_2). These results clearly indicated heterosis in crosses (A, C and E) \times (B, G, H and F). Butorac et al. (2004) and Malla et al. (2010) demonstrated that the predominance of SCA can be easily detection of highly heterotic hybrids of economic importance. The biplot in Figure 3b was divided into six sectors, with entries c, g, b, d, h and a as the vertex. The polygon view demonstrated that entry c produced good hybrid combinations with testers C, E and A due to WUE indicators. In sector h, testers G, H and F were predicted to be the best mating partners for h, whereas the entry d was the best mating partners for D and B. Since H was in the sector h, all crosses between genotype h with H, G and F were not heterotic. Thus, the combination H \times H (Pure line H) is the best among all crosses involving H in produced drought tolerance hybrids (Rastogi et al., 2010). This condition was also honest for sectors c and d. Thus, the combination C \times C (Pure line C) and D \times D (Pure line D) was the best among all crosses involving C and D, respectively. The biplot indicated no tester fell in the, g and b sectors, suggesting that these entries produced the poorest hybrids with some or all of the testers. The best tester in this subset was parent G, as it is closest to the ideal tester represented by the center of the concentric circles (Figure 3a). Many reports have been related to WUE and production, and clearly explained the linear relationship between WUE and drought tolerance in wheat (Blum, 1985; Ehdaie and Waines, 1993; Farshadfar et al., 2011c). The best combination for drought tolerance based on the results of GCA and SCA were: six hybrids involving H \times H, H \times G, H \times F, C \times C, C \times A and C \times E. The hybrids between H with H, F and G have the three

tolerance genes (A_1 , A_2 and D_2). Thus, the crossing between C with C, A and E had set of the three drought tolerance genes (A_1 , A_2 , and D_1). The hybrids $H \times G$ was the best hybrid relative to drought tolerance because they each integrated four tolerance genes (A_1 , A_2 , D_1 , and D_2).

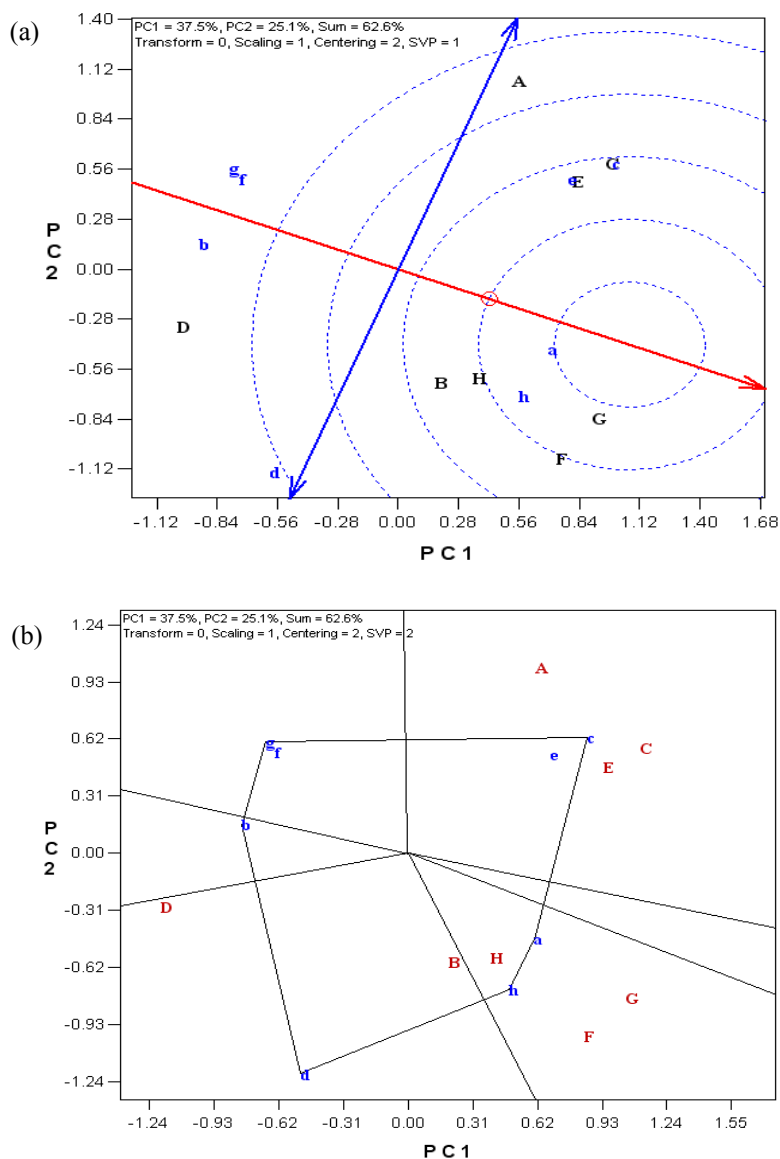


Figure 3. Biplot showing (a) average tester coordinate (ATC) view and (b) polygon view of eight parents for Water use efficiency (WUE) in rainfed condition. Uppercase letters are testers and lowercase letters are entries of eight parents. Parents are: Plainsman (A), Regina (B), Capelle desprez (C), Chinese spring (D), Shakha (E), Saberbeg (F), Karchia (G) and Kobomugi (H)

3.4 Evapotranspiration Efficiency (ETE)

The biplot explained 83.2% ($PC_1 = 61.9\%$ and $PC_2 = 21.3\%$) of the total variation for ETE (Figure 4). Based on ATC abscissa, entries b, c and a have high GCA, entry g has low GCA and d, e, f and h have intermediate GCA. Entry b had the highest GCA followed by $b > c > a > d > e > f > h > g$. To illustrate the differences in GCA can be assumed that entries d, e, f and h (Group 2) had an additive gene (A_1) for drought tolerance relative to entry g (Group 1), also entries b, c and a (Group 3) had an additional gene (A_2) relative to Group 2 (Figure 4a). The testers F and A have the greatest distance from the ATC ordinate, so they had large SCA effects compared to other entries (Figure 4a). Based on SCA, testers can be divided in two heterotic groups: testers A, C, G and D as

one group and F, B, E and H as the other. Groups 1 and 2 interacted positively to produce heterosis in terms of drought tolerance. They are two heterotic groups with different dominant tolerance genes (D_1 and D_2). These results clearly indicated the presence of heterosis in crosses (A, C, G and D) \times (F, B, E and H). Other studies also reported role of different genes effect in the heterosis of respective trait (Kaw and Khush, 1986; Farshadfar et al., 2008a; Khalil et al., 2010). Among the testers, D and H were at the center of the concentric ring, suggesting that it was the ideal parent. Selection of parents with high GCA effects increases the probability of getting heterotic hybrids in crop plants. According to Figure 4b, entries b, f, g and c defined a polygon that was divided into four sectors. Entry b was the best mating partners for D, E, G and H; entry f produced the best hybrid with testers A, B and C, finally entry f were the best mating with F. Thus, the combination F \times F (Pure line F) is the best among all crosses involving F. Since B was not in the sector b, all crosses between genotype B with D, E, G and H were heterotic. Based on that, all crosses between genotype G with A, B and C were heterotic. The biplot indicated no tester fell in the c sector, suggesting that entry c produced the weakest hybrids with some or all of the testers.

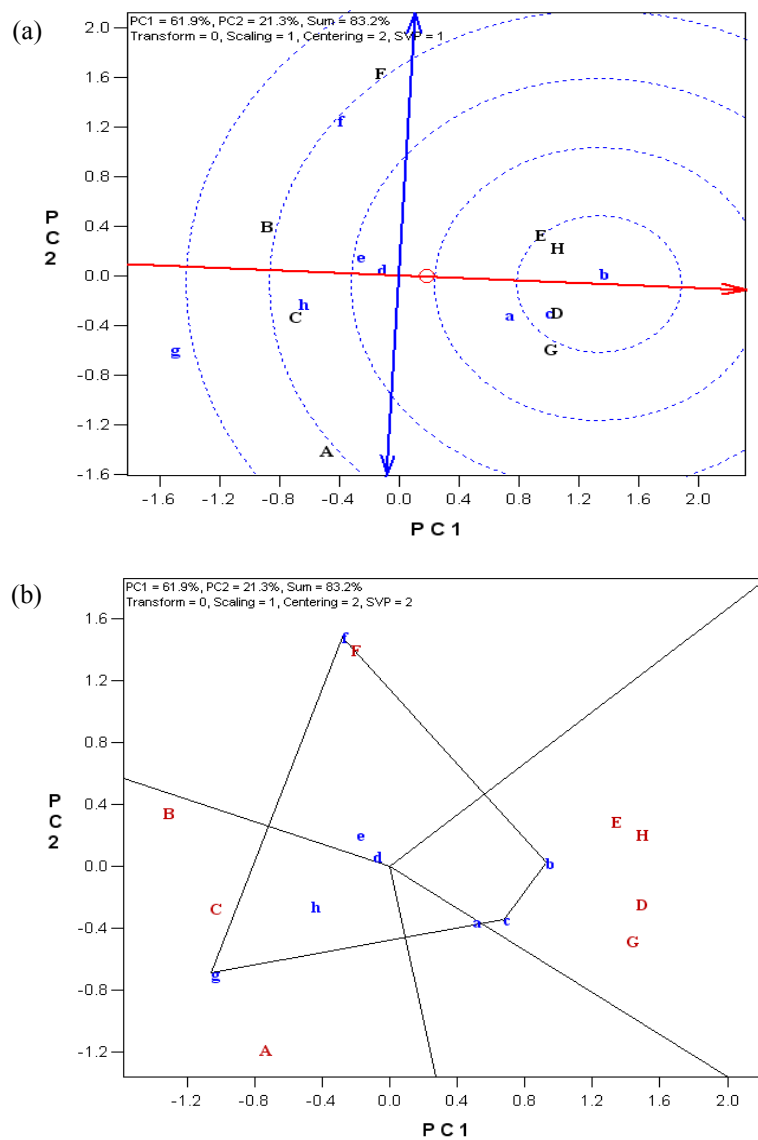


Figure 4. Biplot showing (a) average tester coordinate (ATC) view and (b) polygon view of eight parents for Evapotranspiration efficiency (ETE) in rainfed condition. Uppercase letters are testers and lowercase letters are entries of eight parents. Parents are: Plainsman (A), Regina (B), Capelle desprez (C), Chinese spring (D), Shakha (E), Saberbeg (F), Karchia (G) and Kobomugi (H)

4. Conclusion

In present study, significant differences were found for yield potential (Yp), stress yield (Ys), stress tolerance index (STI), water use efficiency (WUE) and evapotranspiration efficiency (ETE) indicating the presence of genetic variation and possible genetic analysis of these drought tolerance criteria. The result of biplot analysis showed that the Parent A, A, A and B were The best general combiners with positive effects, for improvement of Y, STI, WUE and ETE under drought conditions respectively, also parents A and C exhibited positive GCA for all traits. The high GCA ratio emphasizes the importance of additive gene action to drought tolerance. The crosses (A, D and H) × (C, E, F and G), (A, C and F) × (B, E, H and G), (A, C and E) × (B, G, H and F) and (A, C, G and D) × (F, B, E and H) for Y, STI, WUE and ETE were heterotic, respectively. The heterotic effect might be due to over dominance or epistatic effect of different dominant genes present in parents. The polygon view of the biplot indicated combining A × G and A × C produced the best drought tolerance hybrids for all the traits by integrated the four tolerance genes (A₁, A₂, D₁, and D₂).

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