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Chromosomal Localization of the Genes Controlling Adaptation in *Agropyron elongatum* Using a New AMMI-Based Simultaneous Selection Index of Yield and Yield Stability

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ABSTRACT

Identification of the genetic architecture of phenotypic stability and management of adaptational genes is a prerequisite for the improvement of adaptation. To locate the genes controlling yield and yield stability in a wild relative of wheat (*Agropyron elongatum*), disomic addition lines of *Agropyron* into the genetic background of Chinese Spring were used in a randomized complete block design with three replications for three years under two different conditions (rainfed and irrigated). Combined analysis of variance showed highly significant differences for genotypes, environments and genotype – environment (GE) interaction indicating variability between genotypes, environments and their effect in the GE interaction and possible localization of the genes monitoring yield and yield stability. The results of regression analysis displayed that linear GE interaction accounted for 41% of the variability in the GE interaction, while additive main effect and multiplicative interaction (AMMI) AMMI1 and AMMI2 accounted for 92.4% of GE interaction. Yield stability index (YSI) which incorporate AMMI stability value (ASV) and mean yield in a single non- parametric index indicated that most of the quantitative trait loci (QTLs) involved in controlling phenotypic stability and yield in *Agropyron* are located on the chromosome 7E.

Keywords: disomic addition lines, gene location, phenotypic stability, wild species, yield stability index

INTRODUCTION

The genotype (G) by environment (E) interaction is a major problem in the study of quantitative traits because it complicates the interpretation of genetic experiments and makes predictions difficult. Therefore, the first goal of plant breeders in a crop breeding program is the development of cultivars or genotypes which are stable or adapted to a wide range of diversified environments (Farshadfar and Sutka 2006; Abdulahi *et al*. 2009; Pimsaen *et al*. 2010).

The importance of G × E interactions in national cultivar evaluation and breeding programs have been demonstrated in almost all major crops (Mohammadi *et al*. 2010; Zali *et al*. 2011).

The genotype-environment interaction complicates the identification of superior genotypes and needs to be modeled and interpreted.

Models may be linear formulation such as joint regression (Finlay and Wilkinson 1963; Eberhart and Russell 1966), factorial regression (Abdullahi *et al*. 2009) or additive main effect and multiplicative interaction (AMMI) on multiple environment trials (MET) data (Hassnpanah 2011).

The AMMI model is a powerful multivariate method to multi-environmental trials. This technique also called FANOVA (factorial analysis of variance), incorporates both additive and multiplicative components into an integrated, powerful least square analysis (Mohammadi *et al.* 2007a; Pourdad and Mohammadi 2008; Farshadfar 2008). AMMI is essentially effective where the assumption of linearity of responses of genotypes to a change in environment is not fulfilled (Oliveira and Godoy 2006).

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 1991, 1994; Jalata *et al*. 2011). Various authors have proved that stability indices are genetic and hence heritable (Patanothai and Atkins 1974; Busch *et al*. 1976; Dhillon and Singh 1977; Lin and Binns 1988; Farshadfar *et al.* 1999).

Identification of the genetic architecture of phenotypic stability is a prerequisite for improvement of adaptation, but the studies conducted so for offer very little information on the genetics of stability, therefore, there is a need for approaches to focus more upon the genetic aspects, identification and management of adaptational genes (Morgan 1991; Koszegi *et al.* 1996; Farshadfar and Sutka 2003; Farshadfar 2008).

There are three methods for locating the genes controlling plant characters, namely: agronomic (using mathematical formulas to relate qualitative and quantitative characteristics), cytogenetics (using substitutions, monosomic and disomic addition lines) and molecular (using molecular markers) (Kearsey and Pooni 2004; Farshadfar 2010).

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 identify 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).

Riley and Kimber (1966) provided the first comprehensive review of the transfer of alien genetic variation into wheat. Islam and Shepherd (1991) and Jiang *et al.* (1994) listed the alien genes introduced into wheat. Much less research has been done on the transfer of alien chromosomes or genes into wheat to improve stability.

A large amount of genetic variation exists in the cultivated and wild relatives of wheat. Very few attention has been given to the enormous diversity of gene complexes determining adaptation and productivity, assemble and incorporated over centuries of cultivation in different environ-

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ments (Frankel and Bennett 1970; Sutka *et al.* 1995).

Zohary *et al.* (1969) drew attention to the wild diploid progenitors of wheat which constitute large gene pools largely unexplored by wheat breeders.

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).

In this paper we report the results of phenotypic stability experiments on chromosome addition lines of *Agropyron elongatum* (Host) Beauvois into *Triticum aestivum* L. em. Thell. cv. 'Chinese Spring'.

MATERIALS AND METHODS

To locate the genes controlling yield and yield stability, disomic addition lines of *Agropyron elongatum* (2n=2x=14) into the genetic background of 'Chinese Spring' (CS) wheat (2n=6x=42) were used in a randomized complete block design (RCBD) with three replications in two different environments (irrigated and rainfed) for three years (2000-2003). The plant materials consisted of 9 genotypes including 7 disomic addition lines (DALS) in the genetic background of bread wheat (*Triticum aestivum* L., 2n=6x=42, AABBDD cv Chinese Spring = CS) along with CS (as recipient) and Sardari (as control). The DALS were named as: 1E to 7E indicating addition of chromosomes 1E to 7E from *A. elongatum* into the genome of CS, respectively. The genotypes were cultivated at the field of College of Agriculture, Razi University, Kermanshah, Iran (47° 20′ N latitude, 34° 20′ E longitude and 1351.6 m altitude). Climate in the region is classified as semi-arid with mean annual rainfall of 378 mm. Minimum and maximum temperature at the research station were -27 and 44°C, respectively. Each genotype was planted in 2-m rows and at 15 × 25 cm inter-plant and inter-row distances, respectively. Each plot consisted of 100 seeds (each row 50 seeds). The environments were considered as random factors, while genotypes as fixed factors. At the time of harvesting 5 single plants were selected randomly and grain yield was measured.

Statistical analysis

Additive main effect and multiplicative interaction (AMMI) was performed using IRRISTAT software. Briefly, analysis of variance is used to partition variance into three components: genotype deviations from the grand mean, environment deviations from the grand mean, and GE deviations from the grand mean. Subsequently, multiplication effect analysis is used to partition GE deviations into different interaction principal component axes (IPCA), which can be test for statistical significant through ANOVA. The AMMI analysis is interpreted by plotting the IPCAs of GE in various types of biplots.

AMMI stability value (ASV)

ASV is the distance from the coordinate point to the origin in a two-dimensional scattergram of IPCA1 scores against IPCA2 scores in the AMMI model (Purchase *et al.* 2000). Because the IPCA1 score contributes more to the GE interaction sum of square, a weighted value is needed. This weight is calculated for each genotype and each environment according to the relative contribution of IPC1 and IPC2 to interaction SS as follows:

$$ASV_i = \sqrt{\left[\frac{SS_{IPCA1}}{SS_{IPCA2}}(IPCA1score)\right]^2 + (IPCA2score)^2}$$

SS_{IPC1}/SS_{IPC2} is the weight given to the IPC1 value by dividing the IPC1 sum of square on the IPC2 sum of square. The larger the IPCA scores, either negative or positive, the more specifically adapted a genotype is to certain environments, smaller IPCA scores indicating a more stable genotype across environments.

Table 1 Combined analysis of variance for grain yield under different rainfed and irrigated conditions.

Source of variation	Degrees of freedom	Mean square
Environment (E)	5	10329.86**
Error1	12	83.40
Genotype (G)	8	4760.09**
G×E	40	379.81**
Error2	96	70.64

** Significant at 1% level of probability

Table 2 AMMI[a] analysis of grain yield in *Agropyron*-wheat disomic addition lines over rainfed and irrigated conditions.

Source	df	MS	SS explained%
Genotypes (G)	8	1586.70**	36.3
Environments (E)	5	3443.29**	49.2
G×E	40	126.60**	14.5
AMMI1	12	288.24**	68.3
AMMI2	10	122.16**	24.1
AMMI3	8	22.85ns	3.6
AMMI4	6	25.154ns	3
Residual (noise)	4	12.49	1
Total	53	659.89	-

** significant at 1% level of probability; ns: non- significant;
[a] additive main effect and multiplicative interaction.

Yield stability index (YSI)

A new approach known as yield stability index (YSI) is recommended, calculated by ranking the mean grain yield of genotypes (RY) across environments and rank of AMMI stability value (RASV). YSI incorporate both mean yield and stability in a single criterion as:

YSI = RASV + RY

A low value of this parameter shows desirable genotypes with high mean yield and stability.

RESULTS AND DISCUSSION

The results of combined analysis of variance (**Table 1**) showed highly significant differences for genotypes, environments and GE interaction indicating variability between genotypes, environments and their effects in the GE interaction and possible localization of the genes monitoring yield and yield stability. The percentage of the sum of squares (SS) attributable to the genotype, environment and GE after removing SS due to error and replication was 93.13%.

Mean comparison revealed that average grain yield of genotypes ranged from 72.581 g for Sardary to 24.607 g for disomic addition 4E.

The results of regression analysis (**Table 2**) showed that linear GE interaction accounted for 41% of variability in the GE interaction.

As a general rule the effectiveness of regression analysis is when 50% of the total sum of square is accounted for by linear GE interaction (Hayward *et al*. 1993), hence regression analysis is not useful for stability analysis of genotypes (Wade *et al.* 1995). Nevertheless, using regression analysis of Finlay and Wilkinson (1963) and Eberhart and Russell (1966), because of its wide application, it was concluded that chromosomes 3E, 5E and 7E have regression coefficients greater than 1 with minimum deviation from regression indicating general adaptability for rainfed and irrigated conditions, while chromosomes 2E and 6E with b less than 1 have specific adaptation for rainfed agriculture. Sutka *et al.* (1995) and Farshadfar *et al*. (2002, 2004) reported that most of the genes controlling drought tolerance indicators and general adaptation in *Agropyron* are located on chromosomes 3E, 5E and 7E which are in agreement with the result of this study.

AMMI model and pattern analysis

In the AMMI model, principal component analysis is based on the matrix of deviation from additivity or residual, while pattern analysis employs both classification and ordination techniques. In this respect, the results of AMMI analysis of both genotype and environment will be grouped based on their similar responses (Gauch 1992; Wade *et al.* 1995; Pourdad and Mohammadi 2008).

Using ANOVA, yield sum square was partitioned into genotype, environment and GE interaction. GE interaction was further partitioned by principal component analysis (**Table 2**).

The results of AMMI analysis indicated that 36.3, 49.2 and 14.5% of total variability was justified by genotype, environment and GE interaction, respectively.

AMMI1 and AMMI2 were highly significant and cumulatively accounted for 92.4% of GE interaction, therefore AMMI1 and AMMI2 clearly explain the interpretation of results and possible localization of the genes in the genotypes investigated.

IPCAs crossover and non-cross over interaction

IPCA scores of genotypes and environments displayed positive and negative values (**Table 3**, **4**).

A genotype with large positive IPCA score in some environments must have large negative interaction in some other environments. Thus, these scores presented a disproportionate genotype response (Yan and Hunt 2001; Mohammadi *et al.* 2007b), which was the major source of variation for any crossover (qualitative) interaction. This disproportionate genotype response is referred to as crossover GE interaction for convenience. Diversely, scores with the same sign or near zero represent a non- crossover (quantitative) GE interaction or a proportionate genotype response (Mohammadi and Amri 2008; Farshadfar 2008).

AMMI stability value (ASV)

In fact, ASV is the distance from zero in a two dimensional scattergram of IPCA1 (interaction principal component analysis axis 1) scores against IPCA2 scores. Since the IPCA1 score contributes more to GE sum of square (**Table 2**), it has to be weighted by the proportional difference between IPCA1 and IPCA2 scores to compensate for the relative contribution of IPCA1 and IPCA2 total GE sum of squares.

The distance from zero is then determined using the theorem of Pythagoras (Purchase *et al*. 2000).

In ASV method, a genotype with least ASV score is the most stable, accordingly, genotype Sardari (landrace from Iran) followed by CS and E7 were the most stable, while E2 and E4 showed specific adaptability and E3, E5 and E6 revealed medium adaptability.

Adjusted yield can be obtained by AMMI1, AMMI2, AMMI3 and AMMI4 for each environment by the formula:

$$\overline{Y}_{i0} + \overline{Y}_{0j} - \overline{Y}_{00}$$

where

$\overline{Y}_{i0}$ = mean of genotype i;

$\overline{Y}_{0j}$ = mean of environment j;

$\overline{Y}_{00}$ = grand mean, and used as a selection criterion in breeding programs.

Biplot analysis and ordination techniques indicated highly significant differences for AMMI1 and AMMI2 which justify 92.4% of variability in the GE interaction. Biplot analysis (**Fig. 1**) also revealed that genotype 7E has high positive interaction (their angle is less than 90%) with environments A, B, D and E, genotype 1E with environments B an E, genotypes 2 and 4 with environments B, C, E and F, genotypes 6E and 8 with environments C, F, E and D and genotype 9 with environments A, C, D and F, genotypes 3E and 5E with environments A and D.

Table 3 Mean yield, first and second IPCA scores, ASVi and YSIi of genotypes investigated.

genotypes	Mean	IPCA[a]1	IPCA2	ASV[b]	YSI[c]
E_1	31.394	1.334	1.815	4.190	9
E_2	25.286	3.545	0.658	10.057	15
E_3	42.783	-4.048	-1.628	11.389	12
E_4	24.610	3.534	-0.219	9.995	15
E_5	37.213	-2.815	-0.747	7.922	10
E6	27.647	0.723	-0.726	7.744	10
E_7	58.838	-2.659	4.332	8.687	8
CHS	42.067	0.215	-0.604	0.856	5
SAR	72.581	0.172	-2.881	2.920	3

[a] interaction principal component analysis; [b] AMMI stability value; [c]yield stability index

Table 4 Mean yield, first and second IPCA scores and ASVi of Environments.

code	Mean	IPCA[a]1	IPCA2	ASV[b]
A	75.38	-3.321	-1.205	9.48
B	38.60	2.043	2.082	6.06
C	29.82	2.062	-2.493	6.36
D	48.78	-5.145	-0.449	14.63
E	24.45	0.664	4.243	4.66
F	24.59	3.109	-2.178	9.09

[a] interaction principal component analysis; [b]AMMI stability value

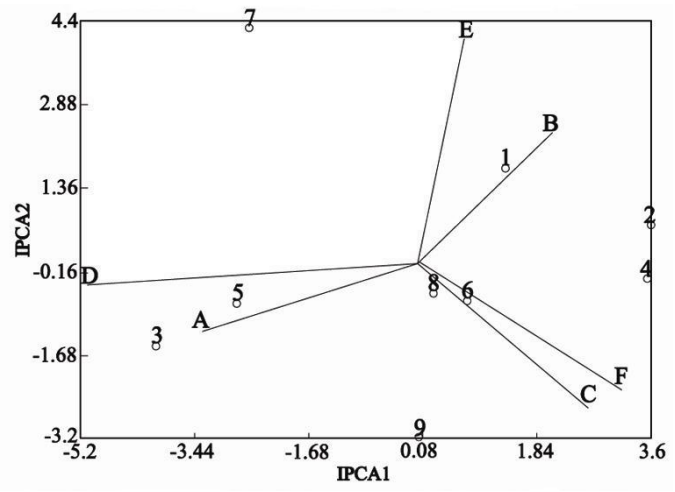

Fig. 1 Interaction biplot for AMM2 model.

In general the importance of AMMI model is in reduction of noise even if principal components do not cover much of the GESS (Gauch and Zobel 1989; Gauch 1992).

It is to be mentioned that genotypes toward the center of biplot have zero interaction, therefore show general adaptation with different grain yield. Genotypes 8 and 6E are located in this category. The other genotypes are around the center of biplot indicating the variation between the entries (Manrique and Hermann 2000; Farshadfar 2008).

As AMMI2 has least RMSPD (root mean square predictive difference), therefore, a recommendation must be based on this model (Crossa *et al.* 1991; Wade *et al.* 1995; Farshadfar and Sutka 2006).

According to AMMI2 the best disomic addition line was 7E. The advantage of biplot analysis is that genotypes are judged in grouping form and therefore save time and precision in interpretation and selection (Wade *et al.* 1995; Alagarswamy and Chandra 1998; Farshadfar and Sutka 2003).

Yield stability index (YSI)

Stability *per se* should however not be the only parameter for selection, because the most stable genotypes would not

necessarily give the best yield performance (Mohammadi *et al.* 2007a, 2007b), hence there is a need for approaches that incorporate both mean yield and stability in a single index, that is why Kang (1991, 1993) introduced three selection criteria for simultaneous selection of yield and stability entitled: rank – sum (RSM), modified rank – sum (MRSM) and the statistics yield – stability (YSi).

In this regard, as ASV takes into account both IPCA1 and IPCA2 that justify most of the variation in the GE interaction (92.4%), therefore the rank of ASV and yield mean in such a way that the lowest ASV takes the rank one, while the highest yield mean takes the rank one and then the ranks are summed in a single simultaneous selection index of yield and yield stability named as: Yield stability index (YSI). The least YSI is considered as the most stable with high yield mean. Based on the YSI most of the genes controlling yield and yield stability are located on chromosome 7E which is in accordance with the result of AMMI2 model.

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