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Locating QTLs controlling genotypic stability in Rye using AMMI model and AMMI based stability statistics

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Abstract

To locate QTLs controlling yield and yield stability in Rye, 7 disomic addition lines of *Secale cereale* into the genetic background of Chinese Spring (CS= recipient) were used in a completely randomized block design with three replications for 3 rainfed and irrigated conditions. The results of combined analysis of variance showed highly significant differences for environments, genotypes and genotype × environment interaction. The first multiplicative axis term explained 94.30% of GEI sum of squares. The average grain yield of the genotypes ranged from 0.72g for addition line 6 to 6.54g in addition line 2 indicating that QTLs controlling grain yield in Rye are located on chromosome 2R. Biplot analysis revealed that QTLs monitoring simultaneously yield and yield stability in Rye are distributed on chromosomes 2R, 5R and 7R. According to the all AMMI based stability measures and mean grain yield genotype 2R was identified with high grain yield with stability followed by 5R, therefore most of the QTLs controlling yield and yield stability are located on chromosome 2R of Rye. AMMI based stability statistics were positively correlated, therefore all of the AMMI based measures discriminate stable entries at the same manner.

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Introduction

Genetic materials such as alien additions, substitutions, translocations, deletions, monosomes, ditelosomes, and nullisomes are valuable genetic resources for both plant breeding and basic research (Szakacs and Molnar, 2010). Alien chromosome addition lines have been developed for a variety of plant species and have been used for many purposes such as introducing valuable traits to the recipient species, mapping genes and markers on introgressed alien chromosomes, examining alien gene regulation, understanding meiotic pairing behavior and chromosome structure, and isolating individual chromosomes and genes of interest (Islam and Sheperd, 1990; Muehlbauer *et al*., 2000; Jin *et al*., 2004).

Bread wheat (*Triticum aestivum* L.) addition lines have been produced with numerous species related to wheat, including Rye (*Secale cereale*). Among these, the 'Chinese Spring' (CS)/'Imperial' wheat-rye disomic addition series (Driscoll and Sears, 1971) have been widely used all over the world to study the effect of individual Rye chromosomes on quality parameters and resistance to biotic and abiotic stresses in the wheat genetic background, and to locate various genetic markers in Rye,such as storage proteins, isozymes, and RFLP or RAPD loci (Aniol, 2004; Jianzhong *et al*., 2001; Szakacs and Molnar, 2010).

Wheat (*Triticum aestivum* L., 2n=42) is an important crop, but its ability to adapt in poor environment conditions, is inferior to some of wild grass species. Rye (*Secale cereale* L., 2n=14), one of its wild grass species, possess some good traits, which help its adaptation to poor soil conditions (Li, 1985, 1990). Because Rye and wheat cross easily, a set of Wheat–Rye disomic addition lines were developed (Jianzhong *et al*., 2001; Farshadfar *et al*., 2011).

By growing the disomic addition lines (DALs) under different growing conditions it may help to find genes useful for making wheat adaptable to unpredictable conditions. However, little is known about the study of genotype × environment (GE) interactions to determine the gene controlling stability performance in Wheat-Rye disomic addition lines.

The GE interactions have been studied regarding genotype stability in different species crops (Eberhart and Russell, 1966; Gauch, 1992; Becker and Leon, 1988; Lin and Bin, 1994; Yan *et al*., 2000; Fan *et al*., 2007; Farshadfar *et al*., 2011).

Various methods of GE interaction analysis exist, including parametric and non-parametric approaches. Parametric approaches are: (1) univariate analysis (regression analysis and stability variance analysis) and (2) multivariate analysis (principal component analysis, factor analysis, canonical component analysis, cluster analysis and biplot analysis) (Roy, 2000). The ordinary form of ANOVA is an additive model and therefore describes only the main effect (Snedecor and Cochran, 1989). Principal component analysis is a multiplicative model and has the opposite problem of not describing the additive main effects. Linear regression models (Finlay and Wilkinson, 1963) combine additive and multiplicative components and thus analyse both main effects and interaction, but in general they confound the interaction with the main effects (Wright, 1971), reducing its power for general significance testing.

The additive main effects and multiplicative interaction (AMMI) model is a powerful multivariate method for multi-environmental trials (Romagosa and Fox, 1993). This technique, also called FANOVA (Gollob, 1968), incorporates both additive and multiplicative components into an integrated, powerful least squares analysis (Gauch, 1992; Voltas *et al*., 1999). Plots showing both the genotypes and the environments simultaneously can be of great assistance in this respect, and are called biplots (Gabriel, 1971; Rubio *et al*., 2004).

Some methods are based on the additive main effects and multiplicative interaction model, e.g., AMMI

stability value (ASV) (Purchase *et al.*, 2000), parameter of Annicchiarico (1997) (Dai), distance of IPC point with origin in space (Dzi), stability statistic based on the first IPC axes (FPi), stability statistic based on the first two IPC axes (Bi), stability statistic based on fitted AMMI model (FAi), Wrick's ecovalance in term of AMMI (Wi(ammi)), modified AMMI stability value (MASV), sums of the absolute value of the IPC scores (SIPC), sum across environments of the GEI modeled by AMMI (AMGE), averages of the square eigenvector values (EV), absolute value of the sum across environments (AV(AMGE)), and absolute value the relative contribution IPCs to the interaction (Zai) (Dehghani *et al.*, 2010). Different AMMI stability parameters reflect various aspects of GE interaction and so introduce different genotypes as the most stable or unstable candidates. It seems plausible that yield stability estimated from AMMI and various stability statistics derived from AMMI model could be more repeatable than other stability statistics (Sneller, 1997; Dehghani, 2010).

Regardless of the definition of stability parameter one important question is whether stability is heritable or not? If stability is not heritable, then using this parameter in breeding programs is fruitless (Lin and Binn, 1991, 1994; Jalata *et al.*, 2011). If stability is heritable, the next step in the genetic analysis is identification of the chromosomal location of the genes controlling adaptation (Farshadfar *et al.*, 2008). 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).

Thus, the main objective of this study was to locate the genes controlling stability and yield performance in Rye using the CS/'Imperial' disomic addition lines grown under different growing conditions by applying the AMMI and AMMI based approaches.

Materials and methods

To locate QTLs controlling yield and yield stability, 7 disomic addition lines (1R to 7R) of *Secale cereale cv.* Imperial (2n=2x=14) into the genetic background of Chinese Spring (CS= recipient) wheat (2n=6x=42) and a check (*Triticum aestivum L. cv.* Sardary = SAR; a stable landrace from west of Iran) and Rye variety Imperial (RIM = donor) together with Rye variety Lovaspatonai (RLO) were used in 3 rainfed and irrigated conditions in the 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 semiarid with mean annual rainfall of 378 mm. Minimum and maximum temperature at the research station were -27°C and 44°C, respectively. The experimental design for each environment was a completely randomized block design with three replications. The plots consisted of 2m 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 and genotypes as fixed factors. At the time of harvesting 5 single plants were selected randomly and grain yield was measured.

AMMI 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, environmental 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 prinicipal 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 based stability statistics

AMMI based stability parameters were calculated according to the following methods.

$SIPC_i = \sum_{K=i}^{N} |\lambda_k^{0.5} \gamma_{ik}|$ (Sneller *et al.*,1997)

$EV_i = \sum_{k=1}^{N} \frac{\gamma_{ik}^2}{N}$ (Sneller *et al.*, 1994)

$Da_i = \sqrt{\sum_{k=1}^{N} (\lambda_k \gamma_{tk})^2}$ (Annicchiarico, 1997)

$FP_i = \lambda_1^2 \gamma_{i1}^2$ (Raju, 2002)

$AV_{(AMGE)} = \sum_{j=1}^{E} \sum_{k=1}^{N} |\lambda_k \gamma_{ik} \delta_{jk}|$ (Sneller *et al.*,1997)

$Za_i = \sum_{k=1}^{N} |\delta_k \gamma_{ik}|$ (Sneller *et al.*,1997)

All genotypes ranked in this manner, and the ranks of yield and stability variance summed for each genotype. Spearman's coefficient of rank correlation was calculated on the ranks to measure the relationship between the statistics. PCA based on the rank spearman correlation matrix used for better understand the relationships among the yield stability statistics. All statistical analyses performed using the STATISTICA and GENSTAT softwares.

Results and discussion

The results of combined analysis of variance (Table 1) showed highly significant differences for environments, genotypes and genotype × environment interaction. The significant interactions of genotypes × environments suggest that grain yield of genotypes varied across irrigated and rainfed conditions. Significant differences for genotypes, environments and GE interaction indicated the effect of environments in the GE interaction, genetic variability among the entries and possibility of selection for stable genotypes. As GE interaction was significant, therefore we can further proceed and estimate phenotypic stability (Farshadfar and Sutka, 2006; Osiru *et al.*, 2009).

Environment significantly explained about 51.04% of the total sum of squares due to treatments. A large yield variation explained by environments indicated that the environments were diverse, with large differences among environmental means causing most of the variation in grain yield. In multi environmental trial (MET), environment explains 80% or higher of the total yield variation. Only the small portion that is, 2.52% of the total sum of squares due to treatments was attributed to genotypic effects. GEI significantly explained 25.94% of the treatments variation in grain yield. The magnitude of the GEI sum of squares was about 10 times larger than that for genotypes, indicating that there were sizeable differences in genotypic response across environments. Analysis of GEI is vital for breeders in order to design the dissemination strategies for new varieties. It is important to identify cultivars with specific and general adaptation. The average grain yield of the genotypes ranged from 0.72g for genotype 6 to 6.54g in genotype 2 indicating that QTLs controlling grain yield in Rye are located on chromosome 2R.

Table 1. Partitioning of the sum of squares (SS) and mean of squares (MS) from the AMMI analysis of disomic addition genotypes evaluated across 3 environments.

S.O.V	Df	Sum of square	SS%	Mean of square
Total	89	1265.9		
Treatments	29	1170.7	92.48	40.37**
Genotypes	9	220.9	2.52	24.54**
Environments	2	646.1	51.04	323.04**
Interactions	18	303.7	25.94	16.87**
$IPCA_1$	10	286.5	94.30	28.65**
Residuals	8	17.3	5.70	2.16^{ns}
Pooled error	60	95.1	7.52	1.59

ns and **: non-significant and significant at 1% probability level, respectively

The application of AMMI model for partitioning of GEI (Table1) revealed the first term of AMMI was significant using an approximate F-statistic. The Gollob's test most often retains the multiplicative axis terms of little practical relevance that is, axis with a low proportion of explained GE variation. In this study, the first multiplicative axis term explained 94.30% of GEI sum of squares, The first IPCAs retained by Gollob's F-test accounted for 94.30% of GE interaction. The AMMI model revealed that there was a more complex interaction of GE and which it could not facilitate graphical visualization of the genotypes in low dimensions and so it is essential to use an alternative procedure to interpretation of GEI using AMMI parameters. The first IPCAs accounted

for 94.30% of the total interaction, the remaining 5.70% being the residual or noise, which is not interpretable and thus discarded. The advantages of the AMMI model or its variants are that, they use overall fitting, impose no restrictions on the multiplicative terms and result in least square fit (Freeman, 1990). Within limits, any model may be expected to fit the data from which it was derived. However, the AMMI model has a good chance of being able to predict for new sites and new years, thus contributing a real advance (Gauch, 1988).

The AMMI method is used for three main purposes. The first is model diagnoses, AMMI is more appropriate in the initial statistical analysis of yield trials, because it provides an analytical tool of diagnosing other models as sub cases when these are better for particular data sets (Gauch, 1988). Secondly, AMMI clarifies the G ×E interaction and it summarizes patterns and relationships of genotypes and environments (Zobel *et al.*, 1988; Crossa *et al.*, 1990). The third use is to improve the accuracy of yield estimates. Gains have been obtained in the accuracy of yield estimates that are equivalent to increasing the number of replicates by a factor of two to five (Zobel *et al.*, 1988; Crossa, 1990). Such gains may be used to reduce testing cost by reducing the number of replications, to include more treatments in the experiments or to improve efficiency in selecting the best genotypes.

Biplot analysis

AMMI1 model justified 94.30% of GEI. The AMMI1 biplot was obtained by plotting average yield and first interaction principal component (IPCA1). By AMMI1 biplot it is possible to screen for simultaneous selection of yield and yield stability. Genotypes with high grain yield and low IPCA1 are the best combination for simultaneous selection of genotypes with high mean yield high stability. According to Fig. 1 genotypes G5 and G7 and G2 revealed stability and high grain yield more than average, hence it can be concluded that QTLs monitoring simultaneously yield and yield stability in Rye are distributed on chromosomes 2R, 5R and 7R.

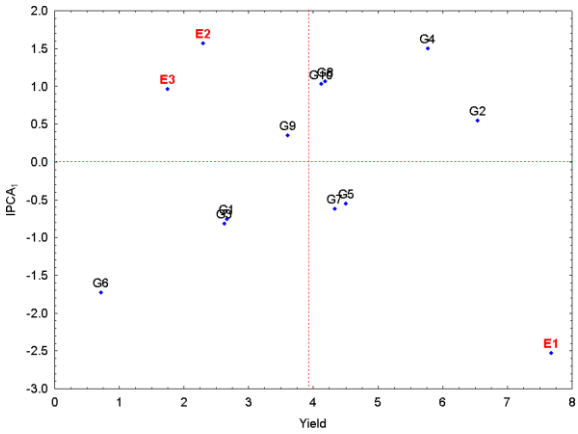

Fig. 1. Biplot of the first interaction principal component axis (IPCA1) versus mean yield for disomic addition lines.

In AMMI1 model it is possible to group the environments. Environment 2 (E2) and 3 (E3) with high IPCA contributed more to the GEI, while E1 contributed more to yield potential. G5 and G7 exhibited specific adaptability with E1.

AMMI stability measure

Seven measures of stability from AMMI model and the mean yield for each genotype over all environments are given in Table 2. Genotypic rank differences over environments indicated the presence of crossover GEI. This was confirmed by the significant effect of the GEI in the analysis of variance (Table 1) and indicated the need to assess the response of the genotypes to environmental variation. The 7 genotypes were ranked with respect to their stability with each of the seven measures of stability from AMMI model such that lesser the value of the rank more is the stability. The stability rank orders displayed by these seven measures of stability from AMMI model presented in Table 2. According to the rank 1 of all stability measures and mean grain yield genotype G2 was identified with high grain yield with stability followed by G5, therefore most of the QTLs controlling yield and yield stability are located on chromosome 2R of Rye.

Table 2. Genotypes numbers, mean yield and measures of stability from AMMI model for disomic addition lines

Gen. no.	$IPCA_1$	γ_{i1}	EV_1	$SIPC_1$	Da_1	$AV_{(AMGE)}$	FP_i	Za_1	Mean
G_1	-0.756	-0.242	0.059	0.76	2.36	3.83	5.59	0.24	2.66
G_2	0.54	0.175 (1)	0.031(1)	0.55 (1)	1.71 (1)	2.77 (1)	2.92(1)	0.18(1)	6.54(1)
G_3	-0.816	-0.261	0.068	0.82	2.55	4.13	6.50	0.26	2.62
G_4	1.500	0.480	0.230	1.50	4.69	7.59	22.00	0.48	5.77
G_5	-0.553	-0.177	0.031 (1)	0.55	1.73	2.80	2.99	0.18(1)	4.51
G_6	-1.729	0.553	0.306	1.73	5.40	8.74	29.20	0.55	0.72
G_7	-0.625	-0.200	0.040	0.63	1.95	3.16	3.82	0.20	4.33
G_8	1.060	0.339	0.115	1.06	3.31	5.36	10.97	0.34	4.19
G_9	0.347	0.111	0.012	0.35	1.08	1.76	1.18	0.11	3.61
G_{10}	1.025	0.328	0.108	0.03	3.21	5.19	10.27	0.33	4.12

$IPCA_1$*:* interaction principle component, γ_{i1}*:* Eigenvectors, *EV_1: Averages of the square eigenvector values, $SIPC_1$: Sums of the absolute value of the IPC scores, Da_1: parameter of Annicchiarico (1997), $AV_{(AMGE)}$: Absolute value of the sum of the environments,* FP_i: Stability statistic based on the first IPC axes of the first IPC axes and Za_4: Absolute value the relative contribution IPCs to the interaction.

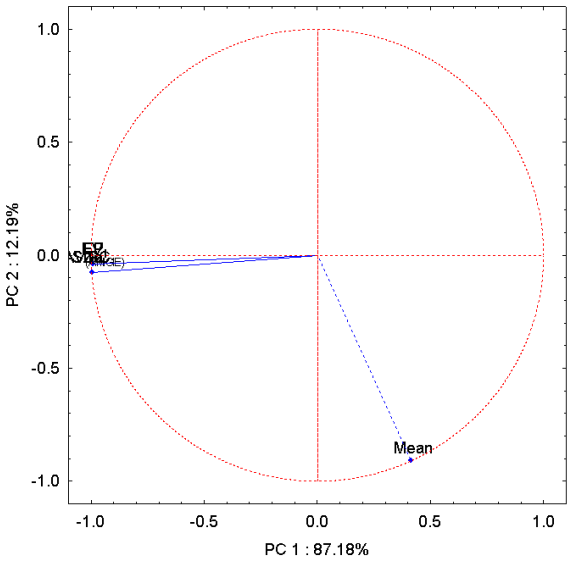

Fig. 2. Principal component analysis (PC1 and PC2) plot of ranks of yield stability, estimated by eight parametric statistics using mean yield of disomic addition lines over 3 environments.

To better understand the relationships, similarities and dissimilarities among the physiological indicators of drought tolerance, principal component analysis (PCA) was used based on the rank correlation matrix. The main advantage of using PCA over cluster analysis is that each statistics can be assigned to one group only (Khodadadi *et al.*, 2011). The relationships among different indices are graphically displayed in a biplot of PCA1 and PCA2 (Fig. 1). The PCA1 and PCA2 axes which justify 99.37% of total variation, mainly distinguish the indices in different groups. One interesting interpretation of biplot is that the cosine of the angle between the vectors of two indices approximates the correlation coefficient between them. The cosine of the angles does not precisely translate into correlation coefficients, since the biplot does not explain all of the variation in a data set. Nevertheless, the angles are informative enough to allow a whole picture about the interrelationships among the in vivo indices (Yan and Kang, 2003). As the cosine of the angle between the vectors of two indices approximates the correlation between them therefore, all the AMMI based stability statistics were positively correlated (an acute angle), and independent from grain yield (right angle). It is concluded that all of the AMMI based measures discriminate stable entries at the same manner.

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