



Chromosomal localization of QTLs controlling phenotypic stability in wheat-agropyron disomic addition lines using performance plots

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Abstract

In order to identify QTLs controlling genotype \times environment interaction (GEI) in Agropyron performance plots were compared in disomic addition lines of Wheat-Agropyrum disomic addition lines. The experiment was conducted in six environments (A, B, C, D, E and F). The genotypes 7E, CHS and Sardary (SAR) were stable in static sense (static stability), as the profile of their mean yield in each environment was parallel to the profile of their environmental mean yield. The same conclusion was observed for genotypes SAR and 7E in dynamic sense (dynamic stability). SAR and 7E also exhibited wide adaptability (genotypes SAR and E7 yielded over the mean in each environment). CHS also revealed wide adaptability, which yielded over the mean in all environments, but it was not consistent in both dynamic and static stability. It was concluded that QTLs controlling stability and wide adaptability in *Agropyrum elongatum* are located on chromosome 7E and can be transferred into wheat genome for enhancement of adaptation. The regular performance plot (RPP) provided better information about environments and genotypic stability in static sense than the two other plots. The environment-centered performance plot (ECPP) better represented genotypic stability in dynamic sense, while the environment-standardized performance plot (ESPP) poorly represented stability in both senses (static and dynamic).

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Introduction

It is obvious that the phenotype of crop plants is influenced by genotype and environment. The genotype-environment interaction (GEI) reduces association between phenotypic and genotypic values, genetic progress resulted from selection, bias in the estimates of gene effects and combining ability for different characters sensitive to environmental fluctuations and confounds precise partitioning of the contributions of improved cultivars and improved environment or technology to yield (Farshadfar *et al.*, 2000; Kearsley and Pooni, 2004). GEI occurs when different varieties or genotypes respond differently to different environments.

Information on existence of GEI is important for plant breeders because it can help them to develop genotypes with general adaptability (stable) for all environments or specific adaptation for target environments. The identification of GEI in trials has led to the development of methods that are called stability analyses or sensitivity analysis (Dyke *et al.*, 1995).

Stability has different concepts. The static concept of stability or biological concept of stability means that a cultivar has a stable performance over environments, with no among-environment variance, i.e., a genotype is nonresponsive to increased levels of inputs (Becker, 1981). This type of stability is not useful in production agriculture. The dynamic concept of stability or agronomic concept implies that a genotype's performance is stable, but for each environment, its performance corresponds to the estimated or predicted level. The estimated or predicted level and the level of actual performance should agree (Becker, 1981; Becker and Leon, 1988).

Apart from the definition and many concepts of stability one important question is whether stability is heritable or not? If stability is not heritable, then using this parameter in breeding programs is not useful (Lin and Binn, 1991, 1994; Jalata *et al.*, 2011). If stability is heritable, the next step in the genetic

analysis is identification of genes controlling stability in the stable genetic resources (Farshadfar, 2008; 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. The chromosome location of such genes is critical for effective utilization and subsequent manipulation. Because of the complex nature of genotypic stability, very little information is available on the chromosomal location of the genes conditioning stability (Morgan, 1991; Koszegi *et al.*, 1996; Farshadfar and Sutka, 2003).

Disomic addition lines (DALs), in which a single pair of homologous chromosomes from a related species are added to the full chromosome complement of the recipient, are valuable genetic materials to detect alien chromosomes carrying desirable genes and prepare the starting point for gene transfer (genetic engineering) and genetic improvement of genotypic stability (Gale and Miller, 1987; Ellis *et al.*, 2000; Farshadfar *et al.*, 2012).

In order to identify chromosome (s) carrying QTLs controlling stability, there are two procedures of stability analysis: statistical procedures [parametric (univariate and multivariate) and nonparametric] and plot procedures (AMMI based biplot, GGEbiplot and performance plots) (Gauch, 1992 ; Yan and Kang, 2003; Kozak, 2010).

Kozak (2010) proposed three plots namely regular performance plot (RPP), environment-centered performance plot (ECPP) and environment-standardized performance plot (ESPP) as a simplest method for analysis of both static and dynamic yield stability in a set genotypes evaluated over diverse environments (Farshadfar *et al.*, 2012).

This study focuses on the simplest type of plot (performance plot) of the genotypes across a range of environments (genotypes' response to environments). Its advantage is simplicity and easy interpretation; in fact, it is used as a standard display to show interaction between two factors, therefore it is easily understood even by non-experts. Its disadvantage is that only a small number of genotypes can be presented on the plot (DeLacy *et al.*, 1996).

The objectives of the present investigation are to (i) compare three performance plots for visual exploration of phenotypic stability in both static and dynamic concepts and adaptability and (ii) locating QTLs controlling stability.

Materials and methods

To locate the genes controlling dynamic stability (represented by ecovalence) (Wrick, 1962) and static stability (represented by variance of yield across environments) (Roemer, 1917) disomic addition lines (DALs) 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 under two different environments (irrigated and rainfed) for three consecutive years. The plant genetic materials consisted of 9 genotypes including 7 disomic addition lines 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 *Agropyron elongatum* into the genom of CS, respectively. The genotypes were cultivated in the field of College of Agriculture, Razi University, Kermanshah, Iran ($47^{\circ} 20' N$ latitude, $34^{\circ} 20' E$ 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 temperatures at the research station were $-27^{\circ}C$ and $44^{\circ}C$, 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.

Stability analysis using performance plots (Kozak, 2010)

Regular performance plot (RPP)

In the regular performance plot (RPP), environments are forming the horizontal axis and genotypes (or more often, groups of genotypes) are forming the traces (profiles). It is common to order environments from the worst to the best, which is done based on environment means. Another useful addition is the mean profile, which represents the mean trait value of genotypes in environments. In addition, it is useful to order genotypes on the legend from the best to the worst in terms of the mean across the environments in that way the reader of the graph can immediately access this important information. Such a performance plot shows at the same time (a) stability of a genotype in a static sense (which can be seen by looking at changes across environments on a profile for the genotype), (b) stability of a genotype in a dynamic sense (which can be seen by looking at changes across environments on a profile for the genotype compared to the mean performance), and (c) adaptability of a genotype (which can be seen by looking at how the genotype outperforms the mean profile across environments).

Environment-centered performance plot (ECPP)

The environment-centered performance plot (ECPP) is constructed in a very similar way as the regular performance plot, but for the data centered for the mean across the genotypes in a particular environment:

$$Y_{ge}^c = Y_{ge} - \bar{Y}_e \quad (1)$$

Where Y_{ge}^c and Y_{ge} are respectively the environment-centered and original trait value for the g th genotype in the e th environment, and \bar{Y}_e is the mean of the trait across all genotypes in the e th environment. Fox and Rosielle (1982) call such

transformed data the “coded data” (hence the index c).

Environment-standardized performance plot (ESPP)

The environment-standardized performance plot (ESPP) is based on data standardized by the following formula:

$$Y_{ge}^s = \frac{(Y_{ge} - \bar{Y}_e)}{S_e}$$

(2)

Where Y_{ge}^s is the standardized trait value for the g th genotype in the e th environment, and S_e is the estimated phenotypic standard deviation of the trait in the e th environment, calculated with the standard formula:

$$S_e = \frac{1}{E-1} \sum_{g=1}^E (Y_{eg} - \bar{Y}_e)^2$$

(3)

E being the number of environments.

Note the difference between the coded and standardized data: in the latter, the former data are divided by the phenotypic environment-wise standard deviations (Fox and Rosielle, 1982; DeLacy *et al.*, 1996). Through the transformation (1), the environment means are all equal to 0, so the mean performance is equivalent to the horizontal line for $Y=0$; the standard deviations in environments are the same as of the original data, so the information about variability in the environments is kept. Through the standardization (2) the environment means are also zero, but in addition the standard deviations in the environments are all equal to 1, so each environment has now an equal variability (so, equal weight) in the plot. In that way, the information on variability (hetero- or homogeneity of genotypes’ performance) in the environments is lost.

Results

The regular performance plot showed that the environments offered quite diverse conditions for wheat genotypes (Fig. 1). Mean yield in the worst environment was slightly above 24.4g, while in the best was almost 75.4g. The genotypes 7E, CHS and SAR were stable in a static sense, the profile mean

yield of them in each environment is parallel to the profile mean of environments (Table 1). The same results observed for SAR and 7E in the dynamic sense of stability. These two genotypes also revealed wide adaptability (yielded over the mean in each environment), the other genotype with wide adaptability was CHS, which yielded over the mean in all environments, but was unstable in both dynamic and static senses (Table 1 and Fig. 3). Genotype 2E was the worst genotype, yielding very low in most environments but one. One environment (A: year 1 and irrigated) offered very homogenous conditions for most of the genotypes, because all of them had almost the same seed yield.

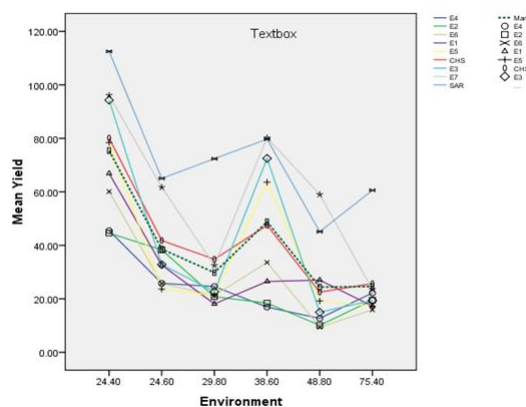


Fig. 1. Performance plot for seed yield of nine wheat genotypes in six environments.

Environments on the horizontal axis are ordered by an increasing mean yield and genotypes in the legend by a decreasing mean yield. Stability in a dynamic sense is much easier to see and interpret on the environment-centered plot (Fig. 2). One needs to compare a profile for a genotype with the mean profile; this means comparing the extent to which these two profiles are parallel. Hence it is easier on the environment-centered performance plot, on which the mean profile is a horizontal zero-line, than on the regular performance plot (Fig. 1). See for example the lines representing the changes from environment D (year 2 and non-irrigated mean = 48.8) to A (year 1 and irrigated mean=75.4) on both plots and note the difficulty in comparing these changes for various genotypes on the regular plot. We can see that all genotypes yielded higher in A than in

B. On the environment-centered performance plot the dynamic stability can be easily seen (Fig. 2) here we compare reactions for different genotypes and see that, for example, for these two environments the greatest increase in yielding compared to the mean performance was obtained for the SAR genotype, and the greatest decrease in yielding compared to the mean performance was obtained for genotype 7E (represented by the horizontal line) was observed. In addition, the difference between the trait value for a genotype and the mean in a particular environment is immediately accessed on the environment-centered plot, while for the regular performance plot one needs to subtract the genotype's value from the mean value (so one needs to judge the vertical distances between two points for two genotypes for each environment). Cleveland (1994) discussed these issues, showing that human eye does such a work poorly. Thus the regular performance plot in this context is less efficient in terms of visual encoding of the data than the environment-centered performance plot.

Table 1. Mean yield and stability in dynamic (represented by Ecovalence) and static (represented by variance of yield across environments) senses for wheat-agropyron disomic addition lines

Genotypes	Mean yield (g/pot)	Variance across environments	Ecovalence
1E	31.4	39.73	328
2E	25.3	214.7	834.8
3E	42.8	278.9	1085
4E	24.6	198.6	772.2
5E	37.2	141.3	549.7
6E	27.6	13.19	51.3
7E	58.8	278.8	1084
CHS	42.1	11.27	43.82
SAR	72.6	1992	7747

The environment-standardized performance plot (Fig. 3) fails to convey most of the information discussed above. No information was provided about stability in static and dynamic sense. Therefore, it is difficult to

interpret the profiles of genotypes. Look at genotype 5E and its reaction to changing environment from F to C: even though this change is the same as that of genotypes 6E, 4E and CHS (Fig. 2), but Fig. 3 expressed that this change was huge. This is because genotype 5E was the worst in environment F, which was homogenous in terms of yielding (the difference between the worst and the best yielding genotypes was 48). Hence standardized data provide no information about stability. It provided information about wide adaptability, showing in which environments a genotype yield is higher than the mean yield, but this cannot be assessed in the original units.

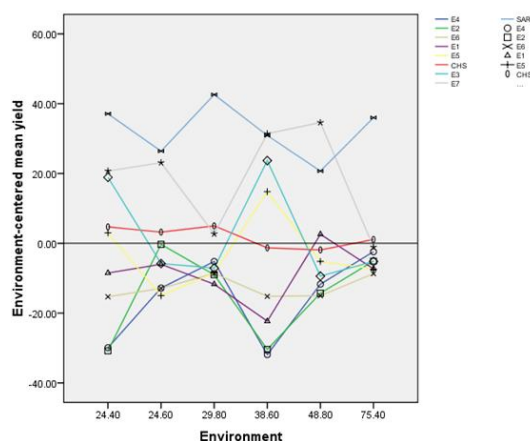


Fig. 2. Environment-centered performance plot corresponding to the performance plot from fig. 1. Environments on the horizontal axis are ordered by an increasing mean yield and genotypes in the legend by a decreasing mean yield.

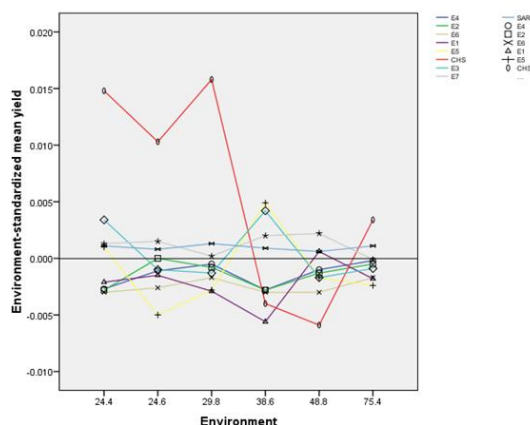


Fig. 3. Environment-standardized performance plot corresponding to the performance plot from Fig. 1. Environments on the horizontal axis are ordered by an increasing mean yield and genotypes in the legend by

a decreasing mean yield. The grey reference line represents the mean profile.

Discussion

Most promising genotypes of a crop species are those which have high and stable yield. Stability can be considered in various ways, which can be grouped in two main types: stability in static and dynamic concepts. The former refers to stable yielding of a genotype over environments, while the latter refers to stable yielding of a genotype over environments as compared to mean yielding of a particular group of genotypes considered (Lin *et al.*, 1986). It is easy to imagine that stability in these two concepts does not have to be related, and that the dynamic stability of a genotype strongly depends on other genotypes being considered in the particular study. A genotype that is very stable statically does not react to changing environmental conditions, while that which is very stable dynamically reacts to changing environmental conditions similarly to the mean reaction within the pool of genotypes. Hence we see that great stability does not have to be a great advantage: for example, a genotype does not have to be stable in a static sense and be the best yielder in every environment, and a genotype that reacts extremely well on one type of environmental conditions (e.g., drought stress), but reacts normally on other conditions, will not be stable in dynamic sense. Hence when studying stability one should look at stability measures as well as genotype performance among environments. Such performance is difficult to see in any type of biplot, but it can be seen on performance plots.

From the results presented in the paper it follows that the regular performance plot, as the only one of the three plots compared, pictures stability in a static sense. Also as the only one it enables us to read the original value of the trait in the environments. It is also the most efficient in conveying information about the environments, although one needs to keep in mind that this information is not rich simply because performance plots are not focused on environments. Its disadvantages are lower (compared to the

environment centered performance plot) efficiency in visualizing stability in a dynamic sense as well as narrow and wide adaptabilities. This is due to less efficient visual encoding of the data in this plot.

The environment-centered performance plot is the most efficient among the three in picturing stability in a dynamic sense as well as narrow and wide adaptability. The adaptability is best shown because one can easily subtract the difference between a particular genotype's value and the environment, so not only one can see whether the trait's value is above the mean, but also how far it is from the mean. This plot is not free of disadvantages, although rather minor ones. Stability in a static sense cannot be seen. Information on environments is poor, although the important information about the diversity of the environments in terms of the trait is kept. Note that this problem is to some extent overcome by ordering environments on the horizontal axis from the worst to the best.

The environment-standardized performance only pictures narrow and wide adaptability, but worse than environment-centered performance plot. This is because the information about the actual difference about the environmental diversity is lost, so one does not know how much the genotype outperforms the mean performance.

One additional problem is that on a regular performance plot the mean performance is usually represented by a thick black line in order to make it easily distinguishable from the genotype-wise performances. Since on the environment-centered and environment-standardized performance plots the mean performance is equal to the horizontal zero line, the corresponding line does not need to be thick; in fact, a thin grey line will suffice, accounting for better readability of the graph (compare Fig. 1 with Fig. 2 and 3).

Note that the considerations in this paper refer to exploratory graphs that aim to facilitate

understanding genotype's performance in terms of stability and adaptability across environments. So these conclusions must not be generalized to other situations, for example as statistical analysis of Fox and Rosielle (1982) showed, in various situations standardized data will work better than coded data (on which the environment-centered performance plot is based). However, in addition to rigorous statistical analysis the plots described in this paper are simple to understand by plant breeders, still being powerful in conveying important information about some aspects of the data (except for the environment-standardized performance plot). All discussions in this paper equally refer to the version of the performance plot in which the horizontal axis is formed by environment means instead of environments treated as levels of a qualitative variable. This all does not mean that any stability or adaptability analysis should be based solely on the performance plots. They aim to visualize stability and adaptability of genotypes, showing at the same time the performance of the genotypes in the environments, thereby supporting further detailed analysis based on various methods of analyzing genotype-by-environment interaction (DeLacy *et al.*, 1996). Laffont *et al.* (2007) concluded that dot plots and performance plots provide a clearer visualization of genotype performance than biplots, so these types of plots should not be considered competing or alternative but rather complementary; therefore, these different types of plots should be applied together, in that way providing a more comprehensive picture of data. It is also desirable to support interpretation of performance plots with stability measures, so that the plots support understanding the sources of stability or its lack. For example, it can be a different performance in just one environment that is a reason of lack of stability, which can be quickly seen from a performance plot. In addition, all that should be accompanied by formal statistical inference to draw final conclusions. Future research should focus on optimizing performance plots in terms of number of genotypes and/or environments that can be

graphed. Interactive visualization might be an idea for that.

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