GENOTYPE BY ENVIRONMENT INTERACTION EFFECTS ON PLANT HEIGHT OF WHEAT GENOTYPES CARRYING *RHT 8* DWARFING GENE

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ABSTRACT

Twenty-five bread wheat genotypes (G), carring *Rht* 8 dwarfing gene, selected from Facultative and Winter Wheat Observation Nursery for Semiarid Environments (FAWWON-SA) of International Winter Wheat Improvement Program (IWWIP) were tested across 14 environments (E) from European, Asian and African Continents during the 2011-2012 cropping season in order to detect the effects of G, E and GE interaction (GEI) on plant height (PH) by means of pattern analysis (PA). It showed that Gs originated from Russia, Ukraine and IWWIP were semi-dwarf taller than those of National Bread Wheat Breeding Program of Turkey (NBWBPT). In this study, medium-tall Gs were favorable to rain-fed Es, due to the positive relationship between PH and grain yield. It has been suggested that ZAF01 (Bethlehem-South Africa) among 14 Es could be more suitable for phenotyping Gs for PH potential. In conclusion, Eastern European germplasm was able to adapt to almost all Es, whereas genotypes from NBWBPT were not. Therefore, the latter needs improving its adaptability to stressful Es.

Key words: Bread wheat, plant height, genotype by environment interaction

INTRODUCTION

IWWIP is a joint program between Turkey, CIMMYT and ICARDA. Its main objective is to develop winter/facultative wheat germplasm for the region of Central and West Asia. It also facilitates the winter wheat germplasm exchange for the global breeding community. Its germplasm development targets both irrigated and dryland conditions. It annually distributes nurseries to more than 100 cooperators in more than 50 countries. In addition, interested breeding programs submit their material to IWWIP for inclusion into international testing (http://www.iwwip.org).

IWWIP oftenly use parents, carring *Rht* (reduced height) genes, in crossing blocks for improving widely adapted Gs. The adoption of 'Norin 10' semi-dwarfing genes *Rht*-B1b (formerly *Rht* 1) and *Rht*-D1b (formerly *Rht* 2) was a major event in wheat breeding, making a substantial contribution to the 'Green Revolution' (Hedden, 2003). These two dwarfing genes are effective in reducing plant height and have been associated with increased wheat yields, improved lodging resistance and higher harvest indices (Worland et al., 1994; Beharav et al., 1998). But they are not beneficial in the Mediterranean environment, where high temperatures and drought are commonly encountered in the period between anthesis and grain filling (Worland et al., 2001). As a result, alternative dwarfing genes, such as the GA (gibberellic acid)-sensitive *Rht* 8, have become widespread among cultivars grown in the Mediterranean basin and Southern Europe (Worland et al., 1998).

Singh et al. (2001) developed a set of near-isogenic lines in 10 modern CIMMYT bread wheat and six durum wheat backgrounds. They assessed the effect of the *Rht*-B1b and *Rht*-D1b dwarfing alleles in six Es with varying levels of drought stress. Trethowan et al. (2001) studied the same germplasm and found that while the presence of a height reducing allele decreased both the coleoptile length and plant height, there was a significant genetic background effect for these traits among the different isolines relative to any height reducing alleles.

Globally distributed FAWWON-SA targets dry Es with the yield level of 1-3 t/ha. Its objective is to offer diverse germplasm for evaluation and selection of the best lines for utilization in crosses or further studies. Most of the entries in this nursery are tall with the height above 100 cm under the dryland conditions of Turkey. The FAWWON-SA germplasm developed by Turkey-CIMMYT-CARDA IWWIP Program is combined with the germplasm from the breeding programs in Eastern Europe, Iran, S. America, Turkey and USA which generously agreed to share their germplasm. This

introduced germplasm is pre-screened in Turkey for adaptation to dry E and diseases.

PA which consists of cluster (Fox and Rosielle, 1982) and biplot (Gauch and Zobel, 1997) techniques was developed to use some of the functions of these methods jointly. The GEI information from MET (Multi-Environment Trial) grown over diverse Es can be studied with PA (DeLacy et al, 1996; Zobel et al., 1988) to identify Gs with similar responses across Es, and to identify those Es which produce similar discriminations among the Gs growing in them. PA has been applied to many MET and shown to be very effective (Abdalla et al., 1996; Lillemo et al., 2004; Zhang et al., 2006).

Using PA, we were interested in detecting effects of GEI on PH of 25 Gs, carrying *Rht* 8 gene, selected from FAWWON-SA tested across 14 Es. Information gained

from this study should facilitate the design of a testing and/or breeding strategy to assist in selecting superior genotypes for target growing sites.

MATERIALS AND METHODS

Field trials

Twenty-five Gs (G1-G25), including 14 advanced lines and 11 cultivars were evaluated in 14 Es representing different ecosystems and climates from Asia, Europe and Africa during 2011-2012 cropping season (Tables 1 and 2). Gs used in this study were selected from FAWWON-SA based on their PH data over 14 Es. The trials were set up using alpha lattice design (Patterson and Williams, 1976) in two replications in a plot size of 2.5 m length, six rows with 0.2 m spacing between rows. Standard agronomic practices were applied as per the recommendation of each E in each country.

Table 1. Code, parentage, cluster and plant height values of the 25 genotypes

Code[†]	Genotype	Origin[‡]	PH[¥] (cm)	SC[§]	Yield (kg/ha)
G1	SONMEZ	IWWIP	80	1	3669
G25	URMAS	MOL	73	1	3879
G13	SARATOVSKAYA90	RUS	77	1	3500
G14	KATIA1	BG	76	1	3860
G3	VEE/TSI//GRK/3/NS55.03/5/C126.15/COFN//6/TAM200/KAUZ	IWWIP	71	1	3513
G19	8272-1-1//MOMT/KATE/4/RPB8-68/CHRC/3/KRMN//NO57/PEX	TR	72	1	3520
G20	ID#840335//PIN39/PEW/3/DMNT	TR	71	1	3730
G21	BEZ//BEZ/TVR/3/KRMN/LOV29/4/KATE/5/MOM	TR	72	1	4126
G5	CHIRYA.3/GK OTHALON	TR	74	1	3529
G24	NI98414 (=NE90614/NE87612//NE87612)/WESLEY	USA	75	1	4011
G10	KOLOS MYRONIVSCHYNY	UKR	79	1	3873
	Mean		74		3746
G6	VP1620 (VF304/TTAU.69.5-33//YANAC)	AUS	66	2	3400
	Mean		66		3400
G18	TİLEK/4/JSW 6/LOV 13//JSW 3/3/EİKA	TR	63	3	3319
G22	DMNT/7/BEZ/TVR/5/CFN/BEZ//SUW92/CI13645/3/NAİ60/4/EMU"S"/6/UNA	TR	69	3	3634
G23	BEZ/SAD1*6 (8)	TR	66	3	3887
	Mean		66		3613
G2	MUFITBEY	IWWIP	83	4	4016
G16	ZHEMCHUZHINA POVOLZHJYA	RUS	80	4	3792
G15	SARATOVSKAYA17	RUS	85	4	3512
G4	VRZ/3/ORF1.148/TDL//BLO/4/PONY/OPATA	IWWIP	81	4	3747
G17	MALAHIT	RUS	83	4	3800
G7	FRTL/NEMURA	MEX	88	4	4162
G8	BEZ/NAD//KZM (ES85.24)/3/MILAN/4/SPN/NAC//ATTILA	IWWIP	85	4	3912
G9	CTK/3/ATL66/CMN//TX2607/4/SS8/LLFN/3/BEZ/NAD//KZM74/BB//CC/CNO*2/3/TOP156/BB/5/GUN91/6/TAM200/KAUZ	IWWIP	83	4	3669
G11	SMUGLYANKA	UKR	81	4	4100
G12	SNIZHANA	UKR	83	4	4129
	Mean		83		3884
	Over All Mean		77		3772

[†] Genotypes were ordered based on genotype clusters; [¥] PH, plant height; [§] SC, Sub-cluster numbers (see Figure 1); [‡]RUS, cultivars from Russian Wheat Breeding Program; TR, advanced lines from Turkish National Wheat Breeding Program; MEX, advanced line Mexico based wheat program of CIMMYT; IWWIP, advanced lines from Turkey based Turkey-CIMMYT-ICARDA International Winter Wheat Improvement Program; BG, cultivar from Bulgarian National Wheat Program; UKR, cultivars from Ukranian National Wheat Breeding Program; USA, advanced line from North American wheat breeding programs; AUS, advanced line from Australian National Wheat Breeding Program; MOL, cultivar from Moldovan National Wheat Breeding Program

Table 2. Code, cluster, plant height values, climatic and geographical characteristics of 14 environments

Code[†]	Country	Location	Latitude	Longitude	Altitude (masl)	Sub-Cluster	Plant Height (cm)	Climate	LTAP[§] (mm)
AFG01	Afghanistan	Kabul	34°25'N	68°07'E	1825	1	88	SA[‡]	312[¥]
AZB02	Azerbaijan	Baku	40°23'N	49°52'E	-28	1	89	SSA	210[¥]
BUL01	Bulgaria	Dobrich	43°39'N	28°01'E	236	1	92	HC	541
ARM02	Armenia	Echmiadzin	40°10'N	44°17'E	853	1	85	C	301
ESP07	Spain	Lleida	41°63'N	0°78'E	243	1	85	SA	369
SRB01	Serbia	Novi Sad	45°3'N	19°8 'E	84	1	85	HC	647
	Mean						87		
ZAF01	South Africa	Bethlehem	28°16'S	28°30'E	1696	2	101	HC	680
	Mean						101		
GEO03	Georgia	Tbilisi	41°43'N	44°47'E	563	3	74	C	568
IRN14	Iran	Ardabil	38°15'N	48°17'E	1350	3	74	SA	303[¥]
KAZ01	Kazakhstan	Almaty	43°24'N	76°61' E	760	3	64	HC	684
KAZ02	Kazakhstan	Saryagash	41°48'N	69°35'E	419	3	63	C	576
RUS01	Russia	Krasnodar	45°02'N	38°95'E	17	3	64	HC	735
	Mean						68		
IRN11	Iran	Maragheh	37°24' N	46°16' E	1852	4	54	SA	353
UKR04	Ukraine	Kharkov	50°0'N	36°13'E	143	4	58	HC	517
	Mean						56		
	Overall Mean						77		

[†] Environments were ordered based on environment clusters; [‡] SA, semi-arid; SSA, subtropical semi-arid; HC, humid continental; C, continental; [§]LTAP, long term annual precipitation (mm); [¥] supplementary irrigated environments (AFG01, AZB02 and IRN14)

Analysis of variance (ANOVA) and pattern analysis (PA)

PH data collected from 25 Gs tested across 14 Es were used to examine the partitioning of sum of squares (SS) to G, E and GEI with the mean squares of the error. Before the application of PA, the data matrix was standardized within Es, whereby the E main effects and the grand mean are removed, with the remainder divided by the within E standard deviation (Fox and Rosielle, 1982; DeLacy et al., 1996). From the standardized data matrix, a squared Euclidean distance matrix (i.e. a distance matrix) was computed for Gs and Es. Hierarchical agglomerative clustering (Williams, 1976) with incremental SS (Ward, 1963) as the fusion criterion was applied to the matrices, i.e. in any part of the dendrogram, members or groups were joined to minimize the new within group SS (Figures 1 and 2).

The biplot derived from PCA (principal components analysis) (using E standardized data) assessed the relationships among Gs, among Es, and between Gs and Es (Kempton, 1984; Figure 3). The statistical software CROPSTAT, which was developed by International Rice Research Institute, was used to perform the ANOVA and PA. In order to draw visually better dendrograms, they were constructed using MINITAB while the biplot was depicted by means of Biplot and Singular Value Decomposition Macros for Excel© (Lipkovich and Smith, 2002).

Genotyping analysis for Rht 8 gene

According to the method described by Korzun et al. (1998), genotyping analysis for *Rht* 8 gene was conducted at CIMMYT in Mexico.

RESULTS AND DISCUSSION

ANOVA

ANOVA indicated that the E main effect was the predominant significant source of variation, followed by G main effect and GEI. The proportion of the total sum of squares due to G, E and GEI during the 2011-2012 cropping season was 18, 71 and 11 % for PH. The ratio of the sum of squares due to GEI and those due to G main effect with respect to E main effect were 3.9 and 0.4 for PH (data not shown).

Genotype and environment means

Mean PH for Gs was 77 cm and varied from 66 cm for G18 to 88 cm for G7 (Table 1). Of 25 Gs, 7, from NBWBPT, were among the shortest ones. On the other hand, Gs from Russia, Ukraine and IWWIP were mostly taller than the other ones.

As for Es, PH ranged between 54 cm at IRN11 (Maragheh-Iran) to 101 cm at ZAF01 (Bethlehem-South Africa) (Table 2). On the other hand, the Es differed in amount of rainfall (Table 2), which caused contrasting growing conditions and therefore a range of PH under

rainfed conditions. The annual rainfall varied from 210 for AZB02 (Baku-Azerbaijan) to 735 mm for RUS01 (Krasnodar-Russia). They also had adverse climatic patterns, ranging from semi-arid for AFG01 (Kabul-Afghanistan) to humid continental for BUL01 (Dobrich-Bulgaria).

Clustering genotypes and environments

Applying distance level where 50 % or more of the sum of squares of the GEI was retained, leads to distinguishing four sub-clusters (SC) for G and E in regard to the PH investigated during the 2011-2012 crop cycle (Zhang et al., 2006). This clustering resulted in an 81 % reduction in data size, while retaining 85 % of the sum of squares of G, 82 % of sum of squares of E for PH (data not shown). The results of cluster analysis based on adjusted PH data from 14 Es and 25 Gs are given in Tables 1 and 2 as well as Figures 1 and 2.
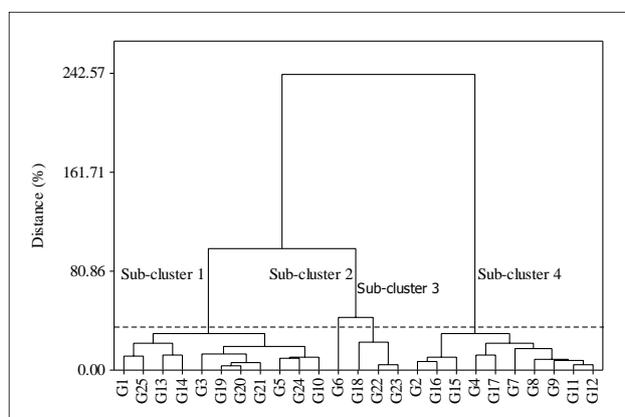

Figure 1. Dendrogram by cluster analysis conducted for plant height data obtained from 25 genotypes tested across 14 environments (For further information about genotypes, see Table 1)
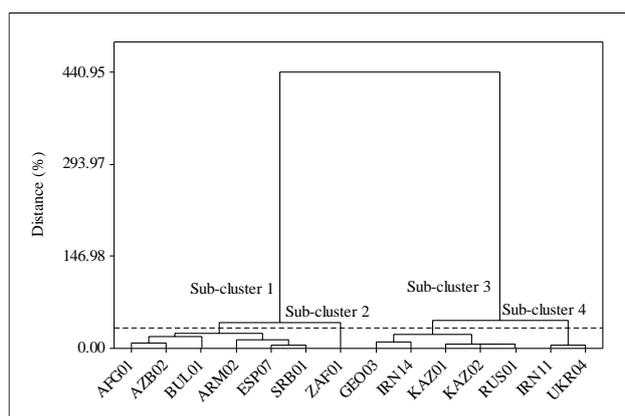

Figure 2. Dendrogram by cluster analysis conducted for plant height data collected from 14 environments (For further information about environments, see Table 2)

Considering G clustering, G1, G25, G13, G14, G3, G19, G20, G21, G5, G24 and G10, respectively, were in the first SC, with mean of 74 cm in PH, ranging from 71

to 80 cm, but the Gs from second and third SCs were the shortest ones, with mean 66 cm. Consequently, all Gs from SCs 1, 2 and 3 (except G1, G13 and G10) were shorter than overall mean (77 cm) in PH. Interestingly, majority of the shortest Gs were from NBWBPT. The fourth SC included G2, G16, G15, G4, G17, G7, G8, G9, G11 and G12, with mean of 83 cm in PH, ranging from 80 to 85 cm. On the other hand, Gs, mostly originated from Russia, Ukraine and IWWIP, in the SC 4 were taller than those in the SCs 1, 2 and 3.

As for E clustering, AFG01, AZB02, BUL01, ARM02, ESP07 and SRB01 were in the first SC of the dendrogram (Figure 2), with mean of 87 cm in PH after E ZAF01, a single member of the SC 2, with mean of 101 cm. The third SC consisted of Es GEO03, IRN14, KAZ01, KAZ02 and RUS01, with mean of 68 cm in PH. IRN11 and UKR04 were in the fourth SC, with mean 56 cm in PH. Certainly, the first result from E clustering showed that Es in the SC 1 and 2 could be used in phenotyping Gs for determining potential PH. The second conclusion was that Gs from NBWBPT exhibited the poor adaptation to SC 3 and 4 Es, due to Eastern European and Asian adverse climatic conditions such as Russia, Kazakhistan and Ukraine and a severe drought occurred in the Northen Iran, during the crop season of 2011-20112.

Biplot analysis

The first two principal components (PCs), which accounted for 68 % of the total variation, were used for depicting the biplot (Figure 3). Gs, which were taller than the overall mean of 77 cm, were grouped at the positive axis of the first PC, whereas Gs, which were shorter than the average, were at the negative side of the PC 1. The biplot revealed that semi-dwarf tall Gs had similar responses across Es; however, semi-dwarf short ones differed considerably. In case of desirability of Gs for PH, the semi-dwarf tall ones should be positively selected, because PH was positively correlated with grain yield ($r = 0.482$; $p<0.01$) in this study. Accordingly it might be resulted that semi-dwarf tall Gs could be more tolerant than the semi-dwarf short ones tested across Es used in this research. As for Es, all of them were grouped at the positive axis of PC 1 (Figure 3). That all E PC1 scores are positive allows PC1 in the biplot to be interpreted as representing proportional G differences across Es, which leads to a non-crossover GE interaction (Yan et al., 2000). In other words, G rankings based on PH were not mostly changed across Es.

Adjacent Es cause similar discrimination among the Gs. Both all Gs, which were taller than the average G (77 cm), and Es were located at the positive axis of PC 1 (Figure 3). This showed that semi-dwarf tall Gs generally were adaptable to almost all Es used in the study. The only AFG01 was separated from the Es, due to the fact that G ranking for PH in this E could be different from those in the rest of Es.
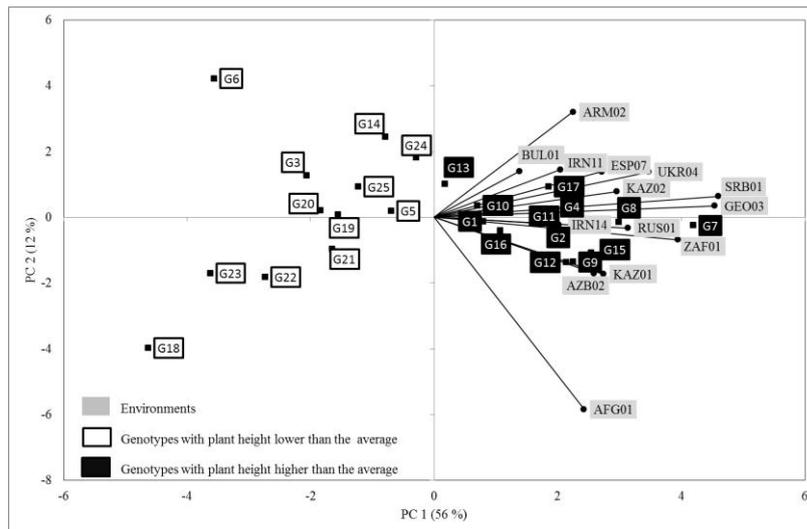
Figure 3. Biplot by Principal Components Analysis conducted for plant height data obtained from 25 genotypes tested across 14 environments (For further information about genotypes and environments, see Tables 1 and 2, respectively)

The rapid global spread of the *Rht*-B1b and *Rht*-D1b dwarfing alleles during the Green Revolution allowed wheat breeders to improve wheat with less risk of lodging. Hence, improvements in yield, quality, and disease resistance have, in general, been made in the presence of one of these dwarfing alleles. However, tall varieties may be desirable for reasons other than high yield, including high biomass and longer straw lengths. The longer coleoptiles and larger root systems of tall cultivars compared with the semidwarfs likely contributes to their relative adaptation to dry Es, where deep sowing ensures contact with available soil moisture (Rebetzke and Richards, 2000; Trethowan et al., 2001). However, other studies have proposed breeding ''tall dwarfs'' for adaptation to dry Es (Borrner et al., 1993; Budak et al., 1995).

One of the winter/facultative wheat breeding goals of the IWWIP is to develop Gs carring *Rht* 8 for where drought and heat stress occur predominantly. Worland and Law (1985) reported that the distribution of GA-insensitive dwarfing genes (*Rht*-B1b and *Rht*-D1b) is restricted to areas where heat and drought stress condition prevails during grain filling. Ellis et al. (2005) have suggested that both *Rht*-1 dwarfing alleles (*Rht*-B1b and *Rht*-D1b) also negatively affect the growth of young plants, but that this effect is not mirrored by *Rht*-8. Therefore, *Rht*-8 might be more suitable in reducing final plant height, without compromising early plant growth (Ellis et al., 2005).

Currently used Gs were distributed across the facultative/winter wheat Es to test them under the FAWWON-SA. Test Es varied widely for levels of precipitation, latitudes ranging from 28.16'S (South Africa) to 50°0'N (Ukraine) and altitudes from -28 m (Azerbaijan) to 1852 m (Iran). Even if Es differed in their geographical and climatic characteristics, E discrimination by cluster analysis was materialized only based on PH, because of lack of the soil and climate data availability for each E. It was shown that currently available E data were

irrelevant in clustering Es considering results of analyses conducted between spatial (e.g. environmental) and phenotypic (e.g. PH) data. But, it is obvious that the more spatial data, including soil and seasonal climatic observations and measurements, should help the more precise discrimination in clustering of Es.

Russian wheat cultivar 'Bezostaya-1' is used in crossing blocks as a source for *Rht*-8 gene in IWWIP, for improving quality as well. Indeed, Bezostaya-1 contains Japanese Aka Komugi in its pedigree, well known as the ancestor for *Rht* 8 gene (Worland et al., 1998). All of the Gs used in this research carry *Rht*-8 gene possibly due to Bezostaya-1 existing in their pedigrees.

Averaged over all Es, the *Rht*-8 containing Gs, which were originated from Russia, Ukraine and IWWIP, consistently were taller (about 10 cm) than the other ones. On the orher hand, Gs selected from NBWBPT to IWWIP showed poor adaptability to almost all Es. To eliminate the poor adaption genes from the Turkish materials, frequency of *Rht*-8 gene should be increased because it was rare (26 %) in Turkish germplasm, comparing with that in Italian (60 %) and Yugoslavian (86 %) wheat (Guedira et al., 2010; Yediay et al., 2011). In the Mediterranean and South-east Anatolian regions of Turkey, where heat and drought stresses are common place from anthesis onwards and especially during grain filling, since the GA-insensitive *Rht*-1 dwarfing genes are not well adapted to these conditions, *Rht*-8 would be a valuable resource for Turkish wheat breeding (Yediay et al., 2011).

We also recommend that 1BL.1RS wheat-rye translocations should be used in Turkish wheat breeding program to enhance the adaptation to stressful Es. It is well documented that 1BL.1RS wheat-rye translocations are useful, because of their positive agronomic traits including yield performance, yield stability, wide adaptation and stress tolerance (Rajaram et al., 1983; Villareal et al., 1991; Waines and Ehdaie, 2007). Yediay et al. (2010) have screened 107 wheat Gs, including

durum and bread wheat cultivars and landraces from Turkey using six rye-specific DNA markers. It has been revealed that only four Turkish bread wheat cultivars carry the 1BL.1RS wheat-rye translocations. Comparing the 1BL.1RS translocation frequencies in wheat cultivars from Turkey with the frequencies found in USA, China, Bulgaria and Hungary shows that Turkish wheat breeding program has not yet exploited these 1RS resources comprehensively. Taken together, the results of this study and the results presented from Altintas et al. (2007) suggest the need of broadening the genetic base of Turkish wheat breeding material, using alternative sources in crossing programs. A more precise knowledge of the genetic background of the breeding stock will contribute greatly to the creation of new populations with boarder genetic basis (Yediay et al., 2010).

There is something else about wheat stature. Straw per se could be more important than its manipulating genes for some reason. In order to better understand one of the reasons why Turkish wheat Gs were able to poorly adapt to Es, it should be taken into accout that wheat cropping in semi-arid areas of West Asia and North Africa is frequently integrated into a cereal–livestock farming system. The wheat straw, mostly used for feeding animals, represents an important commodity, its average sale price per unit weight being not less than 40 % of that of grain. Therefore, modern, short-stature wheat Gs are not mostly accepted by dryland farmers because of their low straw yield (Annicchiarico and Pecetti, 2003).

We took the messages from this study given below:

1.   PA was an efficient method for detecting effects of GEI on PH. It successfully discriminated semi-dwarf tall Gs vs. semi-dwarf short ones and also favorable Es vs. unfavorable ones based on PH data collected from METs.

2.   Gs originated from Russia, Ukraine and IWWIP program were mostly medim tall, indicating that they might be recommended for IWWIP mandate region, Central and West Asia, because of positive correlation between PH and grain yield.

3.   Genoypes selected from NBWBPT showed poor adaptation to almost all Es. Accordingly, Turkish germplasm can be enriched using Gs carring *Rht* genes and rye translocations in crossing blocks to accelerate its adaptability to stressful Es.

ACKNOWLEDGMENTS

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