

Genotype × Environment Interactions and Heritability Estimates of Agronomic Traits in Selected Tunisian Barley Cultivars

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ABSTRACT

Fifty-nine doubled-haploid (DH) barley lines derived from a cross between the two Tunisian cultivars 'Roho' and 'Line 90' were used to assess the genotype × environment interaction ($G \times E$), heritability estimates and genetic correlations between nine agronomic traits. DH lines were planted in a randomised block design with three replications at Mograne during two successive growing seasons. Each line was scored for: heading date (HD), plant height (PH), spikes number per meter (SN), ear length (EL), number of seeds per spike (NSS), 1000-grains weight (TGW), biomass (BM), seed yield (SY) and harvest index (HI). DH lines exhibited better performance for seed production in the first experimental season and an earlier heading associated with a higher vegetative development in the second season. Pooled analysis of variance across environments indicated that the main effects of genotype and environment (year) were highly significant for all traits except SY. The $G \times E$ interaction was also highly significant for all the traits, except TGW. Broad sense heritability estimates for mean values across environments ranged from 0.33 for HI to 0.96 for NSS. Heritability estimates of NSS and TGW were the highest, those of HD, PH and EL were high, but those of SN, BM, SY and HI were relatively low. Genetic correlation analysis indicated significant associations among PH, EL, BM and SY, and among HD, SN, NSS and TGW. Furthermore, HD was also positively correlated with PH and EL. The results obtained suggest that loci for several agronomic traits may be pleiotropic or linked. Selection efficiency to improve BM and SY could be achieved using subsidiary traits that are highly heritable and genetically associated. Thus, PH, LE could be considered as effective selection criteria along with earliness, NSS and TGW.

Keywords: agronomic character, genetic correlation, *Hordeum vulgare*, seed yield, variance component

Abbreviations: BM, biomass; DH, doubled-haploid; EL, ear length; $G \times E$, genotype × environment interaction; HD, heading date; HI, harvest index; QTL, quantitative trait locus; NSS, number of seeds per spike; PH, plant height; SN, spike number per meter; SY, seed yield; TGW, thousand-grain weight

INTRODUCTION

Barley (*Hordeum vulgare* L.) is an important crop in Tunisia. It covers around 500,000 ha annually representing around 33% of the total cereal area. Barley is used mainly for animal feeding as grain, straw or grazed as forage early in the season, as well as for direct human consumption. However, barley average grain yield is low and ranging from 0.4 to 1.7 t/ha during the period 1980-2008. This limited yield is attributed to the prevailing growing conditions of semi-arid areas where marginal soils and reduced cultural practices are frequently used (Anonymous 2009).

The main objectives of the national barley improvement programmes include the development of cultivars with high-grain yield, high-straw quantity, and resistance to biotic and abiotic stresses. The mode of inheritance of grain yield and most agronomic traits is complex, governed by several genes and influenced by environmental conditions (Falcoener 1981; Peighambari *et al.* 2005). Genotype × environment interactions ($G \times E$) can affect breeding progress because they often complicate the evaluation and selection of superior genotypes. Because of their importance in plant breeding and evolution, $G \times E$ of quantitative traits have been the subject of extensive investigations for several crops including barley (Teulat *et al.* 2001; Pillen *et al.* 2003; Peighambari *et al.* 2005; Sameri *et al.* 2006; Shahinnia *et al.* 2006; Von Korff *et al.* 2006). Moreover, multiple traits are of further interest for breeders when searching for indirect traits in selection schemes. By exploiting genetic correla-

tions between traits, subsidiary traits can be used to improve primary ones that have low heritability or are difficult to measure. Many investigations were carried out to study the relationship between agronomic traits in barley (Jui *et al.* 1997; Choo *et al.* 2001; Li *et al.* 2005, 2006; Sameri *et al.* 2006).

Double-haploid (DH) lines are suited for studying the inheritance of qualitative and quantitative traits (Choo *et al.* 2001). Moreover, these lines present an unlimited number of individuals facilitating the estimation of $G \times E$ interactions by increasing the number of possible replications (Choo *et al.* 1985) and thus estimating heritability (Marwede *et al.* 2004; Peighambari *et al.* 2005). This study aims to assess $G \times E$ interactions and heritability of agronomic traits in a DH population derived from Tunisian barley cultivars grown during two cropping seasons and to estimate the genetic correlations between these traits.

MATERIALS AND METHODS

Plant material used in this study consisted of 59 DH barley lines produced from F_1 plants of the cross 'Roho' × 'Line 90'. These two Tunisian parents were selected and crossed, at the National Agronomic Institute of Tunisia, because they differed by several agro morphological traits. 'Roho' is an early two-row and spring barley cultivar with short straw; whereas 'Line 90' is a late six-row and spring barley cultivar with a tall straw. The DH lines were developed by the seed coop. 'Florimond Desprez Veuve and Fils', using anther culture and the *Hordeum bulbosum* method (Devaux

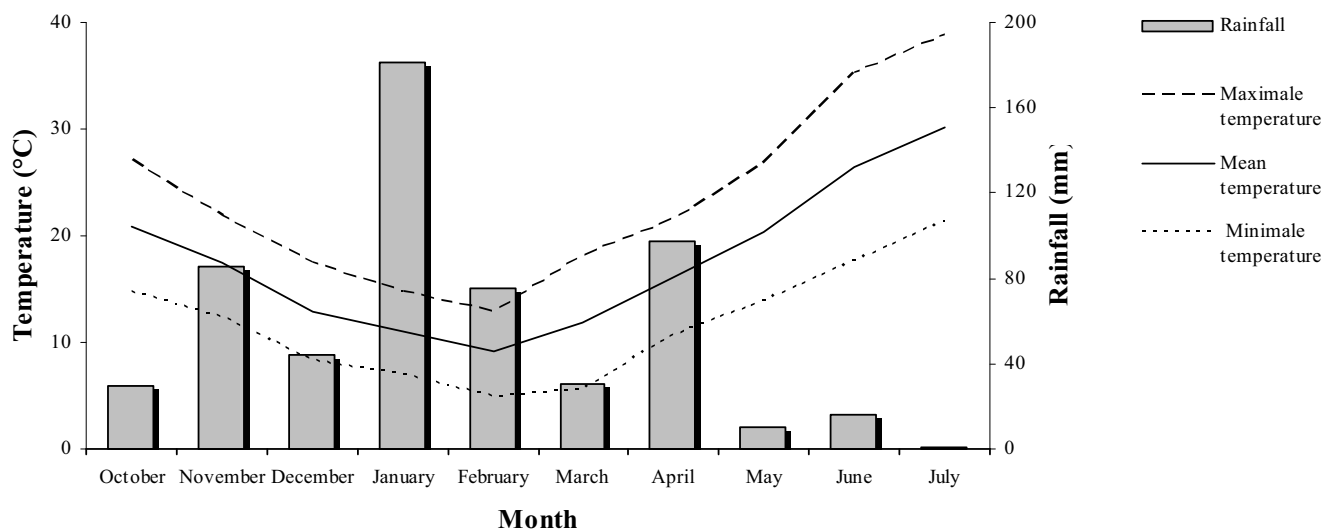


Fig. 1 Repartition of temperatures and rainfall in Mograne during 2002-2003.

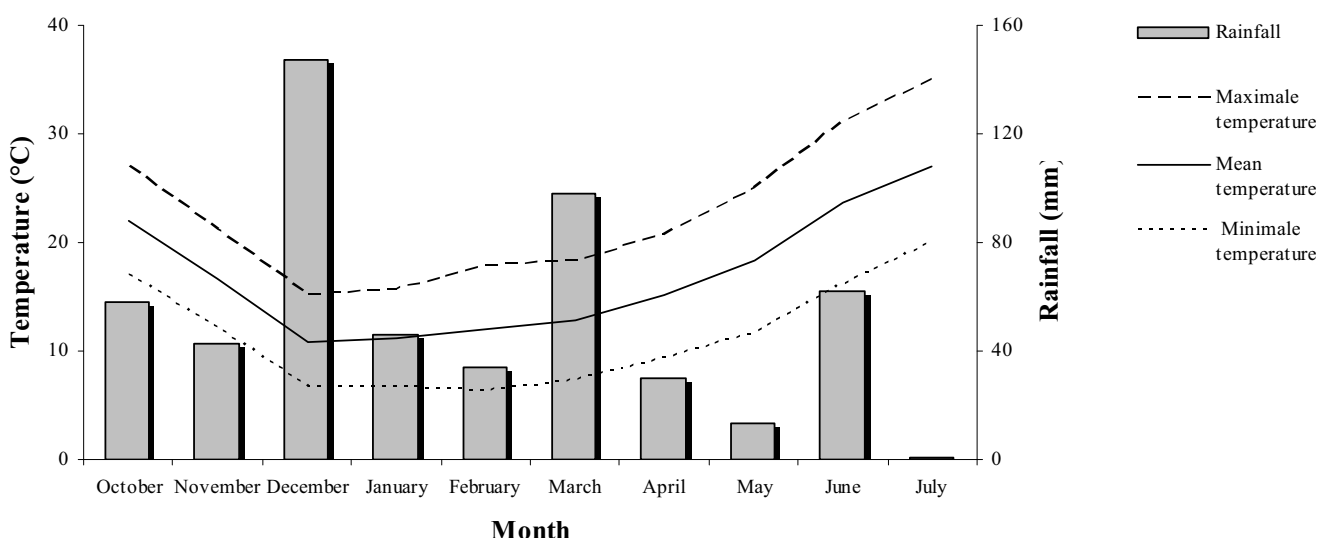


Fig. 2 Repartition of temperatures and rainfall in Mograne during 2003-2004.

and Pickering 2005).

The DH lines were grown in a randomised block design with three replications at the research farm of Superior Agronomic School of Mograne during 2002-2003 and 2003-2004. These two seasons showed great differences in temperatures and rainfall distributions (Figs. 1, 2). Each DH line was sown in single rows on 5 December 2002 and in two rows on 17 November 2003. Row-lines were 1 m long and spaced 0.5 m apart.

The DH lines were evaluated for the nine agronomic traits: heading date (day), plant height (cm), spikes number per meter, ear length (cm), number of seeds per spike, 1000-grains weight (g), biomass (g/m), seed yield (g/m) and harvest index (%). The heading date (HD) was evaluated based on the number of days from sowing to half emergence of the ears. Plant height (PH) was calculated as the average height of five randomly selected plants per line measured from the ground to the top of the terminal spikelet (excluding awns) at maturity. Spikes number per meter (SN) indicated the number of tillers with fertile spikes. Ear length (EL) was calculated as the average length of five randomly selected ears measured from the base of the spike to the tip of the terminal spikelet (excluding awns). Number of seeds per spike (NSS) was counted as the average number from five randomly selected ears collected at harvest, excluding empty or unfilled spikelets from an ear. Thousand grains weight (TGW) was determined as the weight of a sample of 1000 grains after harvest. Biomass (BM) was evaluated as the total weight of all the straw from one meter measured after harvest. Seed yield (SY) was assessed as the total grain weight of a one-meter line measured after harvest. Harvest index

(HI) was calculated as the ratio between seed yield and biomass.

Analysis of variance was performed for data obtained from two-year experiments using PROC ANOVA (SAS Institute 1988). Then, components of variance were estimated for each of the nine agronomic traits using REML of proc MIXED of SAS. The following model was used for these analyses:

$$Y_{ijk} = \mu + E_i + R_j(E_i) + G_k + E_iG_k + \epsilon_{ijk}$$

where Y_{ijk} = observation of genotype k in environment i in replication j, μ = general mean, E_i = effect of environment i, $R_j(E_i)$ = effect of replication j in environment i, G_k = effect of genotype k, E_iG_k = genotype x environment interaction of genotype k with environment i, and ϵ_{ijk} = experimental error.

Broad sense heritability (H^2) estimates were calculated from variance components according to the formula proposed by Marwede *et al.* (2004):

$$H^2 = \sigma^2_g / (\sigma^2_g + \sigma^2_{ge}/E + \sigma^2_{\epsilon}/ER)$$

where, σ^2_g , σ^2_{ge} , and σ^2_{ϵ} are the genotypic variance, the G x E interaction variance, and the environmental variance respectively. E and R are number of environments and replicates, respectively.

Genetic correlation coefficients were estimated between traits investigated in both years. Variance and covariance components were estimated by the REML method of SAS PROC MIXED (SAS Institute 1988).

RESULTS AND DISCUSSION

Summary statistics of the phenotypic performance of the 59 DH lines for nine agronomic traits assessed in Mograne during 2002-2003 and 2003-2004 are represented in **Table 1**. A wide range of variations was found among the DH lines for all the traits. Moreover, the DH lines expressed better performance for seed production in the first experimental season and an earlier heading associated with a higher vegetative development in the second season. Greater number of DH lines grown in 2002-2003, than those grown in 2003-2004 produced longer spikes with higher NSS and TGW. In addition, the averages SY and HI were superior in 2002-2003 than in 2003-2004. Whereas, early heading, taller plant heights were noted for all DH lines evaluated in 2003-2004 than those evaluated in 2002-2003. Results indicated also that more important DH lines proportion were associated with fertile tillering and biomass production during the second cropping season. These results would suggest that high temperature and rainfall distribution during the vegetative growth are among the factors that enhanced the expression of these traits.

Pooled analysis of variance across environments indicated the presence of highly significant genotype effect for all traits and a highly significant year (environment) effect for all characters studied, except SY (**Table 2**). $G \times E$ was highly significant for all traits, except TGW. Previous studies have also reported significant $G \times E$ effect for different agronomic characters in barley populations (Teulat *et al.* 2001; Pillen *et al.* 2003; Peighambari *et al.* 2005; Von Korff *et al.* 2006, 2008; Schmalenbach *et al.* 2009).

Variance components for agronomic traits are summarized in **Table 3**. Although the genotypic effects (σ^2_G) were highly significant, their relative contributions to the total variation were different for the nine agronomic traits. In fact, the variance among the genotypes (σ^2_G) accounted for 29, 11, 28, 34, 82, 43, 24, 23 and 11% of the total phenotypic variance for HD, PH, SN, EL, NSS, TGW, BM, SY and HI, respectively. Furthermore, the variance among environments (σ^2_E) was very high for PH (76% of the total phenotypic variance) and very low to negligible (0% to 6% of the total phenotypic variance) for SN, EL, NSS, BM, SY and HI. The contribution of $G \times E$ interaction to the total phenotypic variance differed with the agronomic character. Thus, the $G \times E$ interaction variance (σ^2_{GE}) represent 24, 5, 42, 19, 5, 3, 34, 48 and 27% of the total variance of HD, PH, SN, EL, NSS, TGW, BM, SY and HI, respectively. **Table 3**

Table 1 Variation of nine agronomic traits^a in 59 doubled-haploid lines of barley evaluated at Mograne during 2002-2003 and 2003-2004.

Agronomic trait	Mean	Min	Max	LSD 0.05
Mograne 2002-2003				
HD	133.58	127.00	138.33	2.32
PH	82.61	59.40	104.00	8.27
SN	185.88	91.00	340.00	37.67
EL	7.75	5.83	9.42	0.86
NSS	30.68	17.50	65.67	4.86
TGW	45.80	31.80	64.00	8.47
BM	486.11	155.50	960.50	112.24
SY	130.26	50.50	300.60	25.29
HI	27.40	16.21	41.60	8.51
Mograne 2003-2004				
HD	129.38	121.00	138.33	3.46
PH	108.40	97.80	131.07	10.11
SN	200.16	88.67	307.50	74.58
EL	7.47	6.32	9.02	0.93
NSS	25.94	14.89	53.22	6.31
TGW	37.75	22.37	50.40	6.20
BM	508.49	300.30	836.30	213.45
SY	125.72	75.85	210.82	47.48
HI	25.02	16.51	33.44	7.86

^a HD: heading date (day); PH: plant height (cm); SN: spikes number per meter; EL: ear length (cm); NSS: number of seeds per spike; TGW: thousand grains weight (g); BM: biomass (g/m); SY: seed yield (g/m); HI: harvest index (%)

indicates that the experimental error contributed by 7% (for PH and NSS) to 58% (for HI) to the total variance. All these data affected the broad sense heritability (H^2) estimates for mean values across environments (**Table 3**). Heritability estimates of NSS (0.96) and TGW (0.89) were the greatest, indicating that these two traits were slightly influenced by the environment effect. This result was supported by the reduced $G \times E$ interaction variance (σ^2_{GE}) and residual variance (σ^2_e). Similar results were reported by Peighambari *et al.* (2005) and by Zhang *et al.* (2010). High heritability values for NSS and TGW suggest that selection for these traits may be effective in early segregating population such as F_2 (Sato and Takeda 1995) using results from one to few sites. Heritability estimates using data from the two experimental seasons were also high for HD, PH and EL (0.67 for HD and EL, and 0.74 for PH). However, $G \times E$ interaction variances (σ^2_{GE}) of these traits represented almost 50% of the genotypic variances (σ^2_G). Therefore, it was

Table 2 Analysis of variance for nine agronomic traits^a in 59 doubled-haploid lines of barley evaluated at Mograne during 2002-2003 and 2003-2004.

Source of variation	df	HD	PH	SN	EL	NSS	TGW	BM	SY	HI
Year	1	1555.26**	58873.02**	$18.04 \times 10^{3**}$	7.06**	1989.24**	5728.98**	$4.43 \times 10^4*$	$1.82 \times 10^3^{ns}$	502.68**
Repetition(Year)	4	2.82	596.00	25.24×10^3	0.63	42.71	145.55	4.50×10^4	4.54×10^3	165.15
Genotype	58	67.05**	392.47**	$13.89 \times 10^{3**}$	2.22**	850.71**	280.49**	$8.67 \times 10^{4**}$	$5.88 \times 10^{3**}$	92.07**
G x E	58	22.24**	100.63**	$6.74 \times 10^{3**}$	0.74**	34.87**	30.63 ^{ns}	$4.39 \times 10^{4**}$	$3.32 \times 10^{3**}$	62.02**
Error	232	3.32	32.63	1.33×10^3	0.31	12.14	21.08	1.11×10^4	0.55×10^3	25.68
C.V.%		1.39	5.98	18.93	7.31	12.31	10.99	21.20	18.38	19.03

^a HD: heading date (day); PH: plant height (cm); SN: spikes number per meter; EL: ear length (cm); NSS: number of seeds per spike; TGW: thousand grains weight (g); BM: biomass (g/m); SY: seed yield (g/m); HI: harvest index (%)

** : ns Significant at $P < 0.01$ and at $P < 0.05$, and not significant at $P < 0.05$

Table 3 Variance components and heritability estimates for nine agronomic traits^a in 59 doubled-haploid lines of barley evaluated at Mograne during 2002-2003 and 2003-2004.

	HD	PH	SN	EL	NSS	TGW	BM	SY	HI
σ^2_G ^b	7.47	48.64	1.19×10^3	0.25	135.97	41.64	7.14×10^3	0.43×10^3	5.01
σ^2_E ^c	8.66	328.86	0.00	0.03	10.87	31.49	0.00	0.00	1.70
σ^2_{GE} ^d	6.31	22.67	1.80×10^3	0.14	7.58	3.18	10.92×10^3	0.92×10^3	12.11
σ^2_e ^e	3.32	32.63	1.33×10^3	0.31	12.14	21.08	11.12×10^3	0.55×10^3	25.68
H^2 ^f	0.67	0.74	0.51	0.67	0.96	0.89	0.49	0.43	0.33

^a HD: heading date (day); PH: plant height (cm); SN: spikes number per meter; EL: ear length (cm); NSS: number of seeds per spike; TGW: thousand grains weight (g); BM: biomass (g/m); SY: seed yield (g/m); HI: harvest index (%)

^b σ^2_G : genetic variance

^c σ^2_E : environmental variance

^d σ^2_{GE} : variance of $G \times E$ interaction

^e σ^2_e : error variance

^f H^2 : broad sense heritability estimates

Table 4 Genetic correlation coefficients between nine agronomic traits^a assessed in Mograne during 2002-2003 and 2003-2004 in a 59 doubled-haploid barley lines.

Agronomic trait	HD	SN	NSS	TGW	PH	EL	BM	SY	HI
HD		-0.49**	0.67**	-0.57**	0.52**	0.47**	0.30 ^{ns}	0.03 ^{ns}	-0.38 ^{ns}
SN			-0.85**	0.47**	-0.34 ^{ns}	-0.15 ^{ns}	0.15 ^{ns}	0.16 ^{ns}	-0.21 ^{ns}
NSS				-0.85**	0.21 ^{ns}	0.46**	-0.18 ^{ns}	0.02 ^{ns}	0.35 ^{ns}
TGW					0.16 ^{ns}	-0.14 ^{ns}	0.38*	0.31 ^{ns}	-0.13 ^{ns}
PH						0.70**	0.63**	0.68**	0.09 ^{ns}
EL							0.51*	0.62*	0.16 ^{ns}
BM								0.80**	-0.53 ^{ns}
SY									0.10 ^{ns}
HI									

^a HD: heading date (day); PH: plant height (cm); SN: spikes number per meter; EL: ear length (cm); NSS: number of seeds per spike; TGW: thousand grains weight (g); BM: biomass (g/m); SY: seed yield (g/m); HI: harvest index (%)

** . * . ^{ns} Significant at P<0.01 and at P<0.05, and not significant at P<0.05

apparent that the preponderance effect of the environment could assist in accurately assess heritability estimates and improve selection gains. Finally, heritability values of SN, BM, SY and HI were relatively low ranging from 0.33 to 0.51. These low heritability estimates were attributed to higher $G \times E$ interaction variances (σ_{GE}^2) and experimental error variances (σ_e^2) than the genotypic variance (σ_G^2). These results are expected because the two growing conditions differed greatly from each other, mainly in temperatures and precipitation distributions, sowing date and the importance of disease (net blotch and scald) development. Thus differential expression of SN, BM, SY and HI would be attributed to the differential responses of the DH lines to climatic and disease tolerance. Hence, effective selection for these parameters require several years of experimentations in different environmental conditions. High values of heritability (0.62 to 0.93) for HD, PH, SN, EL, and SY were reported by Peighambari *et al.* (2005), and by Shahinnia *et al.* (2006) and for HD, PH and SN by Eshghi and Akhundova (2010) using data from two cropping seasons. These estimates could be mainly attributed to insignificant year effect and/or insignificant $G \times E$ interaction effect of these traits. Campbell *et al.* (2003) reported that a high $G \times E$ interaction variance observed in the field was reflected by a high frequency of quantitative trait loci (QTL) showing additive \times environment interaction effects. In addition, $G \times E$ interactions effects were explained by the presence of multiple QTLs in the two parents with environment-specific expression (Campbell *et al.* 2003; Peighambari *et al.* 2005; Zhao *et al.* 2005; Li *et al.* 2006; Shen *et al.* 2006).

The genetic correlations among the nine agronomic traits assessed in 'Roho' \times 'Line 90' population were estimated from data combined across environments (Table 4). Significant positive correlations, ranging from 0.51 to 0.80, were observed among PH, EL, BM and SY. Similar results have been reported by Peighambari *et al.* (2005). It is apparent that taller plants with longer ears produce higher biomass and seed yields. Significant genetic correlation between these traits would be attributed to tight linkage of different loci or by pleiotropic effects of one gene (Li *et al.* 2009). Therefore, the results obtained suggest that loci affecting PH, EL, BM and SY may be pleiotropic or linked. Clustering of identified QTLs, for several agronomic traits, in different genomic regions of the barley chromosomes were reported previously (Tinker and Mather 1994; Li *et al.* 2006; Sameri *et al.* 2006). However in several studies (Choo *et al.* 2001; Peighambari *et al.* 2005; Saleem *et al.* 2006; Schmalenbach *et al.* 2009), often SY showed significant and positive genetic correlation with yield components (spike per plant, seed per spike and 1000 grain weight), which are not in agreement with the results of our investigation. This discrepancy could be attributed to genotypes used and to $G \times E$ interactions since pooled data across years were used to estimate correlation coefficients. Results also showed highly significant correlation coefficients (0.47 to 0.85) among HD, SN, NSS and TGW in all combinations. However, positive correlations were observed only between HD and NSS and between SN and TGW. Therefore, early

heading was associated with high fertile tillering, greater thousand grains weight but low number of seeds per spike. It is apparent that loci controlling these four characters are pleiotropic or linked, and positive alleles for HD, SN and TGW were negative for NSS. Furthermore, HD was also positively correlated with PH (0.52) and EL (0.47), indicating that early heading was associated with short plants and short spikes. Favorable alleles for HD, SN and TGW were provided by 'Roho' which is an early, two-row cultivar with high tillering but short straw and short spikes, whereas favourable alleles for NSS, PH and EL were obtained from 'Line90' which is a late six-row barley cultivar with tall straw and long spikes. It was previously reported that the *vrs1* locus, which primarily determines the row type of spike, exerts a pleiotropic or a linkage effect on many agronomic characters, including the number of rachis nodes, spike length, stem length and heading date (Takahashi *et al.* 1975). Therefore, in the present study, the pleiotropic effect of *vrs1* locus was detected for EL, PH and HD. Selection efficiency to improve BM and SY could be achieved using subsidiary traits that are highly heritable and genetically associated. Thus, PH, LE could be considered as effective selection criteria along with earliness, NSS and TGW.

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