Generation means analysis of traits related to lodging using two crosses of durum×emmer wheat

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Abstract

Lodging is one of the most important factors that affect wheat final yield. Emmer is a likely gene source to improve durum wheat; however, it is highly susceptible to lodging. The genetic studies of traits related to lodging in crosses of durum×emmer remains largely understudied. Here, we used progenies (six generations) derived from two crosses of durum×emmer in a generation means analysis (GMA) to determine gene action, inheritance, and genetic gain from selection in respect to plant height and its related traits. The results indicated that lodging resistance was significantly and negatively correlated with plant height and positively correlated with grain yield and mainly influenced by stem diameter. GMA results indicated that epistasis did not play an essential role in the genetic control of lodging related traits and almost the major portion of the genetic variation in these crosses resulted from additive gene actions. Also for all of the studied traits, the additive variance was higher than the dominance one. Narrow sense heritability was higher than 0.60 for most of the traits, and the genetic gain after one cycle of selection was positive for plant height and its components in both crosses. It was found that, selection in early generations may result in simultaneous reduction of plant height and increased stem diameter to improve lodging resistance in durum×emmer crossings.

Introduction

Durum wheat (*Triticum turgidum* subsp. *durum*) is of significance as a food crop being used to make pasta and a variety of other foods. Emmer (*Triticum turgidum* subsp. *dicoccum*) is an important gene source for durum improvement but less studied in crosses for traits associated to present-day cultivars (Faris et al. 2014; Maccaferri et al. 2019). Plant height is one of the important characteristics in order to improve and produce modern wheat varieties. For a long time, early farmers were looking for cultivars that had higher biomass, height, and yielding potential (Peng et al. 2011). However, in the era of the Green Revolution and beyond, plant breeders increased resistance to lodging and grain yield by reducing plant height (Hedden, 2003; Peng et al. 2011). Lodging destroys the canopy structure, reduces photosynthetic capacity, and therefore, affects the transportation of water, photosynthetic materials and the grain filling process (Acreche and Slafer 2011; Berry and Berry 2015). This may reduce grain yield by 80 % in wheat (Foulkes et al. 2011; Berry and Spink 2012). Yet lodging is a complex phenomenon affected by many factors including cropping system, diseases, wind, rain, soil type, and other factors (Zhang et al. 2016; Ahmad et al. 2020). To increase lodging resistance, improving stem strength of wheat is one of the important breeding goals. The primary reason for improving stem strength is to prevent lodging which in turn can facilitate the selection of other yield-enhancing traits such as large spikes (Zhang et al. 2016).

Tetraploid emmer wheat is known as one of the eight founding crops that have caused the agricultural revolution about 10,000 years ago (Faris et al. 2014). Although the grain yield of emmer is much less than durum wheat and inclined to lodge, emmer is valuable for sustainable farming systems because of its resistance to abiotic and biotic stresses, and also higher grain protein content (Zaharieva et al. 2010; Faris et al. 2014).

Adaptation of plants in the face of environmental constraints largely depends on their genetic background (Manschadi et al. 2008) and a better understanding of genetic mechanisms involved. The inheritance of quantitative traits is not based on a simple addition of individual genes and a high incidence of epistasis effects may play a major role compounded by genotype and environment interactions (Fethi et al. 2011). To address these challenges, generation means analysis (GMA) is applied to estimate epistasis effects and gene actions of

quantitative traits (Mather and Jinks 1977), which allows breeders to get a clear understanding of traits genetic control. Additionally, it helps crop improvement by maximizing genetic gain from selection in breeding programs (Ng et al. 2014).

Using a diallel cross-study in bread wheat, it was determined that plant height, spike length, peduncle length, internode length, and internode diameter were controlled by additive gene action (Yao et al. 2011). Additionally, high narrow-sense heritability was reported for these traits. Similarly, in another report on the F₂ population of bread wheat, additive gene action was recorded for the same traits (Khahani et al. 2018). Berry and Berry (2015) estimated heritability greater than 0.5 for the internode length and diameter. Previous studies reported that emmer wheat had greater values of plant height (30 cm) than durum wheat (Longin et al. 2016). The ancient wheat, such as emmer, tends to lodge due to its long and weak stems (Konvalina et al. 2012). Further, other researchers (Rinki Khobra et al. 2019) reported that stem traits such as diameter, solidness, and wall thickness were the best indicators of strength against lodging. Even researchers found a positive correlation between lodging tolerance and stem diameter, but lodging tolerance had a negative relationship with plant height traits and internode length (Xiao et al. 2015; Mirabella et al. 2019).

To explore emmer genetic potential in durum breeding, stem strength and plant height must be considered to prevent lodging and yield reduction. However, genetic interaction and inheritance of traits related to plant height in generations obtained from the cross between the two species remains poorly documented. Here, we addressed this gap using generation means analysis. The objectives were to determine the gene action controlling plant height and its components in two crosses of durum×emmer wheats using GMA, and also to determine heritability and the number of effective factors associated with these traits.

Material And Methods

Plant material

Filial and backcross populations were expanded from two crosses between a lodging-susceptible locally grown emmer wheat (Singerd) with two lodging-resistant durum cultivars (Shabrang and Yavaros). The three parental genotypes (Shabrang and Yavaros = P₁ and Singerd = P₂) plus F₁, F₂, BC₁P₁, and BC₁P₂, were used for generation means analysis.

Experimental Design And Data Collection

The six-generations (P₁, P₂, F₁, F₂, BC₁P₁, and BC₁P₂) from each cross were grown during 2018–2019 (November 2018 to June 2019) in the Research Farm of Isfahan University of Technology located at the central part of Iran (32°32′ N, 51°23′ E, 1630 masl, 15 ° C mean temperature, average annual rainfall 140 mm). The six generations were arranged in a Randomized complete block design with three replications. Each planting row was 1.5 m long with an inter-row spacing of 30 cm and plant to plant distance of 10 cm. A total of 44 rows were planted in each block, which included four rows for each P₁, P₂, and F₁, sixteen rows for F₂, and eight rows for each BC₁P₁ and BC₂P₂. Agronomic management and prevention of pests and diseases were done according to durum wheat's technical recommendations, and harvesting was done manually.

Given that the non-segregating and segregating generations consisted of homogeneous and heterogeneous populations respectively, the number of plants analyzed in each block was different. This included 30 plants for parents and F₁, 180 plants for F₂ and, 75 plants for BC₁P₁ and BC₁P₂. Parameters recorded for individual plants

in each plot included plant height (PH), spike length (SL), peduncle length (PL), second internodes length (SIL), third internodes length (TIL), peduncle diameter (PD), second internodes diameter (SID), and third internodes diameter (TID). Further, assessments of lodging resistance and grain yield were recorded for each plot as a whole.

Generation Mean And Genetic Parameter Analysis

Before performing data analyses, the normality of the data was tested, and the Bartlett test performed to examine for homogeneity of variance (Kozak and Piepho 2018). For each cross, analyses of variance and comparison of mean traits of the six generations were performed using PROC GLM (SAS v. 9.4, SAS Institute Inc. 2014). The principal component analysis (PCA) performed using Statgraphics program version 17.0 to determine relationships among the studied traits and scattering of generations (Malik and Piepho 2018).

Scaling tests (including A, B, C and D) was carried to test the adequacy of the additive-dominance model (additive and dominance without epistatic effects), which described by Mather and Jinks (1949) and Hayman (1960) by using the following formulas:

$$A = 2\overline{B_1P_1} - \overline{P_1} - \overline{F_1}$$

$$B = 2\overline{BC_1P_2} - \overline{P_2} - \overline{F_1}$$

$$C = 4\overline{F_2} - 2\overline{F_1} - \overline{P_1} - \overline{P_2}$$

$$D = 2\overline{F_2} - \overline{BC_1P_1} - \overline{BC_1P_2}$$

All calculations of genetic parameters, variance components, the heritability of traits, the number of effective factors in genetic control of traits, and genetic gain from one cycle of selection were determined using the SASQuant program defined by Gusmini et al. (2007). It should be noted that all the computational formulas in the SASQuant program are given in the appendix of the article.

Results

Analysis of variance and descriptive statistics

The results of the analysis of variance for the parents and progeny generations of the two crosses showed a significant difference between generations for all the measured traits suggesting the existence of considerable diversity between the studied generations. The mean and standard error for each of the measured traits in different generations are presented in Table 2. The mean of F1 generations for traits PH and PL were higher than the superior parent (Singerd), indicating presence of heterosis for these traits. On the other hand, the mean of F1 generations were closer to the one for emmer parent (Singerd) in traits SL, SIL, and TIL and closer to durum parents (Shabrang and Yavaros) for traits PD, SID, and TID. Notably, for all measured traits, the means of F1 hybrids were higher than the means of F2 populations, which is a common occurrence due to segregation and inbreeding in the F2 generation.

Table 1
Mean squares for plant height and its components in the two crosses of tetraploid wheat

Source	DF	Mean square							
		PH	SL	PL	SIL	TIL	PD	SID	TID
Shabrang × Singerd									
Replication	2	44.64 ^{ns}	0.01 ^{ns}	6.83 ^{ns}	5.69 ^{ns}	1.30 ^{ns}	0.04 ^{ns}	0.16 ^{ns}	0.17 ^{ns}
Generation	5	3297.7**	23.01**	1028.2**	227.9**	183.24**	4.31**	7.12**	10.12**
Error	412	97.38	1.25	35.72	9.28	4.81	0.13	0.17	0.14
Yavaros × Singerd									
Replication	2	51.1 ^{ns}	1.60 ^{ns}	26.41 ^{ns}	3.50 ^{ns}	4.32 ^{ns}	0.14 ^{ns}	0.42 ^{ns}	0.05 ^{ns}
Generation	5	5613.6**	43.38**	1517.8**	221.3**	174.17**	4.81**	11.16**	10.89**
Error	412	120.43	1.19	48.92	9.02	4.95	0.18	0.19	0.14
PH, Plant height (cm); SL, Spike length (cm); PL, Peduncle length (cm); SIL, Second internodes length -top to bottom- (cm); TIL, Third internodes length-top to bottom- (cm); PD, Peduncle diameter (mm); SID, Second internodes diameter (mm); TID, Third internodes diameter (mm)									
**and ^{ns} indicate significant at 0.01 probability levels and non-significant, respectively									

Table 2

Mean and their standard error of plant height and its components in six generations from the two crosses of tetraploid wheat

Shabrang (P1) × Singerd (P2)								
	PH	SL	PL	SIL	TIL	PD	SID	TID
P1	90.3 ± 0.55 d	9.23 ± 0.13 d	41.3 ± 0.40 d	16.73 ± 0.29 c	10.67 ± 0.26 d	3.45 ± 0.04 a	4.2 ± 0.06 a	4.32 ± 0.07 a
P2	111.4 ± 0.62 b	11.43 ± 0.17 a	46.83 ± 0.92 c	23.67 ± 0.38 a	17.43 ± 0.27 a	2.49 ± 0.03 e	3.03 ± 0.05 d	2.94 ± 0.05 e
F1	118.5 ± 0.92 a	10.80 ± 0.12 b	56.23 ± 0.74 a	23.1 ± 0.42 a	15.2 ± 0.27 b	3.23 ± 0.05 bc	3.92 ± 0.05 b	3.79 ± 0.03 c
BC1P1	104.8 ± 1.03 c	9.97 ± 0.13 c	46.19 ± 0.55 c	20.16 ± 0.32 b	12.91 ± 0.22 c	3.28 ± 0.04 b	3.94 ± 0.04 b	3.95 ± 0.05 b
BC1P2	113.7 ± 1.19 b	10.73 ± 0.12 b	52.48 ± 0.76 b	22.48 ± 0.33 a	15.01 ± 0.25 b	2.87 ± 0.04 d	3.4 ± 0.05 c	3.21 ± 0.04 d
F2	109.9 ± 0.88 b	10.02 ± 0.10 c	50.1 ± 0.51 b	20.58 ± 0.27 b	13.66 ± 0.19 c	3.1 ± 0.03 c	3.83 ± 0.04 b	3.69 ± 0.03 c
LSD 5%	4.07	0.46	2.46	1.26	0.905	0.147	0.171	0.157
Yavaros (P1) × Singerd (P2)								
	PH	SL	PL	SIL	TIL	PD	SID	TID
P1	81.47 ± 0.77 d	7.96 ± 0.13 d	36.87 ± 0.5 d	16.03 ± 0.31 d	9.97 ± 0.26 e	3.39 ± 0.04 a	4.47 ± 0.06 a	4.35 ± 0.05 a
P2	112.13 ± 1.41 a	11.10 ± 0.16 a	49.97 ± 0.66 b	23.3 ± 0.43 a	16.67 ± 0.28 a	2.53 ± 0.05 d	2.98 ± 0.06 e	2.86 ± 0.04 e
F1	114.53 ± 1.28 a	10.16 ± 0.17 b	55.63 ± 0.78 a	20.87 ± 0.45 b	14.77 ± 0.36 b	3.11 ± 0.06 b	3.78 ± 0.04 b	3.79 ± 0.08 bc
BC1P1	96.04 ± 1.12 c	9.12 ± 0.13 c	46.24 ± 0.59 c	18.36 ± 0.28 c	12.37 ± 0.25 d	3.31 ± 0.04 a	3.94 ± 0.04 b	3.92 ± 0.04 b
BC1P2	110.03 ± 1.26 a	10.37 ± 0.15 b	53.03 ± 1.01 a	21.01 ± 0.37 b	14.29 ± 0.24 bc	2.73 ± 0.06 c	3.21 ± 0.05 d	3.19 ± 0.05 d
F2	101.12 ± 0.97 b	9.58 ± 0.09 c	48.18 ± 0.6 cb	19.47 ± 0.26 c	13.73 ± 0.19 c	3.06 ± 0.04 b	3.54 ± 0.04 c	3.64 ± 0.03 c
LSD 5%	4.53	0.45	2.88	1.24	0.92	0.174	0.177	0.158
PH, Plant height (cm); SL, Spike length (cm); PL, Peduncle length (cm); SIL, Second internodes length -top to bottom- (cm); TIL, Third internodes length-top to bottom- (cm); PD, Peduncle diameter (mm); SID, Second internodes diameter (mm); TID, Third internodes diameter (mm)								

Table 3

Scaling tests and estimates of gene effects with the six-parameter genetic model for plant height and its components in the two crosses of tetraploid wheat

Shabrang × Singerd								
	PH	SL	PL	SIL	TIL	PD	SID	TID
Scales								
A	0.72 ± 2.33	-0.16 ± 0.32	-5.15 ± 1.39**	0.49 ± 0.81	-0.05 ± 0.58	-0.12 ± 0.1	-0.24 ± 0.11*	-0.21 ± 0.12
B	-2.5 ± 2.63	-0.81 ± 0.31**	1.9 ± 1.92	-1.81 ± 0.87*	-2.61 ± 0.63**	0.02 ± 0.09	-0.15 ± 0.12	-0.31 ± 0.1**
C	1.06 ± 4.07	-2.25 ± 0.51**	-0.19 ± 2.72	-4.28 ± 1.45**	-3.86 ± 1.02**	0 ± 0.16	0.25 ± 0.19	-0.08 ± 0.17
D	1.42 ± 2.37	-0.64 ± 0.27*	1.53 ± 1.39	-1.48 ± 0.70*	-0.6 ± 0.51	0.05 ± 0.08	0.32 ± 0.09**	0.22 ± 0.09*
Genetic components								
m	109.98 ± 0.88**	10.02 ± 0.1**	50.1 ± 0.51**	20.58 ± 0.27**	13.66 ± 0.19**	3.1 ± 0.03**	3.83 ± 0.04**	3.69 ± 0.03**
a	-8.92 ± 2.22**	-0.76 ± 0.24**	-6.29 ± 1.31**	-2.32 ± 0.64**	-2.11 ± 0.47**	0.41 ± 0.08**	0.54 ± 0.09**	0.74 ± 0.09**
d	14.79 ± 9.48	1.81 ± 1.14	9.1 ± 6.08	5.85 ± 3.12	2.37 ± 2.24	0.16 ± 0.37	-0.32 ± 0.42	-0.28 ± 0.39
a×a	-2.84 ± 7.97	1.35 ± 0.87	-3.07 ± 4.67	2.95 ± 2.36	1.22 ± 1.7	-0.1 ± 0.28	-0.62 ± 0.32	-0.43 ± 0.30
a×d	1.61 ± 2.81	0.34 ± 0.39	-3.53 ± 1.98	1.15 ± 0.98	1.28 ± 0.73	-0.07 ± 0.12	-0.05 ± 0.14	0.05 ± 0.14
d×d	4.61 ± 15.43	-0.49 ± 1.89	6.33 ± 10.1	-1.63 ± 5.17	1.44 ± 3.71	0.18 ± 0.61	1 ± 0.71	0.94 ± 0.64
Yavaros × Singerd								
	PH	SL	PL	SIL	TIL	PD	SID	TID
Scales								
A	-3.92 ± 2.69	0.17 ± 0.33	-0.02 ± 1.50	-0.18 ± 0.78	-0.001 ± 0.67	0.12 ± 0.1	-0.37 ± 0.11**	-0.3 ± 0.13*
B	-6.6 ± 3.16*	-0.55 ± 0.39	0.46 ± 2.26	-2.15 ± 0.96*	-2.86 ± 0.65**	-0.18 ± 0.14	-0.34 ± 0.12**	-0.27 ± 0.13*
C	-18.18 ± 4.92**	-1.08 ± 0.54*	-5.38 ± 2.97	-3.19 ± 1.46*	-1.26 ± 1.11	0.1 ± 0.2	-0.85 ± 0.19**	-0.23 ± 0.22
D	-3.83 ± 2.57	-0.35 ± 0.27	-2.91 ± 1.67	-0.43 ± 0.69	0.8 ± 0.51	0.08 ± 0.1	-0.07 ± 0.1	0.17 ± 0.09

Shabrang × Singerd								
Genetic components								
m	101.12 ± 0.97**	9.58 ± 0.09**	48.18 ± 0.6**	19.47 ± 0.26**	13.73 ± 0.19**	3.06 ± 0.04**	3.54 ± 0.04**	3.64 ± 0.03**
a	-13.99 ± 2.38**	-1.25 ± 0.25**	-6.79 ± 1.6**	-2.65 ± 0.65**	-1.92 ± 0.49**	0.57 ± 0.09**	0.73 ± 0.09**	0.73 ± 0.09**
d	25.38 ± 11.01*	1.29 ± 0.25	18.04 ± 6.95*	2.08 ± 3.14	-0.13 ± 2.36	-0.01 ± 0.43	0.2 ± 0.43	-0.16 ± 0.41
a×a	7.64 ± 8.64	0.65 ± 0.87	5.82 ± 5.59	0.88 ± 2.32	-1.58 ± 1.73	-0.16 ± 0.33	0.14 ± 0.33	-0.34 ± 0.30
a×d	1.35 ± 3.47	0.31 ± 0.39	-0.24 ± 2.18	0.98 ± 1.02	1.43 ± 0.76	0.14 ± 0.13	-0.02 ± 0.15	-0.01 ± 0.13
d×d	2.89 ± 18.14	-0.24 ± 1.91	-6.26 ± 11.51	1.44 ± 5.25	4.41 ± 3.96	0.23 ± 0.72	0.54 ± 0.7	0.92 ± 0.69
PH, Plant height (cm); SL, Spike length (cm); PL, Peduncle length (cm); SIL, Second internodes length-top to bottom- (cm); TIL, Third internodes length-top to bottom- (cm); PD, Peduncle diameter (mm); SID, Second internodes diameter (mm); TID, Third internodes diameter (mm); Effects: (m), Midparent; (a), additive; (d), dominance; (aa), additive×additive; (ad), additive×dominance; (dd), dominance×dominance; *, ** significant at 0.05 and 0.01 levels of probability, respectively								

According to the biplot chart (Fig. 1) in both crosses, there was a positive and strong relationship between traits of lodging resistance, grains yield, TID, SID, and PD, which were related to the durum parents (Shabrang and Yavaros). Also, there was a positive and strong relationship between traits SL, PL, and PH as well as between SIL and TIL, which were related to emmer's parent (Singerd). In general, a negative association between PH, SIL, and TIL with lodging resistance, grains yield, SID, TID, and PD was observed.

Genetic Effects

The scaling tests A, B, C, and D of Mather and Jinks (1982) determined that the application of the additive-dominance model was adequate for traits PH and PD in Shabrang × Singerd cross and for traits PL and PD in Yavaros × Singerd cross. Nonetheless, for other remaining traits in both crosses, at least one of the scaling tests (A, B, C, and D) was significant, indicating inadequacy of the additive-dominance model and the presence of non-allelic gene interactions or epistasis. Therefore, the three-parameter model was inadequate for description of genetic control in the inheritance of these traits.

Considering that at least one of the scaling tests was significant, the generation means were separated into six parameters to understand the type of interactions present (Hayman, 1958). In both crosses, two parameters, the mean (m) and the additive (a) were highly significant for all of the measured traits. Also, the dominant parameter (d) was significant and important in controlling traits PH and PL in Yavaros × Singerd cross. In both crosses, the three types of interactions, additive × additive, additive × dominance, and dominance × dominance, were non-significant for all measured traits.

The estimates of dominance, additive, and environmental components of variance for plant height and its related traits are presented in Table 4. The additive variance (σ^2_A) was greater than the dominance variance (σ^2_D) for all of the measured traits in both crosses. The narrow-sense heritability (h^2_n) was greater than 0.60 for traits PH, SL, PL, SIL, TIL, SID and TID in Shabrang $\times$ Singerd cross and also for PH, SIL, TIL, and SID for the Yavaros $\times$ Singerd cross showing the lesser share of environmental variance (σ^2_E) for these traits. In general, the genotypic variance (σ^2_G) was greater than the environmental one for all the measured traits in both crosses.

Table 4
Estimates of broad and narrow sense heritability and components of variance for plant height and its components in the two crosses of tetraploid wheat

Shabrang × Singerd								
	PH	SL	PL	SIL	TIL	PD	SID	TID
σ^2_P	140.24	1.67	47.5	13.03	6.65	0.17	0.23	0.19
σ^2_E	17.89	0.54	15.84	4.4	2.19	0.05	0.08	0.07
σ^2_G	122.35	1.13	31.66	8.63	4.47	0.12	0.15	0.12
σ^2_A	94.43	1.09	29.27	10.53	5.12	0.1	0.18	0.13
σ^2_D	27.92	0.04	2.39	-1.9	-0.66	0.02	-0.02	-0.01
h^2_b	0.87	0.68	0.67	0.66	0.67	0.7	0.65	0.65
h^2_n	0.67	0.65	0.62	0.81	0.77	0.59	0.75	0.67
Yavaros × Singerd								
	PH	SL	PL	SIL	TIL	PD	SID	TID
σ^2_P	169.12	1.51	64.2	11.84	6.45	0.24	0.27	0.19
σ^2_E	44.07	0.53	14.18	5.09	2.99	0.08	0.08	0.09
σ^2_G	125.06	0.97	50.03	6.75	3.46	0.16	0.19	0.10
σ^2_A	125.21	0.62	25.79	7.64	3.98	0.13	0.24	0.09
σ^2_D	-0.15	0.36	24.24	-0.89	-0.52	0.03	-0.06	0.01
h^2_b	0.74	0.65	0.78	0.57	0.54	0.67	0.7	0.54
h^2_n	0.74	0.41	0.4	0.65	0.62	0.54	0.91	0.48
PH, Plant height (cm); SL, Spike length (cm); PL, Peduncle length (cm); SIL, Second internodes length -top to bottom- (cm); TIL, Third internodes length-top to bottom- (cm); PD, Peduncle diameter (mm); SID, Second internodes diameter (mm); TID, Third internodes diameter (mm) σ^2_P , phenotypic variance; σ^2_E , environmental variance; σ^2_G , genotypic variance; σ^2_A , additive variance; σ^2_D , dominance variance; h^2_b , broad sense heritability; h^2_n , narrow sense heritability;								

Table 5

Estimates of the number of effective genes and the predicted response from selection for plant height and its components in the two crosses of tetraploid wheat

Effective gene estimates							Genetic gain		
	Wright's	Mather's	Lande I	Lande II	Lande III	EFm	5%	10%	20%
Shabrang × Singerd									
PH	1.1	2.4	0.5	0.6	0.4	1.0	16.4	14	11.2
SL	0.6	2.2	0.5	0.6	0.6	0.9	1.7	1.5	1.2
PL	1.3	0.5	0.1	0.1	0.1	0.4	8.7	7.5	5.9
SIL	0.9	2.3	0.7	0.6	0.9	1.1	6.0	5.1	4.1
TIL	1.4	4.5	1.3	1.1	1.5	1.9	4.1	3.5	2.8
PD	1.1	4.6	1.0	1.1	0.8	1.7	0.5	0.4	0.3
SID	1.3	3.9	1.1	1.0	1.3	1.7	0.7	0.6	0.5
TID	2.0	7.5	1.9	1.9	2.0	3.0	0.6	0.5	0.4
Yavaros × Singerd									
PH	1.6	3.8	0.9	0.9	0.9	1.6	19.8	16.9	13.5
SL	1.4	8.0	1.3	2.0	0.9	2.7	1.0	0.9	0.7
PL	1.2	3.3	0.4	0.8	0.3	1.2	6.6	5.7	4.5
SIL	1.0	3.5	1.0	0.9	1.1	1.5	4.6	3.9	3.1
TIL	1.8	5.6	1.6	1.4	1.9	2.5	3.2	2.8	2.2
PD	0.6	2.9	0.6	0.7	0.5	1.1	0.5	0.5	0.4
SID	1.5	4.6	1.5	1.1	2.2	2.2	1.0	0.8	0.7
TID	2.8	12.1	2.7	3.0	2.4	4.3	0.4	0.4	0.3
<p>PH, Plant height (cm); SL, Spike length (cm); PL, Peduncle length (cm); SIL, Second internodes length -top to bottom- (cm); TIL, Third internodes length-top to bottom- (cm); PD, Peduncle diameter (mm); SID, Second internodes diameter (mm); TID, Third internodes diameter (mm)</p> <p>Wright's method for estimating genetic factors (1968); Mather's method for estimating genetic (1949); Lande's first method of estimating genetic factors (1981); Lande's second method of estimating genetic factors (1981); Lande's third method of estimating genetic factors (1981); EFM, Mean of genetic factor estimates (Wright, Mather, Lande I, Lande II, and Lande III).</p> <p>Gain from selection at 5%, 10% and 20% progeny selected.</p>									
<p>PH, Plant height (cm); SL, Spike length (cm); PL, Peduncle length (cm); SIL, Second internodes length -top to bottom- (cm); TIL, Third internodes length-top to bottom- (cm); PD, Peduncle diameter (mm); SID, Second internodes diameter (mm); TID, Third internodes diameter (mm)</p>									

Five different methods were used to estimate the minimum number of effective factors (genes) controlling traits. Results showed that the two methods of Lande I and Lande III provided similar estimates for all of the measured traits in both crosses. Also, Mather's method estimated higher numbers of effective factors in comparison to the other four methods. Thereby, based on the average of the five methods (EF_m), it was inferred that a single factor is considerably effecting traits PH, SL, PL, and SIL, while for TIL, PD, SID, and TID more than one factor was involved in Shabrang × Singerd cross. Also, in the cross Yavaros×Singerd, almost one effective factor was recorded for traits PL and PD, while for SL, SIL, TIL, SID, and TID more than one factor was estimated.

Average genetic gain from one cycle of selection with 5, 10, and 20% selection intensities were estimated to be positive for plant height and its components in both crosses. However, it varied between the two crosses for different traits. For example, gain from selection for traits PL, SIL and TIL were higher in Shabrang × Singerd cross while it was greater for PD and SID in the cross Yavaros × Singerd.

Discussion

Generation means analysis is based on the assumption that the studied generations are derived from a cross of two contrasting parents (Mather and Jinks 1982). In the present study, the results of PCA showed that the difference between parents was evident in lodging resistance and other traits related to plant height. The durum parents with larger internode diameter showed higher resistance to lodging when compared to the emmer parent with a higher internode length and plant height. Semi-dwarfism is beneficial in wheat because it increases grain yield without plants being influenced by the lodging effect (Lucas et al. 2017). It has been well-documented that plants containing Rht-B1 allele have shorter strong stems and do not lodge (Hedden 2003). The decrease in wheat plant height due to the introduction of dwarfing genes Rht-B1b and Rht-D1b has increased harvest index which is mainly associated with increased yield potential due to lodging resistance (Hayat et al. 2019; Peleg et al. 2009).

The correlation analysis results showed that lodging resistance was positively correlated with internode diameter and grain yield, while it was negatively correlated with plant height and internode length. Several other studies have also shown that lodging was strongly correlated with plant height in wheat (e.g., Verma et al. 2005; Longin and Wurschum 2014; Berry and Berry 2015; Xiao et al. 2015; Mirabella et al. 2019). Positive correlation between PH and SL has been reported in a RILs population generated from crossing durum and cultivated emmer (Sharma et al. 2019). In line with our findings, Yao et al. (2011) reported that there was a positive and significant correlation between traits PH, SL, PL, SIL, and TIL in the F₁ population of bread wheat. Using path analysis, they also indicated that trait PL had the highest effect on plant height, followed by SIL. In another study on bread wheat, the lodging had a positive correlation with traits, PH, SIL, and TIL, and negatively related with SID, TID, and GY (Xiao et al. 2015). Our results indicated a similar conclusion. Given that stem diameter has a positive and significant correlation with traits such as culm wall thickness and stem strength (Hai et al. 2005; Zhang et al. 2016; Rinki Khobra et al. 2019), numerous studies have reported its positive correlation with lodging resistance (Xiao et al. 2015; Mirabella et al. 2019). Thus, stem diameter can be suggested for indirect selection of lodging resistance during early breeding generations (Rinki Khobra et al. 2019).

The results of the scaling tests (A, B, C, and D) in both crosses showed that at least one of them was significant for most of the traits. Nevertheless, in both crosses, all three types of interactions, dominance × dominance, additive × dominance, and additive × additive, were non-significant for all of the studied traits. It seems likely that

the epistasis effects did not play a significant role in differences among the generation means. This is however, not meaning that epistasis had no role in determining phenotypic variance (Mackay 2014). Insignificant epistatic effects allows breeders to have an unbiased estimate of the effects of dominant and additive gene actions and better estimate of the genetic background of the traits (Hayman 1960; Ng et al. 2015).

The mean parameter was significant for all of the studied traits, indicating that they were quantitatively inherited (Salmi et al. 2019). For all of the measured traits, values observed for environmental variance were of low value when compared with the genotypic variance in both crosses. These data describe a high association between phenotypic and genotypic variances and, consequently, high values for heritability of traits (Cruz et al. 2005). Additive gene effects were significant for all of the measured traits in both crosses, while significant dominance effects were only detected for traits PH and PL in the Yavaros × Singerd cross. Our results are consistent with the one reported by Yao et al. (2011) that showed traits PH, SL, PL, SIL and TIL are controlled by additive gene action in a diallel cross-study of bread wheat. They also reported high h^2_n for these traits. Similarly, in another report on the F2 population of bread wheat (Khahani et al. 2017), additive gene action was found for traits PH, SL, SIL, TIL, SID, and TID. They also obtained high h^2_n for traits mentioned, except SL which was consistent with our results. In general, the result of GMA suggested that almost all genetic variation between generations of these crosses were due to additive gene effects. Additive effects will result in higher narrow sense heritability and provide breeders with the possibility of trait improvement through selection. The additive variance was higher than the dominance variance for all of the studied traits in both crosses, and for most of the traits, narrow-sense heritability (h^2_n) was higher than 0.60. In agreement with our results, Berry and Berry (2015) estimated heritability greater than 0.5 for length and diameter of internodes in winter wheat. In this respect lodging resistance may be improved in durum × emmer crosses by reducing plant height and increasing stem diameter using standard pedigree methods and early generation selections. In general, when the heritability of a trait is high, selection in early generations may result in genetic gain (Kumar and Wehner 2013).

To ensure that the number of effective factors controlling traits are correctly estimated, several hypotheses including lack of linkage, no G×E effects, no epistatic interactions, and no dominance were verified (Wright 1968). The maximum number of effective genes, using the five methods, estimated for traits, PH, SL, PL, SIL, TIL, PD, SID, and TID were four, eight, three, six, five, five, and twelve, respectively. In a diallel cross experiment on bread wheat, Yao et al. (2011) showed that the number of gene groups for traits, PH, SL, PL, SIL, and TIL, were four, one, two, three, and one, respectively. Other researchers found one related QTL for stem diameter in bread wheat (Hai et al. 2005). Lucas et al. (2017) found that in a BCS5 population resulting from crossing durum with emmer wheat, there were seven QTL for PH. Among these six QTL were associated with the *Cln-q1* gene and one QTL with the wild-type *Rht-B1* gene, respectively. Some studies attempting to find plant height-related QTLs using populations of RILs generated from crosses between emmer and durum wheat reported three QTL for SL (Faris et al. 2014; Sharma et al. 2019) and six and three QTL for PH (Tzarfati et al. 2014; Sharma et al. 2019). In the current study four and eight effective genes were estimated for traits PH and SL, respectively.

It was found that the average gain after one cycle of selection was positive for plant height and its related components in both crosses. There is a direct relationship between the rate of genetic advance and inheritance of traits (Matter and Jenks 1982). Besides, gain from selection is influenced by genetic diversity, heritability, and selection intensity (Sharma et al. 2003). Zhang et al. (2016) indicated that stem diameter at the anthesis stage and 25 days after anthesis have increased significantly over the last 70 years in Chinese wheat cultivars. Thereby

the average annual genetic gains in these two stage were 0.37 % and 0.57 %, respectively. In this respect, our results suggest that stem diameter can be increased through selection in early segregating generations. Further, due to the negative correlation between plant height and stem diameter, selection for shorter plants may simultaneously increases stem diameter.

Conclusion

Our results showed that among lodging related traits measured, plant height and stem diameter played a more significant role in distinguishing parental genotypes. In both crosses, the three types of gene interactions (dominance $\times$ dominance, additive $\times$ dominance, and additive $\times$ additive) were non-significant for all studied traits. This suggested that epistasis did not play a significant role in differences among the generation means. It was found that almost all genetic variation in the generations of these crosses resulted from additive gene effects. Also, the additive variance was higher than the dominance one for all the studied traits in both crosses. Genetic gain from selection was positive for plant height and its components in both crosses. A high heritability was estimated for most traits measured, suggesting early generation's selection will result in genetic gain and improvement of resistance to lodging genetically. Since traits related to lodging resistance are largely understudied in crosses of durum $\times$ emmer wheat our results may help gene introgression from emmer to durum wheat without the negative lodging consequences.

Declarations

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Compliance with ethical standards

Conflict of interest The authors have no conflicts of interest to declare that are relevant to the content of this article.

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Figures

Figure 1

Display of biplot six basic generations and interrelationships between traits in two crosses based on principal components analysis, (a) Shabrang × Singerd, (b) Yavaros × Singerd. PH, Plant height (cm); SL, Spike length (cm); PL, Peduncle length (cm); SIL, Second internodes length -top to bottom- (cm); TIL, Third internodes length -top to bottom- (cm); PD, Peduncle diameter (mm); SID, Second internodes diameter (mm); TID, Third internodes diameter (mm)

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