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Original Article

Genetic parameters controlling the inheritance of glaucousness and yield traits in bread wheat

Parâmetros genéticos que controlam a herança de glaucosidade e características de produção em trigo mole

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Abstract

Wheat breeders frequently use generation mean analysis to obtain information on the type of gene action involved in inheriting a trait to choose the helpful breeding procedure for trait improvement. The present study was carried out to study the inter-allelic and intra-allelic gene action and inheritance of glaucousness, earliness and yield traits in a bread wheat cross between divergent parents in glaucousness and yield traits; namely Mut-2 (P_1) and Sakha 93 (P_2). The experimental material included six populations, *i.e.* P_1, P_2, F_1, F_2, BC_1, and BC_2 for this wheat cross. A randomized complete block design with three replications was used, and a six parameters model was applied. Additive effects were generally more critical than dominance for all studied traits, except for plant height (PH) and grain yield/plant (GYPP). The duplicate epistasis was observed in spike length; SL, spikes/plant; SPP and days to heading; DTH. All six types of allelic and non-allelic interaction effects controlled SL, GYPP, DTH and glaucousness. All three types of epistasis, *i.e.* additive x additive, additive x dominance, and dominance x dominance, are essential in determining the inheritance of four traits (SL, GYPP, DTH and glaucousness). Dominance × dominance effects were higher in magnitude than additive × dominance and additive × additive in most traits. The average degree of dominance was minor than unity in six traits (glaucousness, grains/spike, spike weight, days to maturity, 100-grain weight and SL), indicating partial dominance and selection for these traits might be more effective in early generations. Meanwhile, the remaining traits (PH, SPP, GYPP and DTH) had a degree of dominance more than unity, indicating that overdominance gene effects control such traits and it is preferable to postpone selection to later generations. The highest values of narrow-sense heritability and genetic advance were recorded by glaucousness trait followed by SL and SPP, indicating that selection in segregating generations would be more effective than other traits.

Keywords: *Triticum aestivum*, generation mean analysis, gene effects, epistasis, heritability.

Resumo

Os criadores de trigo frequentemente usam a análise da média de geração para obter informações sobre o tipo de ação do gene envolvida na herança de uma característica para escolher o procedimento de melhoramento útil para o aprimoramento da característica. O presente estudo foi conduzido para estudar a ação do gene interalélico e intraalélico e a herança de características de glaucosidade, precocidade e produção em um cruzamento de trigo mole entre pais divergentes em glaucosidade e características de produção; nomeadamente Mut-2 (P1) e Sakha 93 (P2). O material experimental incluiu seis populações, ou seja, P1, P2, F1, F2, BC1 e BC2 para este cruzamento de trigo. O delineamento experimental foi em blocos ao acaso com três repetições e aplicado um modelo de seis parâmetros. Os efeitos aditivos foram geralmente mais críticos do que a dominância para todas as características estudadas, exceto para altura da planta (AP) e rendimento de grãos / planta (GYPP). A epistasia duplicada foi observada no comprimento da ponta; SL, espigas/planta; SPP e dias para o cabeçalho; DTH. Todos os seis tipos de efeitos de interação alélica e não alélica controlaram SL, GYPP, DTH e glaucosidade. Todos os três tipos de epistasia, ou seja, aditivo x aditivo, aditivo x dominância e dominância x dominância, são essenciais na determinação da herança de quatro características (SL, GYPP, DTH e glaucosidade). Os efeitos de dominância × dominância foram maiores em magnitude do que aditivo × dominância e aditivo × aditivo na maioria das características. O grau médio de dominância foi menor do que a unidade em seis características (glaucosidade, grãos / espiga, peso da espiga, dias até a maturidade, peso de 100 grãos e SL), indicando dominância parcial, e a seleção para essas características pode ser mais eficaz nas gerações iniciais. Enquanto isso, os traços restantes (PH, SPP, GYPP e DTH) tiveram um grau de dominância maior do que a unidade, indicando que os efeitos do gene de superdominância controlam tais traços e é preferível adiar a seleção para gerações posteriores. Os maiores valores de herdabilidade no sentido restrito e avanço genético foram registrados pelo traço de glaucosidade seguido por SL e SPP, indicando que a seleção em gerações segregadas seria mais eficaz do que outros caracteres.

Palavras-chave: *Triticum aestivum*, análise da média de geração, efeitos gênicos, epistasia, herdabilidade.

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1. Introduction

Wheat (*Triticum aestivum* L.) is the most important cereal crop in Egypt. In 2019, the wheat cultivated area in Egypt was 1.41 million hectares producing 9.0 million tons and Egypt imported 10.42 million tons of wheat in 2019 to satisfy the local consumption, costing the government about 3024 million US dollars (FAO, 2021). Therefore, increasing wheat production horizontally and vertically is the key to saving hard currency for wheat imports. Thus, all efforts of plant breeders are required to improve the productivity of wheat varieties. This development could be achieved by adding genes of traits that increase the grain yield of current varieties.

Glaucousness, the waxy bloom on the surface of leaves, leaf sheaths and spikes, has been associated with several traits and physiological processes, mainly related to an increased drought and heat tolerance and thus higher yield under dry conditions (Johnson et al., 1983; Richards et al., 1986; Febrero et al., 1998; Merah et al., 2000; Samuels et al., 2008; Bi et al., 2017). Early genetic studies in wheat revealed two loci for wax production, termed *W1* and *W2*, and two inhibitors of wax loci, *Iw1* and *Iw2*, that inhibit glaucousness (Tsunewaki and Ebana 1999). Further analyses revealed the genetic control of glaucousness to be more complex, as several quantitative trait loci (QTL) were identified (Börner et al., 2002; Kulwal et al., 2003; Mason et al., 2010; Bennett et al., 2012). Inheritance of glaucousness has been previously reported in bread wheat (Jensen and Driscoll, 1962; Stuckey, 1972; Liu et al., 2007). In addition, the evidence of additive gene action influencing glaucousness was also reported in bread wheat (Al-Bakry, 2010). The genetics of glaucousness and precise interaction between the genes is still not fully understood.

Yield has prime importance in any breeding program, but it is a much complex trait. Habib and Khan (2003), Mohammad et al. (2003) and Riaz and Chowdhry (2003) described the additive type of gene action with partial dominance controlling this trait. On the other hand, Inamullah and Hassan (2005), Dere and Yildirim (2006), and Hassan et al. (2008) showed that overdominance type of gene action control this parameter. Considerable studies in this concern were conducted by many investigators, *e.g.* Kearsey and Pooni (1996), Farshadfar et al. (2001), Novoselovic et al. (2004), Erkul et al. (2010), Farshadfar et al. (2013), Ljubicic et al. (2016a, b). Epistasis was reported in many studies of wheat, Przulj and Mladenov (1999) and Al-Naggar et al. (2010a, b, 2017) and (Al-Azab et al., 2017) for grain yield traits.

The choice of selection and breeding procedures for genetic improvement of any crop is mainly dependent on the knowledge of the type and relative amount of genetic components and the presence of allelic and non-allelic interaction for different traits in the plant materials under investigation. Information on the type of gene action involved in inheriting a trait helps decide the breeding procedures for plant improvement. The breeding strategy mainly depends on the different gene effects, *i.e.* dominance, additive, and non-allelic interaction. Plant breeders frequently use generation mean analysis to obtain information of allelic and non-allelic gene interaction controlling the economic traits in wheat (Khattab et al., 2001; Esmail and Khattab, 2002; Akhtar and Chowdhry, 2006; Khaled, 2007 and Farag, 2009). Generation means analysis is a tool for designing the most appropriate breeding approaches to develop crop varieties with desired traits and commonly used in studying the inheritance of quantitative traits. The generation means analysis procedure is based on the hypothesis that the studied generations must arise from a cross involving two contrasting genotypes. This model is free from the limitations of other models and can estimate the genetic markers needed for each trait (Mather and Jinks, 1971). In this way, in addition to estimate additive and dominance gene effects, the effects of epistasis can also be estimated using the scaling test.

The present study was carried out to obtain information about gene action, inheritance nature, heterosis, inbreeding depression, the average degree of dominance, broad and narrow sense heritability and expected genetic advance from selection for induced glaucousness, agronomic, and yield traits in a bread wheat cross between a glaucous parent (Mut-2) and non-glaucous parent (Sakha 93). Such information would help plant breeders to implement an exact breeding procedure for developing high-yielding varieties.

2. Materials and Methods

2.1. Plant materials

Two bread wheat genotypes, *i.e.* glaucous wheat mutant (Mut-2) and Sakha 93 cultivar (non-glaucous), were crossed and used as parents in the present study because of their diversity for glaucousness grain yield and yield-related traits. Sakha 93 bread wheat was developed by the wheat research department, field crops research institute, Agriculture Research Center, Egypt, while Mut-2 was developed by the wheat breeding program of Atomic Energy Authority, Anshas, Egypt (Al-Naggar et al., 2013). It was selected in the M_2 population resulting from Sakha 93 with 350 Gy of gamma rays. Mut-2 has high epicuticular wax content on leaf sheath, leaf blade, peduncle and spike. It has too many kernels/spike with long spike, but its tillers number is moderate. However, leaf-blades and spikes of Sakha 93 are completely non-glaucous. Also, it has a moderate number of spikelets/spike and a moderate number of kernels/spike, but it has a high number of tillers/plant.

In the first winter season (2016/2017), the mutant Mut-2 (P1) was crossed to Sakha 93 (P2), and an F_1 seed was produced. Thus, BC_1 ($F_1 \times P_1$) and BC_2 ($F_1 \times P_2$) were developed in 2017/2018 season, while the remaining F_1 plants were self-pollinated to produce F_2 seeds. The two parents and their F_1, F_2, BC_1, and BC_2 populations were grown during the 2018/2019 season for field evaluation.

2.2. Experimental design

The experiment was conducted in a randomized complete block design (RCBD) with three replications at the experimental farm of Plant Research Department,

Nuclear Research Center, Atomic Energy Authority, Egypt. Each replication composed 20 experimental rows; 2 rows for each of P_1 and P_2, four rows for F_1, six rows for F_2, and three rows for BC_1 and BC_2 populations. Individual grains were planted in 3-meter rows. Each row included 30 plants spaced 10 cm apart. Rows were spaced 30 cm apart. The sowing date was 20th November (recommended sowing date for north Egypt). All other Agricultural practices were applied as recommended for wheat planting.

2.3. Data recorded in the field

Data for each replication were noted on ten guarded plants for each P_1, P_2 and F_1, 75 plants of F_2, and 20 plants of BC_1 and BC_2. The following traits were recorded: 1. Days number from sowing date to 50% heading (DTH), 2. Days from sowing date to 50% physiological maturity (DTM), 3. Plant height (PH), 4. Main spike length (SL), 5. Number of fertile spikes per plant (SPP), 6. Grains number per spike (GPS), 7. Main spike weight (SW), 8. 100-grain weight (100-GW) and 9. Grain yield/plant (GYPP).

2.4. Epicuticular wax quantification

Thirty flag leaf blades of each parent, F_1, F_2-glaucous, F_2-moderately glaucous, F_2-nonglaucous, BC_1-glaucous, BC_1-moderately glaucous, BC_2-moderately glaucous and BC_2-nonglaucous plants were immersed individually, each for 15 sec in 15 ml redistilled chloroform. The extracts were filtered and evaporated at 35 °C. After drying for 24 hours at room temperature, the residues were weighed (Silva Fernandes et al., 1964; Ebercon et al., 1977). The amount of wax was considered against leaf area (both leaf surfaces) as mg/dm^2 of each sample.

2.5. Statistical and genetic analysis

The analysis of variance of RCBD for each studied character was performed using SAS v9.4 (SAS Institute, 2011) software package to test the differences among the six studied populations. Scaling tests outlined by Mather (1949) and Hayman and Mather (1955) were achieved to detect the presence of epistasis (non-allelic interaction). The significance of scaling tests was executed using a t-test by dividing the effects of A, B, C and D on their respective standard error. The significance of any scaling test implies the inadequacy of the simple additive-dominance model to explain genetic variances and thus indicates the presence of epistasis. Then the six-parameter model was performed as outlined by Hayman (1958) and Mather and Jinks (1982). The gene effects were estimated for each trait and defined as Hayman's notations; mean effects (m) = mean of the F_2 generation, the allelic gene effects (d) = additive gene effects, (h) = dominance gene effects, and the non-allelic gene effects (i) = additive × additive gene effects, (j) = additive × dominance gene effects, and (l) = dominance × dominance gene effects.

The genetic components of variance were calculated according to Mather and Jinks (1982). Broad sense (h^2bs) and narrow sense (h^2ns) heritability were estimated according to Warner (1952). Expected genetic advance (GA%) from selection as a percent of the mean of F_2 was computed according to Johnson et al. (1955) using selection intensity of 5% (k=2.06). Heterosis was calculated as the percentage deviation of F_1 generation from the mid parent (heterosis) and better parent (heterobeltiosis) according to Fonseca and Patterson (1968). Inbreeding depression was estimated as the percentage decrease of the F_2 from the F_1. The average degree of dominance $(H/D)^{1/2}$ was tested by the formula suggested by Jinks and Hayman (1953).

3. Results and Discussion

3.1. Mean performance

Analysis of variance (Table 1) showed significant ($P \leq 0.01$) mean squares due to genotypes (populations) for all studied traits of the studied cross, except for 100-grain weight, indicating the existence of genetic variation for these traits of the studied materials. The significance among the six populations made it possible to go further for generation mean analysis. The same results were obtained by Ataei et al. (2017) and Feltaous et al. (2020).

Table 1. Mean squares from the analysis of variance of parents, their F_1, F_2, and backcrosses for studied in a cross between Sakha 93 and Mut-2 mutant lines .

S. O. V.	df	Mean Squares				
		Plant height	Spike length	Spikes/plant	100-grain weight	Grain yield/ plant
Replications	2	13.72	0.06	2.67	0.48	4.29
Genotypes	5	164.98**	39.68**	18.36**	0.57	369.7**
Error	10	5.92	1.32	1.33	0.27	5.81
		50% Heading	**50% Maturity**	**Spike weight**	**Grains /spike**	**Wax content**
Replications	2	9.06	7.39	0.01	2.39	0.02
Generations	5	144.2**	127.5**	0.33**	214.8**	0.75**
Error	10	1.66	2.79	0.01	4.86	0.001

S.O.V.: Source of variation, df: Degrees of freedom, ** indicates significance at 0.01 probability level.,

Mean performances of P_1, P_2, F_1, F_2, BC_1, and BC_2 for the ten studied traits are presented in Table 2. The difference between P_1 and P_2 was significant (P≤ 0,05 or 0.01) for all studied traits, except 100-grain weight; such difference was more pronounced for wax content, GYPP, SL, GPS, DTH and DTM. The divergence between parents of the hybrid Mut-2 × Sakha 9 is a prerequisite for studying gene action and inheritance of glaucousness, agronomic, and yield traits using generation mean analysis. A similar conclusion was reported by Al-Naggar et al. (2017), Ataei et al. (2017), Koubisy (2019), Salmi et al. (2019) and Feltaous et al. (2020).

The F_1 mean values surpassed the mid-parent values for 6 out of 10 studied traits, namely PH, SPP, GYPP, 100-grain weight, GPS and wax content, indicating the prevalence of heterotic and dominance effects in controlling these traits. The F_1 mean values significantly (P≤0.01) surpassed the higher parent for three traits, namely GYPP, SPP and PH, indicating that overdominance controls the inheritance of these traits. The means of the F_2 population tended to be less than F_1 means for all studied traits, except days to heading and days to maturity, indicating the presence of non-additive components of genetic variance for these traits. However, means of BC_1 and BC_2 populations tended toward the mean of its recurrent parent. These results agreed with those reported by Tammam (2005), Kumar et al. (2017), Al-Azab et al. (2017), Abd El-Hady et al. (2018), Koubisy (2019) and Feltaous et al. (2020).

3.2. Adequacy of additive-dominance model

The scaling test, *i.e.* A, B, C, and D, were performed to determine the efficacy of the additive-dominance model for the inheritance of the studied traits. The significance of one or more of these scales indicates that the additive-dominance model is inadequate for describing the inheritance of the studied trait and the presence of epistasis (non-allelic interaction).

Estimates of A, B, C and D scaling tests and their significance are presented in Table 3. The significance of the C scale reveals dominance × dominance type of epistasis. The significant D scale reveals additive × additive type of gene interaction, and the significance of both C and D scales indicates additive × additive and dominance × dominance

Table 2. Mean performance of studied traits for parents, their F_1, F_2, and backcrosses in the cross between Mut-2 (P_1) and Sakha 93 (P_2).

Trait	Genotypes						LSD	
	P_1	P_2	F_1	F_2	BC_1	BC_2	0.05	0.01
Plant height (cm)	91.00	86.67	105.67	99.00	97.00	93.33	4.43	6.30
Spike length(cm)	23.00	11.67	18.00	17.67	18.00	19.00	2.09	2.97
Spikes/plant	8.00	10.67	15.00	13.33	13.33	12.67	2.10	2.98
100-Grain weight (g)	4.90	5.50	6.20	5.20	5.53	5.60	0.95	1.34
Grain yield /plant (g)	43.33	67.17	76.37	68.73	64.70	66.03	4.39	6.24
50% Heading (day)	74.67	96.00	86.00	88.00	84.00	88.00	2.34	3.33
50% Maturity (day)	119.00	139.33	129.00	130.33	128.33	131.33	3.04	4.32
Spike weight (g)	4.20	5.23	4.80	4.67	4.67	4.77	0.18	0.26
Grains / spike	90.00	66.67	89.33	83.67	84.33	82.33	4.01	5.70
Wax content (mg/dm^2)	2.95	1.55	2.54	2.31	2.56	1.94	0.04	0.06

Table 3. Estimates and significances of scaling test parameters A, B and C for all studied traits in a cross between glaucous mutant line (Mut-2) and non-glaucous wheat cultivar (Sakha 93).

Trait	A	B	C	D
Plant height	-8.88**	-7.35**	-1.21	7.67**
Spike length	-2.69**	7.11**	0.56	-1.66
Spikes/plant	2.44*	-0.21	4.84**	0.66
100 grain weight	0.27	0.78	-0.31	-0.73
Grain yield /plant	-13.57**	3.95**	2.13	6.73**
50% Heading	-7.70**	6.34**	1.00	4.00**
50% Maturity	-5.29**	9.59**	1.63	1.00
Spike weight	-0.66	0.32	-0.63	-0.10
Grains/spike	-10.08**	12.61**	3.01*	0.68
Wax content	-0.39	-0.25	-0.3	0.12**

*, ** Significant at P ≤ 0.05 and P ≤ 0.01, respectively.

types of gene interaction. The adequacy of scales is vital because, in most cases, the estimation of additive and dominance components of the variance is made assuming the absence of genes interaction.

The values of A, B, C and D scales should significantly differ from zero within the limits of their standard error. However, the results in Table 3 indicate that the scaling test values significantly differed from zero for most studied traits, indicating the presence of non-allelic gene interaction and dominance-additive model are inadequate for explaining the inheritance of these traits. The exceptions are 1000-grain weight and spike weight, which did not show significance in any one of the scaling test parameters, indicating that epistasis was not involved in the genetic control of 1000-grain weight and spike weight and the adequacy of simple additive-dominance model for estimating components of genetic variance of such traits (*i.e*. three-parameters model). Al-Bakry (2010) and Al-Azab et al. (2017) reported that no epistasis was detected for 1000-kernel weight in wheat, indicating that estimates of gene effects for this trait were free from linkage bias. These results are harmony those reported by Tammam (2005), Moussa (2010), El-Aref et al. (2011), Zaazaa et al. (2012), Amin (2013), Abd El-Rahman (2013), Hamam and Negim (2014), El-Hawary and El-Shafey (2016), Kumar et al. (2017) and Abd El-Hady et al. (2018).

3.3. Gene effects

The six-parameter model was used in the present study to determine the nature and magnitude of gene effects involved in the genetic control of eight studied traits; PH, SL, SPP, GYPP, DTH, DTM, GPS and wax content (Table 4).

The estimated mean effect parameter (m), which reflects the contribution due to the overall mean plus the locus effects and interactions of the fixed loci, was significant (P≤0.01) for all traits of the studied cross, indicating that these characters are quantitatively inherited and show the importance of non-allelic interactions. These results are in harmony with earlier results reported by Bilgin et al. (2016), El-Hawary and El-Shafey (2016), Al-Azab et al. (2017), Patel et al. (2018), Abd El-Hady et al. (2018), Salmi et al. (2019), Koubisy (2019) and Feltaous et al. (2020).

The additive (a) gene effects were positive significance (P≤0.05 or 0.01) for PH, SPP, and wax content and negative significance (P≤.01) for SL, GYPP, DTH, DTM and GPS, indicating possible improvement of these traits through selection in early segregating generations. Similar results for yield and its components were reported by Ataei et al. (2017), Al-Azab et al. (2017), Patel et al. (2018), Mahpara et al. (2018), Soliman (2018), Koubisy (2019) and Feltaous et al. (2020). In addition, the evidence of additive gene action influencing glaucousness was also reported in bread wheat (Al-Bakry, 2010).

The dominance effects (d) were positive significance (P≤.01) for SL, SPP, GYPP, GPS and wax content; moreover, negative significance (P≤.01) for DTH. Therefore, to make the selection more efficient in these studied traits, it is preferable to postpone the selection to late generations to increase homozygosity.

The results indicated that both additive and dominance have important contributions in the inheritance of the studied traits, suggesting that selection for desirable traits might be effective in early generations. However, it is better to postpone it to later segregating generations. These results are in agreement with those reported by Ljubicic et al.(2016b), Al-Azab et al. (2017), Koubisy (2019) and Feltaous et al. (2020).

Additive x additive interaction (aa) was found significant (P≤.01) with a positive value (Table 4) for SL. A negative and significant (aa) interaction was found in PH, GYPP, DTH and wax content. These findings agree with previous results reported by Koubisy (2019) and Feltaous et al. (2020).

Additive × dominance interaction (ad) presented positive significance (P≤.01) (Table 4) in SL, GYPP, DTH, DTM and GPS, but found significant (P≤.01) and negative in wax content. Significance of additive x dominance interaction suggests that it is preferred to delay selection for improving such traits to later segregating generations. These results are in harmony with Patel et al. (2018), Soliman (2018), Koubisy (2019) and Feltaous et al. (2020).

Dominance x dominance interaction (dd) effects were found positive and significant (P≤0.01) for PH, grain GYPP, DTH, GPS and wax content, and negative significance (P≤0.01) for SL and SPP (Table 4). Dominance × dominance gene interaction was higher in magnitude

Table 4. Gene effects from generation mean analysis for eight traits in the wheat cross between glaucous mutant line (Mut-2) and non-glaucous wheat cultivar (sakha 93).

Trait	Mean	additive	dominance	aa	ad	dd	Epistasis
Plant height	99**	4.33*	1.495	-15.34**	1.505	23.69**	Complementary
Spike length	17.67**	-11.33**	3.985**	3.32**	4.665**	-6.65**	Duplicate
Spikes/plant	13.33**	2.67*	4.345**	-1.32	-0.675	-2.01*	Duplicate
Grain yield /plant	68.73**	-23.84**	7.66**	-13.46**	10.59**	15.24**	Complementary
50% Heading	88**	-21.33**	-7.335**	-8**	6.665**	6.67**	Duplicate
50% Maturity	130.33**	-20.33**	-2.165	-2.0	7.165**	-0.99	Complementary
Grains/spike	83.67**	-23.33**	9.635**	-1.36	9.665**	3.37*	Complementary
Wax content	2.31**	1.4**	0.05*	-0.24**	-0.08**	0.82**	Complementary

(aa) additive*additive, (ad) additive*dominance, (dd) dominance*dominance*, ** Significant at P ≤ 0.05 and P ≤ 0.01, respectively.

than additive × dominance and additive × additive in most traits, indicating that these traits are greatly affected by dominance and non-allelic interactions. Therefore, it is advisable to delay selection to late segregating generations with increased homozygosity.

The present results reveal that all non-allelic interactions (epistasis), *i.e.* additive x additive, additive x dominance, and dominance x dominance, are essential in determining the inheritance of SL, GYPP, DTH and wax content. Epistasis was involved in the genetic control of kernels/spikelet, spikes/plant and GYPP in wheat by Al-Bakry et al. (2008) and Al-Bakry and Al-Naggar (2011). Similar results were reported by Ataei et al. (2017), Al-Azab et al. (2017) and Feltaous et al. (2020), who stated that all non-allelic interactions are essential factors in controlling the expression of GYPP.

The type of epistasis can be determined only when dominance (d) and dominance × dominance (dd) gene effects were significant. Consequently, the type of epistasis can be determined, as Kearsey and Pooni (1996) concluded. When these effects have the same sign, epistasis is of complementary type. The duplicate epistasis determined when the sign was different. The results in Table 4 showed that five traits were controlled by complementary epistasis (plant height, grain yield/plant, days to maturity, grains/spike and wax content). The duplicate epistasis was observed in SL, SPP and DTH. The presence of duplicate dominant epistasis in the expression of a trait would limit the range of variability (Kearsey and Pooni 1996). This type of epistasis limits the efficacy of selection in early segregating generations; therefore, delaying the selection to advanced generations will be an excellent decision to exploit the transgressive segregations. Various investigators reported similar results (Ljubicic et al., 2016b; Abdallah et al., 2019; Raikwar, 2019; Salmi et al., 2019).

Results showed that all six types of allelic (additive and dominance) and non-allelic (epistasis) interaction gene effects controlled four out of ten studied traits; SL, GYPP, DTH, and wax content.

For the traits grain yield/plant, spike length, grains/spike plant height and wax content, results showed a predominance of additive (a) followed by dominance × dominance (dd), additive × additive (aa), additive × dominance (ad) and dominance (d) gene effects in descending order, suggesting that selection for improving these traits could be started in early segregating generations (F_2). However, it is preferable to postpone selection to later segregating generation (F_4 or F_5) to utilize the non-additive gene effects after homozygosity and release the homozygotes. This conclusion is in complete agreement with that reported by Al-Naggar et al. (2010a, b, 2015, 2017).

For SPP, it is observed from Table 4 that the dominance gene effects are the most predominated type of gene action followed by dominance × dominance gene effects, indicating that it is preferable to postpone selection to later segregating generations for this trait.

Regarding plant height, dominance × dominance was the most predominant gene effect, followed by additive × additive, additive and dominance in descending order (Table 4), indicating that selection for this trait should be postponed to later segregating generations. This result is in agreement with that reported by Nanda et al. (1981).

For the earliness traits; DTH and DTM, it is observed from Table 4 that additive is the major type of gene action followed by dominance, dominance × dominance and additive × additive was controlling inheritance of DTH and by additive × dominance followed by dominance gene effects controlling inheritance of DTM. In general, for earliness traits, selection could be practised in the F_2 generation, but it is also preferred to be postponed to later segregating generations to get more efficient selection gain.

Our results are in agreement with those reported by Tammam (2005), Hussein et al. (2009) and Al-Naggar et al. (2010a, b, 2015, 2017) for earliness and Przulj and Mladenov (1999), Al-Bakry et al. (2008) and Al-Bakry and Al-Naggar (2011) for grain yield traits. On the contrary, our results disagree with those reported by other researchers (Menshawy, 2005, 2007) for days to heading and to maturity and Darwish and El-Hosary (2003), Riaz and Chowdhry (2003) and Al-Naggar et al. (2012) for grain yield traits. The divergence in results can be attributed to the differences in the genetic materials used in different research studies.

3.4. Components of genetic variance

The components of genetic variance, additive and dominance variances in Table 5, revealed that the dominance variance component was higher than the additive one for PH and GYPP, indicating that the dominance gene effect plays a vital role in the inheritance of these characters and selection may be effective in later segregating generations. On the other hand, the additive variance was more important in the genetic system controlling the remaining traits, suggesting the effectiveness of selection in early segregating generations. Similar results were obtained by El-Aref et al. (2011), Amin (2013), Hamam and Negim (2014), Abd El-Hady et al. (2018) and Koubisy (2019).

The average degree of dominance $(H/D)^{1/2}$ given in Table 5 was less than unity in six traits: wax content, grains/spike, spike weight, days to maturity, 100-grain weight, and spike length. These results confirm the role of partial dominance gene effects in controlling these traits and selection for these traits might be more effective in later segregating generations. These findings reveal that additive effects $[(H/D)^{1/2} < 1]$ were more critical in the majority of the traits than dominance effects $[(H/D)^{1/2} \geq 1]$ in early generations. Meanwhile, the remaining four traits (PH, SPP, GYPP and DTH) had a degree of dominance more than unity, indicating that overdominance gene effects control such traits and selection should be delayed to later generations to improve these traits. Similar results were reported by El-Aref et al. (2011), Amin (2013), Hamam and Negim (2014), Ataei et al. (2017), Soliman (2018), Abd El-Hady et al. (2018), Koubisy (2019), Koubisy (2019) and Feltaous et al. (2020).

Table 5. Additive, dominance, genotypic, environmental and phenotypic variances, heritability in broad (h^2_b%) and narrow (h^2_n%) sense, genetic advance (GA %), degree of dominance ("a"), heterosis%, heterobeltiosis% and inbreeding depression (ID%).

Parameter	Plant height	Spike length	Spikes/ plant	100-Grain weight	Grain yield/ plant	Days to heading	Days to mature	Spike weight	Grains/ spike	Wax content
Additive	6.34	14.39	6.75	0.59	1.28	22.94	17.45	0.23	6.7	0.75
Dominance	18.67	6.65	5.01	0.27	8.61	13.13	6.42	0.13	2.17	0.23
Genotypic	25.01	21.04	11.75	0.87	9.89	36.07	23.87	0.36	8.87	0.98
Environmental	1.85	0.46	0.45	0.01	6.72	0.59	40.06	0.01	1.57	0.01
Phenotypic	26.86	21.5	12.2	0.88	16.61	36.66	63.93	0.37	10.44	0.99
h^2_b%	93.08	97.88	96.31	99.1	59.55	98.38	37.34	97.97	84.95	98.89
h^2_n%	23.59	66.94	55.28	68.0	7.71	62.57	27.3	62.77	64.18	75.76
GA %	2.54	36.19	29.84	25.27	0.94	8.87	3.45	16.84	5.11	67.22
"a"	2.43	0.96	1.22	0.96	3.67	1.07	0.86	0.84	0.80	0.78
Heterosis%	18.95**	3.84	60.69**	19.23**	38.23**	0.78	-0.13	1.80*	14.04**	12.89**
Heterobeltiosis%	21.92	-21.74	40.58**	12.73**	13.70**	15.17**	8.40**	-8.22**	-0.74	-13.89**
ID%	6.31**	1.83**	11.13**	16.13**	10.00**	-2.33	-1.03	2.71*	6.34**	9.06**

* ** significant at 0.05 and 0.01 probability levels, respectively.

3.5. Heritability and genetic advance

Estimating heritability, either in broad-sense or narrow-sense, enables plant breeders to choose the right breeding strategy. The broad-sense heritability determines the heritable portion of the total variation, while the narrow-sense heritability determines the portion of an additive effect. Heritability was categorized into three groups; high (≥60%), moderate (30-60%), and low heritability (0-30%). The present results (Table 5) indicate that the broad sense heritability falls between moderate for DTM and GYPP to high for the rest of the studied traits. The broad-sense heritability ranged from 37.34% for DTM up to 99.1% for 100-grain weight. The present results revealed that a high portion of the phenotypic variation could be attributed to the genetic variation for most studied traits.

On the other side, the narrow-sense heritability ranged from 7.71% for grain yield/plant up to 75.76% for wax content. The values of narrow-sense heritability imply that the additive effects have a higher role than the dominance effect in controlling the above mentioned studied traits. The present results indicate that the selection process will be effective, which will result in a higher response. These results are in agreement with those reported previously by Farshadfar et al. (2013), Abd El-Hamid and Ghareeb (2018) and Koubisy (2019).

Genetic advance (GA %) as a percent of the mean was classified into three groups, *i.e*. low (less than 10%), moderate (between 10% and 20%), and high (more than 20%). The results in Table 5 showed that genetic advance values were high for SL, SPP, 100-grain weight, and wax content, moderate for spike weight and low for PH, GYPP, DTH, DTM and GPS.

The highest heritability values in narrow-sense and genetic advance were recorded by glaucousness trait followed by SL and SPP (only in GA%), indicating that selection would be more effective in segregating generations than other traits.

The high genetic advance values indicate that the direct selection is effective, while the low values reveal that indirect selection can be applied for these traits with correlated high heritability traits. These results are in agreement with those reported previously by Farshadfar et al. (2013), Said (2014), Ninghot et al. (2016) and Koubisy (2019).

3.6. Heterosis and inbreeding depression

Percentages of heterosis over mid-parent and better parent (heterobeltiosis) and inbreeding depression are presented in Table 5. Positive and significant (P≤0.05 or 0.01) heterosis and hetrobeltiosis values were observed for all studied traits, except DTH and DTM, and heterobeltiosis for GPS. These results are in harmony with Abd El-Rahman (2013), Hamam and Negim (2014), Abd El-Hamid and El-Hawary (2015), and Abd El-Hady et al. (2018). The positive significance of heterobeltiosis (P≤0.01) for GYPP and SPP, indicates that the studied cross could be promising in wheat breeding programs to produce elite recombinant inbred lines in its early segregating generations.

Inbreeding depression measured as a reduction in performance of F_2 generation relative to F_1 is presented in Table 5. Results showed significant (P≤0.05 or 0.01) and positive inbreeding depression values for all studied characters, except DTH and DTM. These results are expected because the expression of heterosis in F_1 will be reduced in the F_2 generation due to selfing and starting homozygosity. These results are in close agreement with Yadav and Singh (2011); Hamam and Negim (2014); Said, 2014; El-Hawary, 2016; Jaiswal et al., 2018. These results exhibit the importance of inbreeding depression and heterosis jointly in the positive selection process. These results are in good agreement with those reported by Kumar et al. (2017), Jaiswal et al. (2018) and Kumar et al. (2018).

4. Conclusion

This investigation concluded that epistasis was involved in the genetic control of all studied traits, except 100-grain weight and spike weight. Dominance and dominance × dominance type of epistasis was the most dominated types of gene effects controlling SL, SPP, GYPP, DTH, GPS and wax content traits in the genetic material under study, indicating that selection for improving these traits in the future should be practised in the later segregating generations (F_4 or F_5) in order to achieve high genetic gain. The highest values of heritability in narrow-sense and genetic advance were recorded by glaucousness trait followed by spike length and spikes/plant, indicating that selection would be more effective in segregating generations than other traits.

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