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Genetics of peduncle area in durum wheat (*Triticum durum* Desf.)

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Abstract

The inheritance of peduncle area was studied from twelve generations of three inter-varietal crosses of durum wheat (*Triticum durum* Desf.), grown under two environments by using generation mean analysis. The results indicated that among different models, 10-parameter model was adequate in almost all the three crosses under both the environments. Additive (d) gene effect was frequently observed significant than dominance (h). Among non-allelic interactions both digenic and trigenic interactions were found significant in controlling the inheritance of this trait in all the cases in both normal and late sown environments, however, trigenic interactions were higher. Non-fixable gene effects were higher than fixable in all the cases, which indicated greater role of non-additive gene effects. Epistatic interactions had a greater role to cause significant and positive heterosis. Epistatic effects involving dominance in F_2 generation, caused significant inbreeding depression. Reciprocal recurrent selection or the biparental mating and/or mating between selected plants from early segregating generations, could be helpful to improve the peduncle area in durum wheat.

Key words: Durum wheat, peduncle area, non-allelic interactions, epistatic effects, heterosis.

Introduction

Durum wheat (*Triticum durum* Desf.) is the second important species of the wheat grown mostly in the central and peninsular region of India and recently its area is further expending under irrigated condition of North-western plain zone of wheat due to renewed interest after developing dwarf, high yielding and disease resistant varieties in this species. Despite its importance for the human diet, little progress has been made in improving the yield of durum wheat. Historically, durum wheat has received insufficient attention from plant breeders in India. Yield is a very complex character, direct selection for which is not effective. Adams [1] emphasized the need to increase the photosynthetic capacity together with the potential of each of yield component character like flag leaf area, spike area and peduncle area etc., which determine the photosynthetic capacity and sink size particularly with respect to grain formation in cereals. Importance of peduncle area in *aestivum* wheat was recognized earlier by different studies [2-6]. However, its importance was not reported in durum wheat. The present study was undertaken to estimate the nature and relative magnitude of various gene effects for peduncle area in the three inter-varietal crosses of durum wheat over environments by using generation mean analysis.

Materials and methods

The experimental material generated from six diverse parents, comprised three crosses namely, Cocorit71 × A-9-30-1, HI8062 × JNK-4W-128 and Raj911 × DWL5002. In each cross combination one of the parents had (A-9-30-1, JNK-4W-128 and Raj911) higher peduncle area. Twelve basic generations, involved in these studies were two parents, F_1 and F_2, first backcross generations with both parents (BC_1 and BC_2), where BC_1 was the cross between F_1 × female parent and BC_2 was F_1 × male parent, their selfed progenies (BC_1, F_2, BC_2 F_2) and second backcross generations (BC_{11}, BC_{12}, BC_{21}, BC_{22}) i.e. the BC_1 and BC_2 plants again crossed with both original parents (BC_1 × female parent; BC_1 × male parent and BC_2 × female parent; BC_2 × male parent). These twelve populations of each of the three crosses were evaluated in randomized block design with three replications in two parallel experiments, one sown on 20th November (normal sown condition) and other sown on 20th December (late sown condition) in the same cropping season. Each replicate was divided into three compact blocks. The crosses, each consisting of twelve populations were randomly allotted to the blocks. All the twelve generations were than randomly allotted to twelve plots within a block. The plots of various generations contained different number of rows i.e. each parent and F_1 plots consisted of 2 rows, while each backcross generation in 4 rows and F_2 and the second cycle of backcrosses in 6 rows. Each row was 5m long accommodating 33 plants spaced 15 cm apart, row to row distance being 30 cm. Border rows were provided at the beginning as well as at end of experimental rows in each block. The experiment was planted at Agricultural Research Station, Durgapura, Jaipur, Rajasthan. The peduncle area was calculated by multiplying peduncle length × peduncle diameter × 3.1416 as suggested by Yap and Harvey [7]. The data were recorded on 15 random plants in each parent and F_1, 30 plants in each backcross generations and 60 plants in each F_2 and second backcross generations in each replication under both the environments.

Standard statistical procedures were used to obtain means and variances for each generation and each environment separately, as suggested by Snedecor and Cochran [8]. While calculating variances, replicate effect was eliminated from total variances to obtain within replicate variance. These variances were used to compute standard error for each generation mean in each environment. Joint scaling test proposed by Cavalli [9] was used to estimate genetic parameters by 3-parameter non-epistatic model [m, (d), (h)], 6-parsnicter model assuming digenic epistatic interaction [m, (d), (h), (i), j), (l)], 10-parameter model, which allowed specification of digenic and trigenic non-allelic interactions [m, (d), (h), (i), (j), (l) (w), (x), (y), (z)].

The estimates of gene effects were obtained by weighted least square techniques. Initially twelve equations were developed by equating observed generation means with their expectations in presence of digenic and trigenic interactions as proposed by Hill [10] Generation means and their expectations were weighted, appropriate weights being the reciprocals of the square standard errors. Twelve simultaneous equations so obtained were solved by way of matrix inversion as follows:

$$M = J_s^{-1}$$

Where, M = the column vector of the estimates of the parameters; S = the matrix of score (right hand side); J = the information matrix; J^{-1} = the inverse of information matrix J and is a variance-co-variance matrix.

The adequacy of a model was tested by predicting twelve generations mean from the estimates of each of the 3, 6 and 10-parameter model by the comparison of the weighted deviations of the observed and expected generation means in the form of chi-square test with n-p d.f. which provides a test of the goodness of fit of a model. In this situation n is the number of statistics or generations and p is the number of parameters. The estimates of χ^2 (n-p) is obtained as :

$$\chi^2 \text{ (n-p)} = \Sigma_i (O_i - E_i)^2 W_i$$

Where, O_i = is the observed mean of ith generation; E_i = is the expected mean of ith generation; W_i = is the weight of ith generation, which is calculated as:

$$W_i = 1/V_{\bar{x}} = 1/SE^2_{\bar{x}}$$

In the trigenic epistatic model the parameters estimated were: m = mean of all possible homozygous lines; (d) = additive gene effects pooled over all loci; (h) = dominance gene effects pooled over all loci; (i) = over all additive × additive epistatic gene effects; (j) = over all additive × dominance epistatic gene effects; (l) = over all dominance × dominance epistatic gene effects; (w) = additive × additive × additive gene interaction effects; (z) = additive × additive × dominance gene interaction effects; (y) = additive × dominance dominance gene interaction effects; (z) = dominance × dominance × dominance gene interaction effects.

The difference between the mean value of F_1 generation and that of its better parent was taken as a measure of heterosis. From the weighted least square estimates of components of generation mean, components of heterosis in the presence of digenic interactions and trigenic interactions were calculated as suggested by Jinks and Jones [11] and Hill [10] respectively. Inbreeding depression as percentage increase or decrease in the mean value of F_2 over F_1 was calculated in each cross under both the sowing environments. Percent heterosis over better parent and inbreeding depression were calculated as follows:

Heterosis (over better parent) = $\bar{F}_1$-$\overline{BP}/\overline{BP}$] × 100; S.E. ($\bar{F}_1$-$\overline{BP}$) = (2 EMS/r)$^{1/2}$

Inbreeding depression = [$\bar{F}_1$-$\bar{F}_2$ / $\bar{F}_1$] × 100; S.E. ($\bar{F}_1$-$\bar{F}_2$) = (2 EMS/r)$^{1/2}$

BP = Better parent; S.E. = Standard error; EMS = Error mean sum of squares.

Parameters (h), (l) and (z) were not affected by the degree of association 'r' therefore interpretation of the different interactions in this study was based on the basis of magnitude and relative signs of these parameters [10].

Results and discussion

The joint scaling tests revealed that 10-parameter model was found adequate in all the three crosses in both the environments, except in the cross HI 8062 × JNK-4W-128 under late sown condition, where even 10-parameter model did not fit to the data to explain the difference among the generation means. However, the various gene effects were estimated following this model, in view the fact that the chi-square value for 10-parameter model was lowest. Thus, it is clear, that epistatic interactions had a greater role in controlling the inheritance of this trait (Table 1).

The analysis of gene effects revealed that additive (d) gene effect was frequently observed significantly in most of the cases. However, dominance (h) gene effect was observed significantly only in two cases under normal sown condition and its magnitude was higher than additive (d) gene effects. The relative signs and significance of additive (d) and dominance (h) gene effects changed frequently with the change in the cross as well as sowing environments. Both the epistatic interaction *viz.*, digenic and trigenic interactions were found significant but their relative magnitude and signs changed in the crosses as well as in environments. Among digenic interactions either additive × additive (i) or dominance × dominance (l) alone or both had an important role in controlling the inheritance of this trait. However, one or more of the trigenic interactions were also involved in the inheritance of all the cases in both the environments (Table 1).

The results of absolute totals of epistatic effects further revealed that the second order interactions [(w), (x), (y), (z)] were much higher than the main effects and first order digenic interactions [(i), (j), (l)] in the inheritance of this trait in all the cases in both the sowing environments (Table 2). Earlier, Patel [5] and Dhindsa [6] in *aestivum* wheat also reported the role of digenic and trigenic epistasis, which was predominant as compared to the additive and dominance effects in the inheritance of peduncle area. Conclusion regarding any type of epistasis could not be drawn in any case because either (h) or (l) or both parameters were found non-significant.

Absolute totals of non-fixable gene effects [(h), (j), (l), (x), (y), (z)] were many times higher than the fixable [(d), (i), (w)] in all the three crosses in both the environments, indicating greater role of non-additive effects in the inheritance of peduncle area in durum wheat. Earlier in *aestivum* wheat Bariga [4] reported the role of non-additive gene effects, whereas Virk and Aulakh [2] reported the role of additive gene effects in controlling the inheritance of this trait. However, Jain and Singh [3] reported that both additive as well as non-additive gene effects governed the inheritance of peduncle area.

Table 1. Results of Joint scaling test and gene effects for peduncle area in durum wheat over environments

Effects	Cocorit71 × A-9-30-1		HI8062 × JNK-4W-128		Raj911 × DWL 5002	
	Normal sown	Late sown	Normal sown	Late sown	Normal sown	Late sown
m	46.44**	36.13**	28.85**	32.90**	36.33**	29.84**
	±2.26	±1.60	±2.08	±2.38	±1.84	±1.48
(d)	–2.05	–2.22*	–8.28**	–5.01*	3.13**	0.90
	±2.14	±1.03	±1.93	±1.90	±1.04	±0.98
(h)	–4.24	–3.17	15.39**	2.20	–5.29*	–2.80
	±4.29	±2.08	±3.87	±3.81	±20.9	±1.97
(i)	–23.23**	2.67	9.59*	4.02	2.18	10.27*
	±3.69	±5.19	±4.72	±5.84	±6.25	±4.53
(j)	–14.13	3.40	–16.74	–9.42	–2.58	–8.61
	±9.86	±4.37	±10.03	±7.82	±5.0	±4.62
(l)	–40.40*	20.98	–24.74	–53.80*	15.24	44.34**
	±19.43	±16.56	±16.92	±23.13	±20.21	±15.57
(w)	3.61	6.13*	7.94	–12.27	–10.36*	–6.36
	±8.18	±3.00	±4.69	±7.68	±4.08	±3.73
(x)	–81.76**	15.80	–6.96	–38.87	22.10	51.85**
	±21.41	±21.41	±20.25	±27.64	±25.89	±19.61
(y)	–44.95*	–14.64	–56.42**	34.24**	27.20*	7.48
	±19.89	±11.57	±19.78	±12.07	±12.01	±10.59
(z)	108.05**	8.74	26.56	112.27**	11.44	–33.40
	±32.11	±25.85	±32.25	±29.70	±29.59	±23.64
χ^2 value for 10-parameter model	3.99(2)	0.68(2)	5.29(2)	95.37(2)	2.19(2)	0.08(2)

*, **Significant at 5% and 1% level, respectively;
Note: Degree of freedom for χ^2 is given in parentheses

Analysis of components of heterosis revealed that epistatic interactions had a greater role to cause significant and positive heterosis in the cross Cocorit 71 × A-9-30-1 (under late sown condition) and Raj911

Table 2. Absolute totals of epistatic effects, fixable and non-fixable gene effects for peduncle area in durum wheat over environments

Cross	Environment	Main effects		Epistatic effects		Total gene effects	
		(d)	(h)	I order	II order	Fixable	Non-fixable
Cocorit71 × A-9-30-1	Normal	–2.05	–4.24	77.86	238.33	28.99	293.49
	Late	–2.22	–3.17	27.05	45.30	11.02	66.71
HI8062 × JNK-4W-128	Normal	–8.28	15.39	51.08	97.88	25.80	146.62
	Late	–5.01	2.20	67.23	197.66	21.30	250.80
Raj911 × DWL5002	Normal	3.13	–5.29	20.00	71.00	15.67	83.05
	Late	0.90	–2.80	63.22	99.10	17.54	148.48

First order interactions: [(i), (j), (l)]; Second order interactions: [(w), (x), (y), (z)]
*and ** Significant at 5% and 1% level, respectively; Note: Degree of freedom for χ^2 is given in parentheses
Fixable components: [(d), (i), (w)]; Non-fixable components: [(h), (j), (l), (x), (y), (z)]

× DWL5002. Additive × additive × additive (w) and additive in the former cross and additive × additive × additive (w), followed by additive × dominance × dominance (y), dominance (h) and additive (d) under normal sown and additive × additive × dominance (x), followed by additive × additive (i) interactions under late sown condition in the latter cross causes significant heterosis. Absence of significant heterosis in remaining cases could be explained due to the internal cancellation of heterosis components (Table 3). Significant inbreeding depression was also observed in a few cases due to the dissipation of non-additive dominance effects of epistatic effects involving dominance in F_2 generation.

Table 3. Components of heterosis for peduncle area in durum wheat over environments

Effects	Cocorit71 × A-9-30-1		HI8062 × JNK-4W-128		Raj911 × DWL5002	
	Normal sown	Late sown	Normal sown	Late sown	Normal sown	Late sown
(h)	–4.24	–3.17	15.39	2.20	–5.29	–2.80
-(l)	23.33	–2.67	–9.59	–4.02	–2.18	–10.27
$^{1}/_{2}$(x)	–40.88	7.90	–3.48	–19.44	11.05	25.92
$^{1}/_{4}$(z)	27.01	2.18	6.64	28.07	2.86	–8.35
-(d)	2.05	2.22	8.28	5.01	–3.13	–0.90
$^{1}/_{2}$(j)	–7.06	1.70	–8.37	–4.71	–1.29	–4.31
-(w)	–3.61	–6.13	–7.94	12.27	10.36	6.36
-1/4(y)	11.24	3.66	14.1	–8.56	–6.80	–1.87
Heterosis (%)	5.53	7.76*	7.82	4.03	18.58**	12.62**
Inbreeding depression (%)	2.34	12.10**	11.99*	5.29	6.94	16.13**

* and ** Significant at 5% and 1% level, respectively.

Thus, the results of the present investigation showed that as a consequence of higher magnitude of interactions particularly of trigenic type, the non-fixable gene effects were higher than the fixable. This indicated the major role of non-additive gene effects. Naturally, the successful breeding methods will be the ones, which can mop-up the genes to form superior gene constellations interacting in a favorable manner. Some forms of recurrent selection namely, diallel selective mating [12] or biparental mating in early segregating generations [13] might prove to be effective alternative approach. The restricted recurrent selection by the way of intermating the most desirable segregants followed by selection [14], might also be a useful breeding strategy for the exploitation of both additive as well as non-additive type of gene actions. These breeding approaches could be helpful in developing durum wheat populations, which upon selection will result in higher peduncle area to develop new plant type. Such new plant type could stand better under high production management conditions to get maximum yield in durum wheat. In the cross Cocorit71 × A-9-30-1 (under late sown environments), additive (d) gene effect and additive × additive × additive (w) epistasis were observed in controlling the inheritance of the trait, which indicated that this character can be easily improved by using simple progeny selection procedure.

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