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Inheritance of Heading Date, Plant Height, Ear Length and Spikelets per Spike in an Intervarietal Cross of Wheat

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Summary. A study to obtain information on early segregating generations of an intervarietal cross 'WG 357' × 'Tobari 66' in spring wheat on the genetics of days to heading, plant height, ear length and spikelets per spike was conducted. 'WG 357' has amber, hard and lustrous grains and is a well adapted high yielding variety of North India whereas 'Tobari 66' is red grained introduction from CIMMYT.

The parental F_1, F_2, B_1, B_2, biparentals, F_3 (parents of biparentals), F_3 bulk and F_4 bulk generations were studied in order to provide analysis of generations means (Mather 1949; Hayman 1958) and variance component analysis (Kearsay 1965; Perkins and Jinks 1970).

There were highly significant differences among the generations for all the characters studied. There were significant differences among the F_3 lines as well as among the biparental progenies. Only in case of ear length was the contrast between the two also significant. The mean value of most of the generations arising from the cross fell between the parental range.

The three-parameter model failed to account for the variation in generation means in the case of days to heading. This character was concluded to be influenced by linkage and higher order interactions. For the other characters the three parameter model was adequate. For all characters, additive gene effects were most important as compared to dominance gene effects.

The analysis of gene action as provided by the generation variance indicated that additive variance was much more pronounced as compared to dominance variance. The heritability was high for days to heading (71 per cent for narrow sense and 80 per cent in broad sense) and plant height (62 and 93 per cent in narrow and broad sense respectively.

The implications of the results in breeding programmes have been discussed.

Key words: Analysis of generations – Spring wheat

Introduction

Early maturity is a desirable attribute, especially in those areas where it is associated with escape from certain diseases and high temperatures that occur late in the growing season. In wheat the qualitative reduction of plant height has been possible due to the use of 'Norin' dwarfing genes. In breeding programmes where both the parents involved are semi-dwarf the quantitative differences in height would assume more importance. Ear length and number of spikelets per spike are the two important ear characters in which the breeder is usually interested when selecting in the field.

Genetic information concerning the nature of gene action for the above mentioned characters would be a valuable tool for breeding better cultivars. Although studies have been conducted in the past (Nandpuri 1959; Johnson et al. 1966; Singh 1969; Walton 1969; Hsu and Walton 1970; Amaya et al. 1972; Bhatt 1972; Aulakh and Virk 1973; Kalashnik and Molin 1974; Gill et al. 1977, etc.), these are usually based on the basic six generations of a cross between two varieties or on a diallel cross among a set of varieties and not on a larger number of Bip's. For this reason the present study was conducted and the results are reported in the present paper.

Material and Methods

The basic parental material used for this study was 'WG-357', a double dwarf variety known for its uniform, bold hard grains and chapati-making properties and 'Tobari-66', also a two-gene dwarf variety with red grains and a high resistance to rusts. The F_2 generation of this cross was space planted during rabi 1975-76. Forty biparental crosses were made between randomly selected pairs of F_2 plants. At the same time the seeds of the F_1, F_2, F_3, B_1 and B_2 generations were also obtained. The F_3 generation was raised in the off-season nursery in order to provide the F_4 generation. The final experiment was conducted during rabi 1976-77 and involved the P_1, P_2, F_1, F_2, F_3, F_4, B_1, B_2 and Bip's. The number of rows, number of plants selected for recording data per row and total plants sampled for each generation are given below:

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Generation	Rows per replication	Plants selected per row	Total plants sampled
P_1 (WG 357)	2	5	20
F_2 (Tobari 66)	2	5	20
F_1	2	5	20
F_2	12	8	192
Bip's	40	5	400
F_3 selfs (parents of Bip's)	80	5	800
F_3 bulk	24	5	240
F_4 bulk	24	5	240
Backcrosses	5	8	160

The plot size was a single row 1.5 m long. The row to row and plant to plant distance was 23 cm and 10 cm, respectively. The observations were recorded for the heading date (difference in number of days between sowing date and date of 50 per cent earing), plant height (cm), ear length (cm) and the number of spikelets per spike.

The statistical analysis was conducted for the generation means and variances as suggested by Mather (1949). Where the three parameter model for generation means did give a satisfactory fit the data were extended to the six parameter model as suggested by Hayman (1958). The analysis of augmented biparentals design was conducted as suggested by Kearsey (1965) and Perkins and Jinks (1970).

Results

Days to Heading

The analysis of variance revealed highly significant differences among the generations for days to heading, as was expected (Table 1). A perusal of the mean values of different generations indicate that 'WG-357' was earlier by 3 days to heading (100.45) as compared to 'Tobari-66'. The F_1 was as late as 'Tobari-66'. The F_2 was earlier than either of the parents, as well as of F_1. Irrespective of the parent involved, the backcrosses were close to 'WG-357'. The mean values of biparentals and F_3 were more than that of F_2. However, the number of days to heading taken by F_4 were significantly less than those taken by the other generations.

The analysis of variance of biparental progenies and their parents (F_2 lines) indicated that the differences among those were highly significant (Table 2). When this variance was seperated into that due to biparental progenies, F_3 lines and the contrast between the two groups, it becomes evident that the two groups were variable within themselves. The contrast was not significant.

The estimation of genetic parameters based on the generation means was conducted involving all nine generations. The three parameter model was not sufficient to explain the genetic variation for this character. Therefore, the six parameter model was applied, which was also not adequate to explain the variation fully, as shown by highly significant chi-square (Table 3). This indicated that the inheritance of heading date is influenced by higher order interactions or/and linkage in the material under study. The number of generations was not sufficient so the model could not be extended further to account for still higher order interactions. However, it was interesting to note that in both the three-parameter and six-parameter models the additive effects were larger than the respective standard errors.

Table 1. Mean performance of different generations and analysis of variance for different characters

Generation/ analysis of variance	Days to heading	Plant height (cm)	Ear length (cm)	Number of spikelets per spike
P_1 (WG 357)	100.45	90.82	12.14	19.45
F_2 (Tobari 66)	103.60	97.61	13.16	21.75
F_1	103.85	95.94	11.63	19.07
F_2	98.64	92.21	12.33	20.70
B_1	100.37	93.64	12.36	20.71
B_2	101.24	94.03	12.46	20.55
Bips	102.84	91.26	12.12	19.78
F_3 (Selfs)	101.71	90.24	12.28	19.99
F_3 (bulk)	102.27	90.60	12.13	19.88
F_4 (bulk)	98.10	93.04	12.43	20.28
Replication mean squares	0.5378	1.0169	0.1746	0.0072
Generation mean quares	21.3141**	15.4135**	0.2739**	1.1161
Error mean squares	0.3289	4.8324	0.0167	0.1515
C.D.0.05	1.27	4.89	0.28	0.86

** Significant at $p < 0.01$

Table 2. Analysis of variance for different characters in F_3 (Selfed) lines and biparentals

Source of variation	df	Mean squares			
		Days to heading	Plant height	Ear length	Number of spikelets per spike
Genotypes	119	20.07**	335.63**	1.07**	2.21**
F_3 Lines	79	20.50**	389.72**	1.17**	2.64**
Biparentals	39	19.07**	233.46**	0.84**	1.35**
F_3 Lines vs biparentals	1	1.49	46.68	1.84*	1.53
Error	119	3.59	32.85	0.34	1.02

* Significant at $p < 0.05$
** Significant at $p < 0.01$

Table 3. Estimates of genetic parameters based on generation means for different characters

Parameter	Characters				
	Days to heading		Plant height	Ear length	Number of spikelets per spike
	3 parameter	6 parameter	3 parameter	3 parameter	3 parameter
m	100.47** ± 1.08	99.36* ± 2.38	91.81** ± 1.08	12.63** ± 0.31	20.73** ± 0.31
d	– 1.43 ± 1.29	– 1.57 ± 1.38	– 3.59 ± 1.28	– 0.42 ± 0.38	– 0.88 ± 0.37
h	1.90 ± 2.26	0.75 ± 8.56	2.68 ± 2.25	– 0.84* ± 0.65	– 1.20 ± 0.66
Chi-square	28.76**	–	12.21	1.73	7.47
i	–	2.54 ± 2.61	–	–	–
j	–	1.42 ± 6.18	–	–	–
l	–	3.63 ± 7.48	–	–	–
Chi-square		16.95*	–	–	–

*, ** See table 2.

Table 4. Estimates of genetic parameters based on the variances of different generations for various characters.

Parameter	Characters			
	Days to heading	Plant height	Ear length	Number of spikelets per spike
D	14.30 ± 18.40	666.81** ± 187.75	3.44** ± 0.80	4.98* ± 1.79
H	16.00 ± 29.50	521.96 ± 301.00	2.31 ± 1.81	1.87 ± 2.86
F	9.76 ± 7.53	1.28 ± 76.83	0.31 ± 0.33	0.45 ± 0.73
E_1	5.58 ± 2.96	64.84* ± 30.18	0.60** ± 0.13	1.30** ± 0.29
E_2	26.38 ± 30.96	38.30 ± 315.66	– 2.52 ± 1.34	– 2.33 ± 3.01

*, ** See Table 2.

Estimation of the components of variation (Table 4) indicated that although none were significant, the dominance component was larger than the additive one. However, the estimates of variance components from biparentals showed an additive variance of a much larger magnitude as compared with the dominance variance (Table 5). The estimate of heritability was high.

Table 5. Estimates of genetic parameters including augmented bips by covariance of bips means on the mid-parental values

Parameter	Characters			
	Days to heading	Plant height	Ear length	Number of spikelets per spike
VA	12.79	160.99	0.4916	0.6492
VD	1.54	80.75	–0.1344	–0.3592
VE	3.58	19.20	0.6340	1.8113
Heritability % in narrow sense	71.39	61.69	49.59	30.89

Plant Height

There were highly significant differences between different generations for plant height (Table 1). Although the parents were two-gene dwarfs, 'WG 357' was significantly dwarfer than 'Tobari-66'. The F_1 and F_2 were intermediate between the parental limits. However, F_2 was dwarfer but not significantly shorter in height as compared to 'Tobari 66'. The remaining three generations B_1, B_2 and F_4 were intermediate between the two parents and did not differ significantly from either of these. The analysis of variance involving the biparental progenies and their parents showed a trend similar to days to heading (Table 2). The overall differences among the genotypes were highly significant. This variation was mainly due to the variation in F_3 lines and biparental progenies and the contrast between these groups was not significant.

Estimation of genetic parameters from the generation means indicated that three-parameter model was adequate for explaining the variation in generation means as the chi-square was non-significant (Table 3). The additive effects were significant. Although the estimate of dominance effects was not significant its value was larger than its standard error. The estimation of gene action from generation variances indicated that additive gene action was significant whereas dominance gene action was not important although it was larger than its standard error. Similarly, the estimate of 'F' was also not significant. The results obtained from biparental progenies (Table 5) collaborated these findings. The heritability estimate was high.

Ear Length

The analysis of variance (Table 1) indicated that there was a highly significant variation among the generations for ear length. A perusal of the mean values of different generations indicates that 'WG-357' had relatively smaller ears as compared to those of 'Tobari 66'. The F_1 had small ears even when compared to 'WG-357'. In fact, F_1 had the smallest ears as compared with the ears of all the other generations. The ear size of all the other generations was intermediate between the two parents and approached that of the parent with smaller ears ('WG-357'). The analysis of variance of the biparental progenies and their parents (F_3 lines) indicated that overall differences were highly significant (Table 2). All three components of this variation, the F_3 lines, the biparental progenies and the contrast between these two groups were important.

The analysis for partitioning the variation in generation means showed that the three parameter model was adequate as the residual chi-square was not significant (Table 3). The dominance effects were significant and its magnitude was almost twice the magnitude of the additive effects. The inheritance of ear length is highly influenced by additive variance. Similar results are indicated by the estimates of variance components from biparental progenies (Table 5).

Number of Spikelets Per Spike

The analysis of variance for the design of experiment (Table 1) indicated highly significant differences among the generations. 'WG-357' had a fewer number of spikelets per spike as compared to 'Tobari 66'. The pattern of variation of the mean values of different generations for number of spikelets per spike was more or less similar to that of the ear length. The F_1 was lower in quantity than even 'WG-357'. All the other generations were intermediate between the two parents and approached the parent with the least number of spikelets per spike. The analysis of variance involving biparental progenies and their parents (F_3 lines) indicated highly significant differences (Table 2). This variation was primarily due to the differences among the biparental progenies and F_3 lines. The contrast between the two groups was not significant.

The variation in the generation means was adequately accounted for by the three parameter model (Table 3) as the residual chi-square was non-significant. The estimate of additive gene effects was significant. Although dominance effects were of larger magnitude as compared to additive effects, the estimate was not significant due to the larger error component. The variance due to additive gene action was more important than the dominance variance (Table 4 & 5).

Discussion

The basic experimental material for the present study consisted of an exotic strain 'Tobari 66' and a well-adapted local variety 'WG-357'. The exotic strain is slightly late in maturity and is slightly taller than 'WG-357', however, it had characteristics of long ears and higher number of spikelets per spike. The analysis of variance (Table 1) indicated highly significant differences for all the characters studied. This revealed that there was enough variability present in the material under study. The F_2 generation took significantly fewer days to heading than the parents and the F_1, and was closer to the dwarfer parent in height. On the other hand, for the rest of the characters, i.e., ear length and number of spikelets per spike, the F_2 mean exceeded the F_1 mean. This signified the possibility of combining the better characteristics of the parents.

A comparison of the means of the F_2, bips and F_3 (Table 1) for different characters indicated that the means of the biparentals was higher only in the case of days to heading. The analysis of variance of the F_3 lines and biparental progenies (Table 2) indicated that the variance due to the F_3 lines was much larger than the variance due to biparentals for all characters except heading date. In this latter case the two were no way superior for any of the characters of the progenies arising out of the selfing series, except for heading date. In the simple additive dominance model, the mean of biparentals and F_2 generations can differ only if linkage among genes is present (Mather and Jinks 1971). In the generation mean analysis (Table 3) the chi-square was significant on both the three-parameter and six-parameter models, indicating the presence of linkage and/or higher order interactions among the genes governing the inheritance of heading date. A test of linkage (Table 6) revealed that the mean square for linkage was sig-

Table 6. Test of linkage for different characters

Source	df	Mean squares			
		Days to heading	Plant height	Ear length	Number of spikelets per spike
Linkage	1	697.74**	1190.41	0.0828	0.0248
Residual	2	18.37	870.36	0.217	0.0072

** See Table 2.

nificant only in case of heading date. In the presence of linkage the estimation of variance components are biased and the dominance is over-estimated. Apparently the heritability estimates are lowered. Although in the present study the heritability estimate for heading date is the largest among the characters studied, it may still have been biased downwards. The present study illustrates the point very clearly that recurrent selection or biparental mating is useful only when linkage between the genes governing the inheritance is pronounced. Pederson (1974), Bos (1977) and Stam (1977) have also shown, through simulation techniques, that the recurrent selection is of rather limited use in self-pollinated crops.

The results of parent investigations have shown that additive gene action is more important for the inheritance of all the characters under study. This indicates that selection in early segregating generations should be effective. Predominance of additive gene action has been reported in wheat for heading date by Amaya et al. (1972), Ceccarelli et al. (1973); for plant height by Johnson et al. (1966), Tai (1969) Amaya et al. (1972), Bhatt (1972), Ceccarelli et al. (1973), Fick and Qualset (1973) and Edwards et al. (1976); for ear length by Rachinski (1971), Ceccarelli et al. (1973) and Gill et al. (1976); for spikelets per spike by Chapman and McNeal (1971), Ketata et al. (1976) and Sidwel et al. (1976).

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