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Genetic control of grain yield and its related traits in bread wheat

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Summary. Genetic control of tiller number, grain number, grain weight, harvest index and grain yield in six generations, along with the biparentals, F_3s, $F_2 \times$ parental progeny, and $F_2 \times F_1$ progeny were investigated in an intervarietal cross of bread wheat involving two highly competitive varieties, 'WL 711' and 'HD 2009'. The performance of F_1, B_1, B_2, $F_2 \times P_1$, $F_2 \times P_2$ and $F_2 \times F_1$ progeny was midway between the parents involved with respect to all the evaluated characters. The biparental progeny excelled the mean performance of their corresponding F_2 and F_3 progeny in tiller number, seed weight and grain yield. The estimates of variance components obtained from the two models deployed were almost similar. Considerable additive genetic variance was observed for grains per spike, seed weight and grain yield while dominance variance was more pronounced for harvest index. The additive-dominance model was adequate for grains per spike and harvest index. Epistatic effects of additive × additive and additive × dominance type for tiller number and grain yield, and of additive × dominance type for seed weight were observed. The digenic epistatic model was inadequate for explaining the nature of gene action for tiller number, seed weight and grain yield. The studies indicated that non-allelic interactions should not be ignored in formulating wheat breeding programmes and that a biparental approach could be adopted as an extremely useful tool for enhancing genetic variability and the creation of transgressive segregants. The usefulness of breeding methodologies utilising a biparental approach is discussed.

Key words: Bread wheat – Genetic variability – Gene action – Conventional approach – Biparental matings – Undesirable linkages

Introduction

Grain yield is complex in inheritance and is difficult to manipulate through a per se approach. However, selection based on certain component traits may lead to considerable improvement in grain yield. To affect improvement in yield it would be desirable to bring about improvement in yield component traits but in order to achieve this more information on the inheritance pattern of different economic traits is essential.

The studies conducted so far on the inheritance pattern of grain yield and its component traits have mostly remained confined to the evaluation and analysis of only six basic populations: P_1, P_2, F_1, F_2, B_1 and B_2 (Sun et al. 1972; Bhat 1972; Ketata et al. 1979; Joarder et al. 1983). However, there is a need to collect more accurate information on the inheritance pattern of grain yield and its related traits in wheat and this could be achieved through investigating larger number of generations than simply these six basic populations. This type of analysis should yield more reliable information on the inheritance pattern of various economic traits and help in devising a suitable breeding methodology. The utilization of a biparental approach is being emphasised in self-pollinated crops. To evaluate its application in wheat improvement, information on this aspect is needed.

The present investigation involving six basic populations along with some additional generations, F_3, biparentals, $F_2 \times$ parental progeny and $F_2 \times F_1$ progeny were studied and an estimation of the D, H and E components was undertaken in order to collect comprehensive information on the inheritance pattern of grain yield and its related characters.

Material and methods

The experimental material was developed from a cross involving two varieties of bread wheat: 'WL 711' and 'HD 2009'. 'WL 711' possesses such characters as a higher number of grains per spike, greater seed weight and better grain yield whereas 'HD 2009' shows a good tillering ability and medium sized grains. The F_2 generation of this cross was sown in 1980–1981. Ninety-six biparental crosses were attempted between one hundred and ninety-two randomly selected F_2 plants. In order to obtain $F_2 \times P_1$, $F_2 \times P_2$ and $F_2 \times F_1$ progeny, 15 F_2 plants were selected and each plant was crossed with both parents as well as with their respective F_1s. The seeds of the F_1, F_2, F_3, B_1 and B_2 generations were also obtained by making fresh crosses and advancing the generations. The final experiment was conducted during 1982–1983 with the experimental material comprising P_1, P_2, F_1, F_2, F_3, BIPs, B_1, B_2, $F_2 \times P_1$, $F_2 \times P_2$ and $F_2 \times F_1$ generations. The row length was kept to 1 metre and intra- and inter-plant distance was maintained at 10 and 30 cm, respectively, providing two replications. Details on numbers and types of plants used, and sampling procedures are presented in Table 1.

Table 1. Generations of plants studied and the sampling procedures

Generation	No. of rows planted per replication	No. of plants selected per row	Total no. of plants selected
P_1('WL 711')	4	5	20
F_2('HD 2009')	4	5	20
F_1	4	5	20
F_2	30	8	240
F_3	192	5	960
BIP's	96	5	480
B_1	15	8	120
B_2	15	8	120
$F_2 \times P_1$	15	8	120
$F_2 \times P_2$	15	8	120
$F_2 \times F_1$	15	8	120

Data were collected on number of tillers per plant, number of grains per spike, 1,000-grain weight (gm), harvest index and grain yield per plant (gm). The statistical analysis for generation means was made according to Hayman (1958). The analysis of Mather (1949) was utilised for the estimation of components of variance. The study was carried out at the experimental farm of the Punjab Agricultural University, Ludhiana which is situated at 30°52'N latitude and 48°48'E longitude.

Results and discussion

Mean performance

The analysis of variance revealed highly significant differences among the generations with respect to all the characters studied indicating that sufficient genetic variability existed in the material under investigation (Table 2). 'WL 711' showed a significantly higher number of grains per spike, seed weight and grain yield than 'HD 2009' while the number of tillers per plant and the harvest index were almost equal. A perusal of mean performance in the case of different generations revealed that the F_1 mean performance of all the characters was midway between the parents involved (Table 2); a similar observation was also made for B_1, B_2, $F_2 \times P_1$, $F_2 \times P_2$ and $F_2 \times F_1$ progeny for all the evaluated characters. However, the limited heterosis observed may have been caused by the absence of genes with dominance effects at most of the loci. Similarly, a low degree of the inbreeding depression from F_2 to F_3 for all the characters was also indicative

Table 2. Mean performance of different generations and analysis of variance with respect to various evaluated characters

Generation/ mean squares	Character				
	No. of tillers/plant	No. of grains/spike	1,000-grain wt	Grain yield/ plant	Harvest index
P_1('WL 711')	11.72	71.10	46.28	25.12	0.46
P_2('HD 2009')	11.06	61.59	38.26	19.75	0.45
F_1	11.44	71.39	45.22	24.32	0.46
F_2	10.17	66.84	39.84	24.30	0.46
F_3	9.91	62.25	38.95	22.72	0.44
BIP's	12.93	65.56	42.87	28.92	0.47
B_1	10.12	69.65	45.24	23.27	0.47
B_2	11.23	65.08	39.94	23.58	0.47
$F_2 \times P_1$	11.36	67.27	41.38	24.92	0.46
$F_2 \times P_2$	10.97	64.09	39.08	22.36	0.45
$F_2 \times F_1$	12.07	66.24	41.15	26.18	0.46
Replication mean squares	1.15	0.89	3.95	0.83	0.0001
Generation mean squares	0.45**	27.19**	16.29**	17.49**	0.005**
Error mean squares	1.07	1.01	0.25	3.38	0.0003
C.D. (0.05)	2.24	2.16	1.09	3.97	0.04

** Significant at $P = 0.01$

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

Parameter	Character				
	No. of tillers/plant	No. of grains/spike	1,000-grain wt	Harvest index	Grain yield/plant
m	11.32** ±0.55	67.32** ±1.35	45.38** ±0.95	0.45** ±0.01	22.38** ±1.35
[d]	0.62 ±0.36	6.17** ±2.03	5.32** ±0.47	0.01 ±0.01	1.68* ±0.80
[h]	−0.33 ±0.87	3.97* ±1.71	1.95 ±1.03	0.02* ±0.01	2.17 ±2.07
x^2 (8 df)	27.35**	8.19	22.35**	7.75	25.38**
Heterosis (%)	0.57	7.61	6.98	1.12	8.68
Inbreeding (%)	11.15	6.38	12.54	0.00	0.38

* Significant at $P=0.05$; ** Significant at $P=0.01$

Table 4. Estimates of six genetic parameters based on different generation means

Parameter	Character		
	No. of tillers/plant	1,000-grain wt	Grain yield/plant
m	10.45±1.27**	43.37±0.93**	28.35±3.76**
[d]	0.68±0.39	4.95±0.38**	1.63±0.84*
[h]	7.35±4.15	5.35±6.17	4.15±4.18
[i]	3.17±1.35*	3.37±3.11	−6.37±2.98
[j]	−3.98±1.38*	5.38±1.92**	−5.35±2.38*
[l]	−5.17±3.17	1.37±3.38	3.88±4.15
x^2 (5df)	7.15**	11.19*	12.08*

* Significant at $P=0.05$; ** Significant at $P=0.01$

of the absence of loci with dominance effects. The above results substantiated the findings of Gill et al. (1973) and Jatasara and Paroda (1980) for grain weight; of Carvalho and Qualset (1978) for tiller number and of Paroda and Joshi (1970) and Singh and Dwivedi (1978) for grain yield (who reported partial dominance for these characters).

The biparental progenies excelled their corresponding F_3 and F_2 progeny in mean performance for tiller number, seed weight and grain yield. The biparentals were superior to their corresponding F_3s for all characters except harvest index. Similarly, a considerable increase in the means of biparentals over those of the corresponding F_1s was also observed in the case of grain yield per plant. The superior performance of biparental progeny could probably be attributed to the accumulation of favourable low frequency genes, thus generating segregants which could be rarely obtained in the simple F_2 generation. Intermating generated tremendous variability through breakage of undesirable linkages by offering additional opportunity for the emergence of genetic recombinants through random mating of F_2 plants.

As such, the present study confirmed the findings of Gill et al. (1973); Singh and Dwivedi (1978) and Yunus and Paroda (1982) who reported that random mating in early segregating generations was an effective mode of creating potentially high yielding transgressive segregants.

Gene action

The generation means analysis was performed for the additive-dominance model on eleven generations for all the characters. The X^2 value was significant for tiller number, seed weight and grain yield (Table 3). The digenic epistatic model was still found to be inadequate to explain the nature of gene action for these characters (Table 4). In order to detect the effects of linked epistatic genes, the F_2, $F_2 \times F_1$ and $F_2 \times F_2$ progeny can be utilised as these provide the same expectations in the absence of linkage (Mather and Jinks 1971). This test also gives an indication of the type of linkage present in the population. In the case of the predominantly repulsion phase linkage, the mean of the $F_2 \times F_2$ is higher than the mean of the F_2 generation. As such, repulsion phase linkage was evident for tiller number, grain weight and grain yield. Therefore, the inheritance of these attributes may have been complicated by linkage and or higher order interactions.

An additive type of gene action was very pronounced in grains per spike, seed weight and grain yield. The non-significance of component [d] in tiller number and harvest index indicated that the genes in the parents were in a dispersed form. The dominance effects [h] were significant for grains per spike and harvest index. The estimation of genetic variances by Mather (1949) and Hayman (1958) revealed similar results about the nature of gene action operative with respect to the different evaluated traits (Table 5).

The predominance of additive gene effects has already been reported by Bhat (1972) and Singh (1980) for seed weight and Gill et al. (1973) and Singh (1978) for grain yield. Both dominance and additive type of effects for grains per spike were reported by Walton (1971) and Joarder et al. (1983). The dominance type of gene action for harvest index has been reported by Gill et al. (1980) and Nanda et al. (1982).

The substantial amount of digenic epistatic effects of additive × additive and additive × dominance type

Table 5. Estimates of genetic parameters and average degree of dominance based on variances of six generations

Parameter	Character				
	No. of tillers/plant	No. of grains/spike	1,000-grain wt	Harvest index	Grain yield/plant
D	14.28 ±16.08	84.27** ±32.32	78.32* ±38.14	12.18 ±15.35	45.42** ±17.14
H	3.32 ± 8.18	17.32 ±16.45	45.49 ±39.80	10.35* ± 4.48	38.12* ±17.35
E	10.32* ± 4.48	15.18* ± 7.35	18.12 ± 6.22	13.38* ± 6.14	4.47** ± 1.49
H/D	0.48	0.45	0.76	0.92	0.92

* Significant at $P=0.05$; ** Significant at $P=0.01$

for tiller number and grain yield and additive × dominance type for seed weight indicated that epistasis also played a role in determining the inheritance of tiller number, seed weight and grain yield. However, the digenic epistatic model was still found to be inadequate to explain the nature of gene action for these attributes.

The existence of large epistatic effects for different characters has also been reported by Sun et al. (1972) and Singh (1981) for grain weight, and Ketata et al. (1976); Singh and Singh (1978) and Singh (1981) for grain yield. Linkage and higher order interactions have also been observed by Bhullar et al. (1980) and Patil (1981). As such, it is evident that the existence of non-allelic interactions should not be ignored in formulating breeding programmes in wheat and the biparental approach could be ulitised as an extremely useful tool for enhancing genetic variability in the population for creation of transgressive segregants.

From the above results it seems difficult to make rapid improvements in yield through conventional breeding approaches which may not produce quick and desirable results. The investigation has shown that, in addition to digenic and higher order interactions, additive and dominance gene effects are also important for grain yield and its related traits. With respect to important economic traits it is also apparent that the biparental progeny are superior in performance to their corresponding F_2 and F_3 progeny and the respective F_1 crosses. As such, a conventional approach may lead to considerable improvement but the variability hidden in the heterozygotes shall remain concealed and unexploited. In order to get transgressive segregants, break undesirable linkages and simultaneously exploit additive, dominance and non-additive gene effects, biparental matings among potentially desirable plants may be resorted to in the early segregating generations. Such an approach would provide transgressive segregants for exploitation and further selection. The materials thus generated could be subjected to population improvement techniques later on.

Recurrent selection, which has revolutionized population improvement in cross-pollinated crops, may also be used in autogamous crops but because of certain physical and economic reasons this procedure has not been widely employed even though there is no genetic reason to exclude its use. Intermating in early segregating generations means reassembling adaptive genes. This approach not only increases the population mean but also retains greater variability for selection over a longer span of time. The strict inbreeding or pure line selection from early generations may not produce the best balanced genotypes. Intermating magnifies the chances of reassembling a maximum number of potentially functional genes and leads to the isolation of stable and widely adapted genotypes. Keeping in mind the limitations of the conventional breeding methodology and the need for breaking the present yield barriers there is an immediate need for exploiting this type of technique in these crops. Gill et al. (1974) suggested the adoption of biparental matings for generating populations possessing higher proportion of favourable and adaptive genes. This procedure has also been suggested by Redden and Jensen (1974) for wheat.

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