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Predicting the Frequencies of Transgressive Segregants for Yield and Yield Components in Wheat

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Summary. Genetical analysis of the F_2 triple test cross design combined with conventional early generations was used to elucidate the genetical control of yield and yield components in two crosses of winter wheat. From estimates of the additive, $\{d\}$, and additive × additive, $\{i\}$, components of means, together with the additive genetical variance, D, predicted frequencies of recombinant inbred lines that would transgress the parental range were calculated for each cross. The accuracy of predictions was evaluated by comparing expected frequencies with observed numbers in populations of F_6 lines previously developed by single seed descent.

For both crosses and all characters where an adequate genetical model was found to explain the observed variation between the early generations, good agreement between predicted and observed frequencies of transgressive segregants was obtained. Furthermore, for characters exhibiting significant epistasis, allowance for additive × additive $\{i\}$ epistasis in the prediction equations was sufficient to allow for skewness of the recombinant inbred population.

These results demonstrate that cross performance in wheat can be predicted from genetical analysis of early generations, and the value of this approach in breeding new varieties is discussed.

Key words: Wheat – Genetical analysis – Cross prediction

Introduction

Genetical analysis of quantitative variation for yield and yield components in wheat has mainly been used to describe the genetical control in terms of the components of variation: additive, dominance, epistasis, linkage and genotype-environmental interaction. By understanding the mode of inheritance the genetical consequences of different selection procedures and breeding strategies on these characters can be predicted. However, little emphasis has been placed on more specific use of the information for distinguishing between particular crosses or for predicting the performance of homozygous lines that could be produced from inbreeding the F_2.

Recently Jinks, Pooni and coworkers (1976, 1978, 1979, 1981b) have shown how estimates of genetical parameters from mating schemes involving early generations of crosses between inbred varieties can be used to predict the distributions of recombinant inbred lines that could be obtained. Experiments in *Nicotiana rustica* have shown that in practice estimates of these parameters can accurately predict cross performance, for example, in terms of the frequencies of lines transgressing the parental range, even when genetical control is complex. These experiments have illustrated that genetical analysis of quantitative characters can be predictive as well as descriptive.

The relevant parameters for prediction can be estimated from different mating designs. The most common design in wheat is to grow the parental varieties together with their F_1, F_2 and backcross progenies. However, on theoretical grounds Pooni and Jinks (1979) have shown that, in addition, including an F_2 triple test cross (Jinks and Perkins 1970) is more satisfactory since this provides a comprehensive description of the genetical architecture and a more satisfactory estimate of the additive genetical variance necessary for cross prediction. This estimate is uncorrelated with dominance variance, has a lower sampling error when epistasis is present and, if linkage disequilibrium is present, provides an estimate which more accurately reflects the variance of the derived inbred population (Jinks and Pooni 1981b).

The present paper describes experiments to evaluate the usefulness of this design for predicting the frequencies of transgressive segregants in two crosses of winter wheat for yield and yield components. The accuracy of predictions were assessed by comparing the expected frequencies of lines with the frequencies observed in populations of F_6 lines of these crosses which had previously been developed by single seed descent.

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The Experiments

Two crosses involving the Plant Breeding Institute semi-dwarf winter wheat, Hobbit 'sib', were investigated; the first with the Dutch variety 'Manella', and the second with the Yugoslavian variety 'Sava'.

(a) Triple Test Crosses

F_1's of the crosses Hobbit 'sib' × 'Manella' and Hobbit 'sib' × 'Sava' were produced by hand-pollination, grown and selfed to produce the F_2's. Fifteen random F_2 plants of each cross were then crossed to both parents and their F_1 to produce L_1 ($F_2 \times P_1$), L_2 ($F_2 \times P_2$) and L_3 ($F_2 \times F_1$) families. F_1, F_2, F_3 and backcross generations were also produced.

The progeny of this crossing programme were grown, together with the parental varieties, in a completely randomised plot experiment. Because of the differing amounts of crossed and selfed seed available, different numbers of plots of each generation were sown. The numbers of families and plots/family are shown in Table 1.

Each plot consisted of a single row of eleven plants with 10 cm spacing between plants and 30 cm between rows. The characters yield/plant, tiller number/plant, spikelet number/ear, grain no./ear and 50 grain weight were measured individually on eight plants, chosen at random, from each plot.

(b) Single Seed Descent Lines

Development of single seed descent (SSD) lines of each cross was initiated by sowing 250 F_2 seeds in seed trays in potting compost at a density of approximately 3,500 plants/m^2. These were vernalised, then grown to maturity and 1 seed/plant harvested. This cycle was repeated for two further generations. A single seed of each F_5 family was then grown under low density conditions to produce sufficient F_6 seed for experimental purposes.

Table 1. Experimental design for early generations

Generation		No. families	No. plots/ family
Hobbit 'sib'		1	4
'Manella'		1	4
'Sava'		1	4
Hobbit 'sib' × 'Manella'	F_1	1	4
	F_2	1	8
	B_1	1	6
	B_2	1	6
	F_3	14	2
	L_1	15	2
	L_2	15	2
	L_3	15	2
Hobbit 'sib' × 'Sava'	F_1	1	4
	F_2	1	8
	B_1	1	6
	B_2	1	6
	F_3	15	4
	L_1	15	4
	L_2	15	4
	L_3	15	4

A total of 71 Hobbit 'sib' × 'Manella' and 116 Hobbit 'sib' × 'Sava' lines were used. These, together with the parental lines, were grown in randomised block experiments, each consisting of 4 replications, adjacent to the experiment containing the early generations. In each block, each SSD line was represented by a single plot of eleven plants sown at the same spacing as the early generations. At harvest, yield and yield components were measured on a plot basis and converted to an individual plant basis where appropriate.

Genetical Analysis

(a) Detection and Estimation of Components of Variation of Means

From the data on individual plants of the crossed generations, means and variances of the parental, F_1, F_2, F_3, B_1, B_2, L_1, L_2 and L_3 generations were calculated and the mean performance of these generations is shown in Table 2. There was significant genetical variation for all characters in the Hobbit 'sib' × 'Sava' cross and for all except tiller number/plant in the Hobbit 'sib' × 'Manella' cross. Joint scaling tests (Mather and Jinks 1971) were used to elucidate the genetical control of each character in terms of additive, dominance and epistatic effects.

(i) Detection of Epistasis

Epistasis may cause the distribution of recombinant inbred lines to be skewed (Snape and Riggs 1975). Therefore, in predicting cross performance it is necessary to detect and estimate its contribution to the genetical variation of family means so that allowance for additive × additive (i type) epistasis can be made in the prediction equations (Jinks and Pooni 1976; Pooni et al. 1977). Thus, a joint scaling test was carried out where an additive, dominance model was fitted to the means of all ten generations for each character. Failure of this model reveals the presence of epistasis. The contribution of linked epistatic genes to this epistatic variation was tested by comparing the means of the F_2, B_1 and B_2 generations with the L_3, L_1 and L_2 generations, respectively. These tests of epistasis were supplemented by the analysis of variance of the comparisons $(2L_{3i} - L_{1i} - L_{2i})$ of the F_2 triple test cross which enables i type interactions to be distinguished from combined additive × dominance (j type) and dominance × dominance (1 type) interactions. The results of these tests for each character and cross are shown in Table 3.

For both crosses, epistasis was detected for spikelet number, grain number/ear and 50 grain weight, although the tests were not consistent in detecting its presence. For spikelet number the predominant type of epistasis was i type in the Hobbit 'sib' × 'Sava' cross and j + l type in the Hobbit 'sib' × 'Manella' cross. The triple

Table 2. Mean performance of cross generations

Generation		Yield/plant (gm)	Tiller no./plant	Spikelet no./ear	Grain no./ear	50 grain weight (gm)
Hobbit 'sib' (P_2)		20.26	8.92	20.54	62.04	2.436
'Manella' (P_1)		25.42	9.69	22.22	59.16	2.777
'Sava' (P_1)		19.60	8.88	21.34	38.76	2.526
Hobbit 'sib' × 'Manella'	F_1	28.78	9.66	22.28	70.19	2.821
	F_2	27.12	9.53	21.53	65.73	2.853
	F_3	24.47	10.20	21.11	60.06	2.636
	B_1	26.14	9.58	21.96	62.81	2.774
	B_2	25.69	9.94	21.15	67.48	2.509
	L_1	27.66	10.27	21.47	59.96	3.013
	L_2	27.19	10.62	21.17	66.62	2.611
	L_3	26.77	10.43	21.25	62.47	2.706
Hobbit 'sib' × 'Sava'	F_1	28.82	11.53	23.22	63.94	2.674
	F_2	27.30	11.56	21.63	60.89	2.614
	F_3	24.75	9.92	22.32	65.26	2.514
	B_1	24.82	12.35	22.06	50.39	2.641
	B_2	27.56	11.08	22.40	72.37	2.357
	L_1	27.70	11.94	22.41	58.07	2.565
	L_2	28.87	10.11	22.19	71.33	2.609
	L_3	27.94	11.06	22.52	65.16	2.531

Table 3. Tests for the presence of epistasis

Cross	Test	Yield/plant	Tiller no.	Spikelet no.	Grain no./ear	50 grain wt
Hobbit 'sib' × 'Manella'	1. Joint scaling test	Absent	–	Absent	Present	Present
	2. Linked epistatic effects	Absent	–	Absent	Absent	Present
	3. Triple test cross	Absent	–	Present	Absent	Absent
	'i' type	–	–	Absent	–	–
	'j' + 'l' type	–	–	Present	–	–
Hobbit 'sib' × 'Sava'	1. Joint scaling test	Absent	Absent	Present	Present	Absent
	2. Linked epistatic effects	Absent	Absent	Absent	Present	Absent
	3. Triple test cross	Absent	Absent	Present	Absent	Present
	'i' type	–	–	Present	–	Present
	'j' + 'l' type	–	–	Absent	–	Absent

test cross did not reveal the significant component of epistasis for the other two characters. However for grain number/ear and 50 grain weight at least some of the epistatic effect must be due to the linkage of interacting genes.

(ii) Estimation of Components of Means

Following the results of the tests for epistasis, sequential model fitting was applied to the means, where appropriate, to obtain the best fitting model for each character. From these models, estimates of the additive component, $\{d\}$, and the additive × additive epistasis $\{i\}$, were obtained for use in predicting the frequencies of transgressive segregants. However the values of the other components, dominance $\{h\}$, additive × dominance $\{j\}$, and dominance × dominance $\{l\}$ epistasis enabled the genetical architecture of each character to be interpreted. The parameter estimates for each character are shown in Table 4.

These models provided an adequate description of the variation between the observed means with the exception of 50 grain weight in both crosses, and grain number/ear and spikelet number in the Hobbit 'sib' × 'Sava' cross. For these characters no combinations of parameters gave an adequate fit to the observed means. The presence of linked epistatic effects will contribute to this failure since, with the generations available, no adequate model to take account of this effect could be fitted. For 50 grain weight, the additive, dominance model provided the best fit even though epistasis was present in both crosses.

Table 4. Best fitting models of components of means

Cross	Parameter	Yield/plant (gm)	Tiller no.	Spikelet no.	Grain no./ear	50 grain wt (gm)
Hobbit 'sib' × 'Manella'	$\hat{m}$	23.47***	–	21.20***	57.84**	2.600***
	$\{\hat{d}\}$	1.60**	–	0.84**	1.38	0.210***
	$\{\hat{h}\}$	6.14***	–	–0.66	9.29	0.222***
	$\{\hat{i}\}$	–	–	0.13	2.50	–
	$\{\hat{j}\}$	–	–	–0.90	8.78*	–
	$\{\hat{l}\}$	–	–	1.71	3.15	–
Hobbit 'sib' × 'Sava'	$\hat{m}$	20.80***	9.14***	20.85***	55.93***	2.819***
	$\{\hat{d}\}$	0.67	1.50*	0.38*	11.97***	0.042*
	$\{\hat{h}\}$	13.98***	4.46*	3.07*	24.26**	0.184***
	$\{\hat{i}\}$	–	1.16*	0.14	–5.06	–
	$\{\hat{j}\}$	–	0.54	–0.69	–11.29**	–
	$\{\hat{l}\}$	–	–1.99	0.91	–16.84*	–

* 0.05–0.01, ** 0.01–0.001, *** <0.001

Table 5. Triple test cross analyses of variance

Cross	Item	df	Mean squares				
			Yield/plant	Tiller no.	Spikelet no.	Grain no./ear	50 grain wt
Hobbit 'sib' × 'Manella'	Sums	14	32.128**	–	1.2905***	49.899***	0.11589
	Differences	14	22.244	–	0.3688*	15.729	0.14764
	Plot error	45	10.350	–	0.1810	10.942	0.11318
	$\hat{D}'$		29.04	–	1.4793	51.94	0.00036
Hobbit 'sib' × 'Sava'	Sums	14	48.205***	6.6283**	5.8143***	317.252***	0.24240***
	Differences	14	24.534	2.3672	0.7252	14.616	0.01874
	Plot error	135	14.021	2.7560	0.5870	17.598	0.02435
	$\hat{D}'$		22.79	2.5815	3.4849	199.77	0.14537

* 0.05–0.01, ** 0.01–0.001, *** <0.001

The large positive values of $\{h\}$ relative to $\{d\}$ for all characters, except for spikelet number in the Hobbit 'sib' × 'Manella' cross, indicate the dispersion of dominant genes, which increase expression, between the parents, since $(H/D)^{1/2} < 1$ for all characters showing that no overdominance occurs. This type of genetical architecture is commonly found for yield and yield components in wheat (Law et al. 1978) and results in positive heterosis in the F_1. This should also ensure transgressive segregation for these characters and, in the case of yield, recombinant inbreds with a yield as large as the F_1 should be possible.

The magnitudes and signs of the epistatic parameters differ between characters and crosses and it is difficult to classify the interactions into the classical complementary or duplicate types (Mather 1967). Only for grain number/ear is a pattern discernible with duplicate interactions in the Hobbit 'sib' × 'Sava' cross.

(b) Detection and Estimation of Components of Variance

Analysis of variance of the Sums $(L_{1i}+L_{2i}+L_{3i})$ and Differences $(L_{1i}-L_{2i})$ of the F_2 triple test cross families allows a test for the presence of additive and dominance components of variation, respectively. In the absence of epistasis, the Sums mean square is a function of $\frac{1}{8}D$, and thus gives an estimate of the additive variance, D, necessary for prediction. This is obtained from the analysis of variance by equating the observed mean squares to their expectations, appropriate to the experimental design (Mather and Jinks 1971). This estimate is independent of dominance, but will be biased by epistasis, if present. Nevertheless, it is still likely to provide the best source for prediction of the variance of the recombinant inbred population (Jinks 1981).

The analyses of variance of Sums and Differences for both crosses, together with the estimates of the additive genetical variance are shown in Table 5. There was significant additive variance for all characters except 50 grain weight in the Hobbit 'sib' × 'Manella' cross. Surprisingly, in view of the strong directional dominance detected from the analysis of means, significant dominance variance was only detected for spikelet number.

Frequencies of Transgressive Segregants

(i) Calculation of Expected Frequencies

From the estimates of the components of means, $\{d\}$, and where appropriate $\{i\}$, and the additive genetical variance D′ (D ± epistasis), the proportions of recombinant inbreds expected to transgress the parental range were calculated using the method of Jinks and Pooni (1976).

The proportion expected to achieve a performance less than the lower scoring parent was calculated from statistical tables (Fisher and Yates 1963) for the one-tail probability integral corresponding to:

$$-\{d\}+\{i\}/D'^{\frac{1}{2}}$$

and the proportion exceeding the higher scoring parent from the integral

$$\{d\}+\{i\}/D'^{\frac{1}{2}}.$$

The calculated proportions for each character for the two crosses are shown in Table 6, using the estimated components from Tables 4 and 5. Transgressive segregants are predicted for all characters. For yield itself, 76% of the Hobbit 'sib' × 'Manella' lines and 90% of the Hobbit 'sib' × 'Sava' lines are expected to be outside the parental range. These high frequencies indicate the high degree of dispersion of increasing alleles for yield between the parents. This might be expected from parents of such diverse origins. This dispersion is also characteristic of all the individual yield components and indicates that relatively few random inbred lines should be required to obtain recombinants with a performance better than the parental material.

The effect of including $\{i\}$ type epistasis in the prediction equations is to make the expected proportions asymmetrical around the parent values and thus to take into account the expected skewness of the recombinant inbred population. The relative frequencies will depend on the relative sizes of $\{d\}$ and $\{i\}$, and the sign of $\{i\}$. An extreme example of this asymmetry in the present data is the high frequency of lines expected to possess a tiller number less than Hobbit 'sib' in the Hobbit 'sib' × 'Sava' cross, but the low proportion to have a tiller number greater than 'Sava', caused by $\{i\}$ being positive and of similar magnitude to $\{d\}$.

(ii) Performance of Single Seed Descent Lines

The SSD lines of both crosses exhibited significant genetical variation for all characters measured and the overall cross mean, range and genetical variance (V_G) are shown in Table 7. For tiller number and 50 grain

Table 6. Expected frequencies of transgressive segregants

		Yield/plant	Tiller no.	Spikelet no.	Grain no./ear	50 grain wt
Hobbit 'sib' × 'Manella'	$>P_1$	0.38	–	0.44	0.31	–
	$<P_2$	0.38	–	0.12	0.44	–
	Total	0.76	–	0.56	0.75	–
Hobbit 'sib' × 'Sava'	$>P_1$	0.45	0.06	0.39	0.32	0.46
	$<P_2$	0.45	0.42	0.45	0.12	0.46
	Total	0.90	0.48	0.84	0.44	0.92

Table 7. Mean, range and genetical variance of single seed descent populations

Cross		Yield/plant (gm)	Tiller no./plant	Spikelet no./ear	Grain no./ear	50 grain wt (gm)
Hobbit 'sib' × 'Manella'	Mean	22.49	9.37	20.89	59.22	2.785
	Range	9.35–30.46	6.21–11.49	17.31–23.18	44.50–74.73	2.085–3.255
	V_G	15.848	0.922	1.379	30.428	0.0797
Hobbit 'sib' × 'Sava'	Mean	21.35	9.35	21.78	62.09	2.687
	Range	10.06–30.17	6.41–12.77	18.69–26.94	31.66–94.32	1.515–3.375
	V_G	14.415	0.986	2.342	111.78	0.1115

Table 8. Observed and expected numbers of transgressive segregants

		Yield/plant			Tiller no.			Spikelet no.			Grain no./ear			50 grain wt		
		O	E	Sign. of diff.	O	E	Sign. of diff.	O	E	Sign. of diff.	O	E	Sign. of diff.	O	E	Sign. of diff.
Hobbit 'sib' ×	$>P_1$	18	27	N.S.	4	–		24	31	N.S.	23	22	N.S.	5	–	
'Manella'	$<P_2$	23	27	N.S.	10	–		11	9	N.S.	35	31	N.S.	19	–	
(71 lines)	Total	41	54	N.S.	14	–		35	40	N.S.	58	53	N.S.	24	–	
Hobbit 'sib' ×	$>P_1$	64	52	N.S.	3	7	N.S.	71	45	*	52	37	N.S.	84	53	**
'Sava'	$<P_2$	40	52	N.S.	38	49	N.S.	28	52	*	3	14	*	22	53	***
(116 lines)	Total	104	104	N.S.	41	56	N.S.	99	97	N.S.	55	51	N.S.	106	106	N.S.

N.S. = non significant (> 0.05)
* 0.05–0.01, ** 0.01–0.001, *** <0.001

weight in the Hobbit 'sib' × 'Manella' cross, the inability of the triple test cross analysis to detect significant genetical effects cannot be due to the lack of genetical variation. This is possibly a sampling problem in the choice of the F_2 parents used.

A comparison with the parental values in Table 2 shows that, as predicted, both SSD populations possess lines transgressing the parental range for all characters. Furthermore, inbreds with a performance exceeding the heterotic F_1 are found in these recombinant populations indicating that the observed heterotic level can be fixed in an inbred line. The accuracy of the triple test cross analysis in predicting the variance of the inbred population can be examined by comparing D′ in Table 5 with V_G. Reasonable correspondence is obtained although in all cases where significant additive variation was detected, the estimate of D′ exceeds V_G, although never significantly so. A small difference is expected in this direction since V_G is the variance of an F_6 population whose expectation is $^{31}/_{32}\,D + {}^{31}/_{1024}\,H$. This overestimation of the variance should result in an overestimation of the proportions of transgressive segregants, although the bias should be small.

(iii) Comparison of Observed and Expected Frequencies

The observed frequencies of transgressive segregants were scored on the family means of the SSD lines in comparison to their parents grown in the same experiment. The expected numbers were calculated by multiplying the expected frequencies (Table 6) by the numbers of lines grown and rounding off to a whole number. These values are shown in Table 8, together with the significance of differences between observed and expected, calculated from χ^2 tests on expectations of equal frequencies.

In both crosses, and for all characters, the total numbers of observed lines agree very well with the predicted numbers. For yield/plant, where an additive, dominance genetical model accounted for the observed variation, lines higher and lower yielding than the parents are predicted to occur equally frequently, and this agrees well with the observed, although a slight asymmetry is apparent in the Hobbit 'sib' × 'Sava' cross. Asymmetry in the distributions of the lines for the other characters is expected because of significant epistatic effects. This asymmetry is observed and accurately predicted for characters where an adequate genetical model including epistasis was obtained, as in the case of tiller number in the Hobbit 'sib' × 'Sava' cross, and spikelet number and grain number/ear in the Hobbit 'sib' × 'Manella' cross. However, for spikelet number, grain number/ear and 50 grain weight in the Hobbit 'sib × 'Sava' cross, failure to obtain an adequate model to explain variation between the generation means is reflected in significant discrepancies between observed and expected numbers of lines transgressing the parental range. With respect to grain number/ear the error is not serious, and the asymmetry is apparent but has not been allowed for sufficiently. However, for the other two characters gross distortions are obtained. It is apparent that for these characters inadequate or no allowance for epistasis in the prediction equations leads to spurious estimates of the frequencies of transgressive segregants. These results apart, however, the predicted and observed numbers agree extremely well and reinforce the conclusion of Pooni et al. (1977) that prediction equations that assume normality but make a correction for $\{i\}$ type epistasis in the expected mean of the recombinant population can accurately predict the frequencies of transgressive segregants.

Discussion

These experiments clearly demonstrate that genetical analysis of yield and yield components in early generations of a cross of wheat can provide the information necessary to predict accurately the likely outcome of inbreeding the F_2. The frequency of inbred lines superior to the better parent can be predicted so that objective decisions concerning discrimination between different crosses as well as the likelihood of securing a recombinant inbred with any desired level of performance, can be formulated. The limitation of this approach, however, is the amount of practical work required to produce the experimental generations, which in a wheat breeding programme, will restrict the number of crosses that can be handled.

To achieve as accurate data as possible the F_2 triple test cross was used in the present work. This mating design has the advantage that its analysis produces an accurate and uncorrelated estimate of the additive genetical variance, and it is this prediction parameter, rather than the components of means, that is the most difficult to estimate accurately. However it does require an extensive crossing programme to develop the necessary generations. In the present work, fifteen F_2 plants were used for each cross but this is likely to be the lowest limit if sampling problems are to be avoided. Kearsey (1980), for example, on the basis of a computer simulation study recommends that twenty F_2's as a minimum should be used. In the Hobbit 'sib' × 'Manella' cross, it was probable that failure to detect additive variation for tiller number and 50 grain weight was the result of inadequate sampling. Thus to increase the numbers of crosses handled in wheat will require either a restriction on the grains per cross and therefore the degree of replication, or a simplification in the design, and thus a reduction in the number of cross progeny grown per cross.

Additive genetical variance can be estimated from the F_2 and backcross generations alone. However in the present crosses such estimates were very small, or even negative, and significantly different from the triple test cross estimates. This may have been due to the fewer numbers grown and to correlations in estimation between the additive variance and other variance components. This is also compounded by the difficulty of assessing genetical variances for yield and its components on individual plant data in wheat because of effects of within plot competition. A further advantage of the F_2 triple test cross is that by working with plot means, heritabilities are effectively increased.

An alternative approach to an extensive crossing programme has been suggested by Jinks and Pooni (1980). They advocate growing samples of random F_3 lines and using twice the variance of F_3 family means as a measure of additive genetical variance, although this estimate has an upward bias of $\frac{1}{8}$H. In wheat this would have the advantage that no crossing is required after development of the F_1, and plots rather than individual plants would form the basic unit of assessment. Preliminary results of comparisons of F_3 variances with triple test cross variances using the crosses described here (Snape, unpublished) suggest that this approach is promising, although a slight overestimation of frequencies of transgressive segregants is obtained, which on genetical theory would be expected.

Predicting the frequency of transgressive segregation in a cross does not, of course, guarantee that such lines can be identified and selected to form the nuclear seed of a new variety. Problems of assessment remain even if a promising cross is identified. Whether selection is commenced in the early generations or delayed until greater homozygosity is achieved using single seed descent or doubled haploid procedures, will depend on the preference of particular breeders. However it is becoming apparent that delaying selection for quantitative characters until later generations can be advantageous (Snape and Riggs 1975; Jinks and Pooni 1981).

A problem that could occur in applying prediction methods in practice relates to the relationship between the different methods used in the assessment of experimental generations and breeding material. Generally predictions are based on generations which, because seed is limiting or for ease of experimental procedure, are grown at a lower density than breeding plots. Thus genetical parameters measured on spaced plants must relate to performance under agricultural conditions. This necessitates that genotype × method of assessment interaction be absent or small. Evidence from experiments in wheat (Law et al. 1978; Snape, unpublished) suggests that there is a strong correlation between performance under the spaced plant conditions used in the present experiments and drilled plot performance for yield and yield components. Thus the predictions described above should relate closely to the expected performance of the crosses under agricultural conditions.

The predictions described above are for characters considered individually. However the equations can be extended to a multivariate distribution to include genetical correlations between different characters (Pooni and Jinks 1978). Thus probabilities of securing an optimum genotype based on a number of important characters can be calculated. Using this approach in wheat offers an objective method of cross selection. Limitations in application are likely to be based on practical considerations rather than genetical ones.

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