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Cross Prediction Studies on Spring Barley

2. Estimation of Genetical and Environmental Control of Yield and Its Component Characters

C. R. Tapsell
Rosewarne Experimental Horticulture Station, Rosewarne, Camborne, Cornwall (UK)

W. T. B. Thomas
Scottish Crop Research Institute, Pentlandfield, Roslin, Midlothian (UK)

Summary. The genetical and environmental control of yield and its components in spring barley, tillers per plant, grain number and grain weight has been investigated by triple test cross and linear modelfitting analyses.

Additive and dominance effects were observed for both grain number and grain weight, but tiller number was almost totally controlled by environmental factors. Epistatic effects were usually absent, only grain number exhibited such effects. The heritabilities of the yield components varied from low (0.15) for tiller number to high (0.51) for grain weight. Yield itself, measured on a single plant basis was mainly under additive and dominance control, with little evidence for epistasis. The heritability for single plant yield was low (0.22).

The possibilities for early generation selection for yield are discussed, and the relative contributions of each genetic and environmental component are described.

Key words: Cross prediction – Genetical control – Spring barley – Yield – Yield components

Introduction

Selection on a single plant basis for yield in the early generations of a cereal breeding programme is generally unsuccessful (Grafius et al. 1952; Rasmusson and Cannell 1970; Riggs and Hayter 1975; Briggs et al. 1978; Hanson et al. 1979; Valentine 1979) because of the low heritability. Selection for characters with higher heritabilities such as plant height, maturity and the grain weight component of yield has been successful (McKenzie and Lambert 1961; Rasmusson and Cannell 1970; Yap and Harvey 1972; Briggs et al. 1978; Valentine 1979).

Since early generation selection for yield is difficult it would be worthwhile being able to predict which crosses produce inbred lines with a significant improvement over the parental or other varieties. This would reduce the considerable wastage of resources resulting from the continuation of low yielding lines into later generations (Frey 1954), and from discarding lines with good yield potential in early generations (Lupton and Whitehouse 1957).

One method for predicting the range of inbred lines which can be derived from a cross between two inbred parents has been described recently, which allows for the presence of epistasis, genotype × environment interactions and linkage (Jinks and Pooni 1976). This has been tested and extended in later papers (Pooni et al. 1977; Pooni and Jinks 1978, 1979).

In this paper we present the results of an investigation of the genetical and environmental control of yield and its component characters in five barley crosses.

Materials and Methods

A more detailed account of materials and methods is given in the previous paper (Thomas and Tapsell 1983).

Data are presented on the following characters:

TN:	Number of fertile tillers per plant
GNF:	Number of grains on the main tiller measured before harvest
GNL:	Number of grains on the main tiller measured after harvest
TY:	Grain yield on the main tiller (g)
SPY:	Grain yield of the whole plant (g)
TGW:	1000 grain weight (g), obtained using GNL and TY.

Results

1 Tiller Number (TN)

With few exceptions (Tables 1 a and b) there was little evidence for genetical control of TN in any of the five crosses, nearly all of the variation observed being environmental in origin. Heritabilities were low, in the

Table 1a. Components of variation for tiller number (from TTC)

	GP × M	U × M	GP × AR	BH4 × AR	C × Y
D	3.2701***	0.9538 NS	1.8074*	1.0051 +	1.1851*
H	0.0000 NS	0.9767 NS	0.5899 NS	2.3271*	0.0000 NS
F	– 0.0069 NS	0.5213 NS	0.5601 NS	0.9598*	0.0510 NS
E′	8.3988	9.5432	8.1128	9.9815	7.5059
h^2_b	0.2802	–	0.1002	0.0980	0.1364
h^2_n	0.2802	–	0.1002	0.0454	0.1364
$(H/D)^{1/2}$	0.0000	–	0.0000	1.5216	0.0000
Epistasis [i]² type	NS	***	NS	NS	+
J + L type	NS	NS	NS	NS	NS

Significance levels:
NS = probability > 0.10 (not significant)
+ = probability 0.10 – 0.05
* = probability 0.05 – 0.01
** = probability 0.01 – 0.001
*** = probability < 0.001
Heritabilities and dominance ratios were not calculated in those crosses where H and D were not significant

Table 1b. Model-fitting for the character tiller number

	GP × M	U × M	GP × AR	BH4 × AR	C × Y
Best model	#	#	m[d] [h]	m[d]	#
m	–	–	9.8849***	9.2957***	–
[d]	–	–	1.5762***	2.3422***	–
[h]	–	–	– 3.1910***	–	–
Parental means					
Female	8.2000	9.3750	8.3250	7.6500	8.7000
Male	7.4750	8.6250	10.9250	11.1750	8.4250

\# In these crosses the means of the parents did not differ significantly for this character

range 0.0454–0.2802 and 0.0980–0.2802 for h^2_n and h^2_b respectively. However, it should be stressed that the detection and analysis of genetical variation for characters with low heritabilities requires large experimental sizes (Kearsey 1970; Pooni and Jinks 1976), and future studies on TN should be based upon larger sample sizes.

2 Grain Number (GNL)

Grain number was measured both in the field (GNF), shortly before the plants reached maturity, and in the laboratory after harvest (GNL), the latter being used to calculate 1,000 grain weights.

Measurements in the field were made on five randomly chosen plants. The same five plants were not necessarily chosen at harvest for the post harvest characters to be scored. Both estimates of grain number were analysed and similar conclusions were reached. However, since all of the remaining characters were scored on those five plants recovered at harvest, the measurement of GNL is presented here.

Environmental effects contributed more to the variation of this character than genetic effects (Table 2a). The exception was in the cross C×Y where larger genetic effects were found. The presence in 'Clipper' of a day-length insensitivity factor may have been responsible for this. Heritabilities were therefore low, in the range 0.0827–0.1012 and 0.1477–0.1698 for h^2_n and h^2_b respectively with C×Y once again being the exception with both h^2_n and h^2_b of 0.8521.

Highly significant additive effects were found in GP×M, GP×AR, BH4×AR and C×Y in the TTC analysis, and in GP×AR and C×Y by model-fitting. The parents in GP×M, U×M and BH4×AR did not differ significantly (Table 2b), consequently the non-significant additive component in U×M was not unexpected.

Evidence for dominance was not conclusive. Only GP×M, GP×AR and BH4×AR had a significant dominance component in the TTC analysis, and only C×Y in the MF study. Where present, dominance was complete, $(H/D)^{1/2}$ ranging rom 0.96–1.45, and in the direction of increasing grain number.

There was evidence of epistasis, with GP×M, GP×AR and BH4×AR all exhibiting $[i]^2$ type epistasis in the TTC analysis and GP×AR and C×Y J+L types. C×Y also exhibited [l] type epistasis in the MF study.

3 1000 Grain Weight (TGW)

Unlike the previous characters, more of the variation in TGW was genetical in origin, with the exception of C×Y. The heritability of TGW was in the range 0.2664–0.5423 and 0.5038–0.6508 for h^2_n and h^2_b respectively but, in C×Y, h^2_n was equal to h^2_b having a value of 0.2479.

Highly significant additive effects were observed in all crosses in both TTC and MF studies (Tables 3a and b), again with the exception of C×Y where the significance was borderline. In the MF study U×M and C×Y showed no significant difference between the parents.

Dominance or epistasis was found in all crosses in both analyses, with the exception of U×M and C×Y in the MF studies. Dominance was observed in GP×M, GP×AR and BH4×AR in both analyses. Epistasis was detected on fewer occasions and with lower significances. U×M exhibited $[i]^2$ and J+L interactions in the TTC analysis, and C×Y exhibited an $[i]^2$ interaction in the TTC analysis.

The higher scoring parent (P_1) contained an excess of dominant alleles in GP×M, GP×AR and BH4×AR (F positive and significant), which was consistent with the positive [h] parameters found in the corresponding MF analyses. Both indicated that the direction of dominance was for high thousand grain weight.

4 Single Plant Yield (SPY)

Grain yield was measured in two ways; as main tiller yield, and single plant yield. It is unwise to extrapolate directly to commercially grown crop yields because of the considerable differences in growing conditions. However, for the purpose of this study it was important to obtain an estimate of yield which was directly comparable with the yield components, which were measured on, or calculated from measurements on, single plants.

Single plant and single tiller yields showed a phenotypic correlation of 0.58, and additive genetic correlations ranging from 0.64–0.92 in the five crosses. Since there was little evidence of significant genetical variation in tiller number in these crosses tiller yield was not analysed.

The environmental component (E′) and the genetical components (D and H) have approximately equal roles in the control of variation in single plant yield (Table 4a). Estimates for both narrow and broad

Table 2a. Components of variation for grain number

	GP × M	U × Y	GP × AR	BH4 × AR	C × Y
D	1.7285***	0.1079 NS	1.6975*	1.8342***	37.1897***
H	1.5814***	0.2686 NS	3.5777***	1.6849**	0.0092 NS
F	1.0475**	0.3412 NS	−0.0463 NS	0.0282 NS	−0.6715 NS
E′	7.8133	8.4544	8.5211	7.7221	3.2266
h^2_b	0.1619	–	0.1698	0.1477	0.8521
h^2_n	0.0927	–	0.0827	0.1012	0.8521
$(H/D)^{1/2}$	1.2221	–	1.4518	0.9584	0.0000
Epistasis $[i]^2$ type	**	NS	**	+	NS
J + L types	NS	NS	*	NS	**

Table 2b. Model-fitting for the character grain number

	GP × M	U × M	GP × AR	BH4 × AR	C × Y
Best model	#	#	m[d]	#	m[d] [h] [l]
m	–	–	27.1461***	–	18.1010***
[d]	–	–	0.9560***	–	5.2159***
[h]	–	–	–	–	6.1572***
[l]	–	–	–	–	−5.4583***
Parental means					
Female	26.1750	28.3500	26.2750	24.1250	12.5500
Male	28.6500	29.2750	27.5250	27.4500	24.6750

For levels of significance see Table 1

Table 3a. Components of variation for thousand grain weight

	GP × M	U × M	GP × AR	BH4 × AR	C × Y
D	37.9689***	35.1014***	21.5615***	62.9931***	14.2422*
H	44.6341***	7.7344 NS	41.3028***	25.2227**	0.0000 NS
F	17.9058**	5.3435 NS	14.1055***	20.2636***	4.3807 NS
E′	16.2161	17.2875	19.3580	20.2825	43.2167
h^2_b	0.6502	0.5038	0.5216	0.6508	0.2479
h^2_n	0.4095	0.5038	0.2664	0.5423	0.2479
$(H/D)^{1/2}$	1.0842	0.4694	1.3840	0.6328	0.0000
Epistasis $[i]^2$ type	NS	*	NS	NS	***
J + L types	NS	*	NS	NS	NS

Table 3b. Model-fitting for the character thousand grain weight

	GP × M	U × M	GP × AR	BH4 × AR	C × Y
Best model	m[d] [h]	#	m[d] [h]	m[d] [h]	#
m	32.0585***	–	33.0707***	30.4022***	–
[d]	6.9773***	–	3.1187**	8.2984***	–
[h]	12.4081***	–	7.3721***	15.5440***	–
Parental means					
Female	25.9988	32.2888	27.5263	25.3373	43.0725
Male	36.9488	38.8688	38.4950	40.1763	30.9288

For levels of significance see Table 1

Table 4a. Components of variation for single plant yield

	GP × M	U × M	GP × AR	BH4 × AR	C × Y
D	3.2342***	0.9739 +	0.7947 +	3.3160***	3.3006***
H	2.4860***	1.9154*	3.5764**	2.7696***	0.0000 NS
F	0.8379 NS	0.0805 NS	0.6402 NS	2.1090***	0.0012 NS
E′	5.4970	6.1523	5.4746	6.6063	2.3110
h^2_b	0.2894	0.1357	0.1909	0.2624	0.5882
h^2_n	0.2090	0.0684	0.0587	0.1851	0.5882
$(H/D)^{1/2}$	0.8767	1.4024	2.1214	0.9139	0.0000
Epistasis $[i]^2$ type	*	**	NS	NS	NS
J + L types	NS	NS	NS	NS	NS

Table 4b. Model-fitting for the character single plant yield

	GP × M	U × M	GP × AR	BH4 × AR	C × Y
Best model	m[d] [h]	#	m[d]	m[d] [h][a]	#
m	4.5678***	–	5.8184***	6.2484***	–
[d]	0.8988*	–	1.7005***	2.6003*	–
[h]	1.5436 +	–	–	2.9358 +	–
Parental means					
Female	4.0888	6.7575	4.2400	3.4638	3.4513
Male	5.2150	6.6363	7.5600	7.9963	4.5450

[a] This model was fitted excluding the B2 generation since the mean of this generation was considerably deviant from a reasonable value

For levels of significance see Table 1

heritabilities were low (0.06–0.59 and 0.14–0.59 for h_n^2 and h_b^2 respectively).

Significant additive variation was detected in all crosses in both TTC and MF analyses, with the exception of U×M and C×Y where there were no significant parental differences.

There was some evidence for dominance variation with all crosses except C×Y having a significant H component. In the MF study GP×M and BH4×AR also exhibited a directional dominance effect. On the whole, the TTC suggested that dominance was complete, or nearly so, and the significant positive value of F and positive [h] in BH4×AR indicated an excess of dominant genes in the higher scoring parent of that cross. The positive [h] parameter in GP×M supported the view that dominance was towards higher single plant yield.

Only GP×M and U×M exhibited epistasis in the TTC analysis, and this was not highly significant, suggesting only a minor role, if any, in the control of single plant yield.

Discussion

Our finding that the heritability of tiller number is low in spaced plants is in agreement with the results of previous workers (Fiuzat and Atkins 1953; Rasmusson and Cannell 1970; Riggs and Hayter 1975).

Previous studies of grain number have found both additive and dominance effects to be common (Hayes 1965; Riggs and Hayter 1975; Surma 1978), but reports on epistatic effects have been conflicting. Johnson and Whittington (1978) found no evidence for non-allelic interactions, whereas Riggs and Hayter (1973) detected epistasis in a 9-parent diallel of 2-row barley types. In our studies we found evidence for additive effects in four crosses, the exception being U×M, where there was no evidence of any genetical difference between the two parents. Dominance effects were observed in three crosses (GP×M, GP×AR and BH4×AR), and epistasis was detected in all but U×M. The environment played a major role in the control of this character; consequently heritabilities were fairly low.

1,000 grain weight is generally found to be controlled by additive and dominance effects (Riggs and Hayter 1975), although evidence for epistasis has also been reported (Surma 1978). Our results suggest that TGW is indeed largely controlled by additive and dominance effects with a minimal role, if any, for epistasis.

Previous workers have reported difficulties in studying single plant yield due to both the inconsistency of results, and a generally low heritability. In this study we found considerable variation in the magnitude of the genetic effects among the five crosses, although there were significant additive and dominance effects in all crosses, with the exception of C×Y where there was no dominance. Epistasis did not appear to play a large role in the control of single plant yield and was detected in only GP×M and U×M.

From the viewpoint of the possibility of early generation selection on these characters, our results are in agreement with previously published reports. The comparatively low heritabilities obtained for SPY, TN and GNL suggest that response to early generation selection for these characters would be small. On the other hand, TGW possessed much higher heritabilities and would therefore be expected to show a more reasonable response to early generation selection. Selection for increased yield by selecting for increased TGW could prove fairly successful, as a high correlation between them has been reported several times in the literature.

These conclusions require investigation and studies of the reliability and efficiency of the cross-prediction methods are continuing. The effectiveness of the TTC for estimating the genetical components which are necessary for these prediction studies is illustrated. However, the TTC is very labour intensive, particularly in the crossing and field work involved (Thomas and Tapsell 1983). It may be wise only to use it for experimental analyses to identify those characters in those crosses which show large effects and high heritabilities.

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C. R. Tapsell
Rosewarne Experimental Horticulture Station
Rosewarne
Camborne, Cornwall TR14 0AB (England)

W. T. B. Thomas
Scottish Crop Research Institute
Pentlandfield
Roslin, Midlothian EH25 9RF (Scotland)