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Cross Prediction Studies on Spring Barley

1. Estimation of Genetical and Environmental Control of Morphological and Maturity Characters

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Summary. The genetical and environmental control of three height characters, two maturity characters and neck length in five barley pair crosses was studied using both F_2 triple test cross and model fitting analysis.

Significant additive and dominance effects were found for all six characters with some evidence of epistasis for each character. Generally, dominance was incomplete for the height characters but was significantly directional for increased height in those crosses where dwarfing genes were segregating. Variable dominance effects were found for both the maturity characters. Complete dominance was found in three cases, otherwise incomplete dominance was found. Significant directional dominance for earliness was found for both maturity characters in one cross but this was attributed to the presence of a daylength insensitivity factor in one of the parents. Most of the genetic variation for neck length was additive, though some evidence of dominance was found.

Broad sense and narrow sense heritability estimates generally were found to be high for the height and maturity characters but low for neck length. It was concluded that early generation selection for height at ear emergence, for final height and for awn emergence was worthwhile. Early generation selection for neck length was not recommended from the results of this study.

Key words: Cross prediction – Genetical control – Spring barley – Height and maturity

Introduction

In most cereal breeding programmes, selection is concentrated not only on yield but also on agronomic, pathological and quality characters at various stages. Various authors suggest that it is possible to practise single plant selection for plant height and maturity in the early generations of a self-fertilising cereal breeding programme (Briggs et al. 1978; Hanson et al. 1979; McKenzie and Lambert 1961; Valentine 1979). These and other authors such as Rasmusson and Cannell (1970) and Riggs and Hayter (1975) have suggested that selection for yield and its components is largely ineffective at the same stage owing to the comparatively low heritabilities of these characters.

In a subsequent paper (Tapsell and Thomas 1983) we will describe the estimation of the genetical and environmental control of yield and its components. In this paper, we present the results of a study of the genetical and environmental control of three height and two maturity characters and a morphological character.

Where a considerable number of loci are segregating independently in a cross, a large F_2 population is required in order to have a high probability of recovering one or more 'desirable' inbred lines from that cross (England 1982; Sneep 1977). Hence, with only a small number of crosses, a breeder is faced with examining large numbers of single plants in the F_2 generation, the majority of which will be discarded. It would therefore be of great benefit to be able to predict which crosses would eventually produce the greatest number of 'desirable' recombinant inbred lines. Various schemes have been described. For example, the diallel cross and its derivatives has been widely used in this respect. Baker (1978) points out that this approach has not been successful, probably because two of the assumptions in the analysis, independently distributed genes and the absence of epistasis, are frequently not true. A third disadvantage is that the analysis is performed on univariate data.

Jinks and Pooni (1976) describe a method of predicting, for a single character, a range of inbred lines which can be derived from a pair cross, using estimations of the genetical components of family means and variances. Whilst epistasis, genotype × environment interaction and linkage may be present, only epistasis should be allowed for in practice. This

approach has been extended subsequently to allow prediction for two or more characters simultaneously (Pooni and Jinks 1978).

Various experimental designs are available for the estimation of these components. Model fitting analysis (MF) of the basic generations P_1, P_2, F_1, F_2, B_1 and B_2 (Mather and Jinks 1971) is the simplest and most rapid; the F_2 Triple Test Cross (TTC) (Kearsey and Jinks 1968; Jinks and Perkins 1970) is the most complex and reliable. In this experiment, we have used both to analyse the control of the characters studied.

The TTC analysis provides estimates of the genetical and environmental components of variation and the MF analysis provides estimates of the components of the means for each character. The TTC detects and estimates additive (D), dominance (H) and environmental (E′) components of variation (Kearsey and Jinks 1968), together with estimates of directional dominance variation (F) (Jinks et al. 1969) and tests for $[i]^2$ and J+L types of epistasis (Jinks and Perkins 1970). Estimation of E′ can be affected by genotype × environment interactions and is not, in their presence, an estimate of E as defined in Mather and Jinks (1971). The dominance ratio $(H/D)^{1/2}$ can be computed from the results. The MF analysis fits the parameters m, [d], [h], [i], [j] and [l] to the means of the basic generations by a weighted least squares technique (Mather and Jinks 1971).

In this and a subsequent paper, Tapsell and Thomas (1983), the results obtained from both methods have been used to estimate the genetical control of a number of characters in five spring barley crosses. The estimates of [d], [i] and D will later be used to predict the proportions of inbred lines (Jinks and Pooni 1976; Pooni and Jinks 1978) exceeding the parental range for a number of characters for each cross. These results will be presented in a third paper (in preparation), together with a comparison of the predictions with the observed distribution of a number of inbred lines derived from each cross.

Materials and Methods

Seven varieties were used to produce five pair cross populations, studied by both TTC and MF analysis. All were two-row spring barleys and, with one exception, were typical of European spring barleys grown at the time of the experiment.

The five pair crosses studied were:

GP×M : 'Golden Promise'×'Mazurka'
U×M : 'Universe'×'Mazurka'
GP×AR: 'Golden Promise'×'Ark Royal'
BH4×AR: 'BH4/143/2'×'Ark Royal'
C×Y : 'Clipper'×'Ymer'.

The first-named variety was always the female parent. BH4 is derived from the cross 'Akka'×'Midas'. Plants were emasculated by the clipping method (Pope 1944), and heads were then bagged and pollinated 3–5 days later. Enough hybridisations were made to produce approximately 5,000 F_2 seeds for each pair cross. The F_1 seeds were multiplied in the glasshouse, where some were used to produce the backcross generations. From the bulk of F_2 seeds, 20 were picked at random to construct the TTC generations as follows:

$L_{1i} = P_1 \times F_{2i}$, $i = 1–20$
$L_{2i} = P_2 \times F_{2i}$, $i = 1–20$
$L_{3i} = F_1 \times F_{2i}$, $i = 1–20$.

Thus, for each pair cross TTC analysis, 60 cross combinations were required. Each successful pollination of one barley ear yields approximately 20 seed and at least 80 seeds (four successful pollinations) were required for each L_{1i}, L_{2i} and L_{3i}. Thus, 12 fertile tillers were required from each F_2 plant. To encourage development, the F_2 plants used to construct the triple test crosses were grown in 30 cm pots and fed with a nitrogenous fertilizer. This generally proved successful, although there were insufficient seeds in a few cases. For C×Y, seed was scarce in one F_2 family and it was discarded from the experiment. It is worth noting that, to perform TTC analysis on five crosses, at least 1,200 successful pollinations of barley ears were required.

For the MF analysis, the following generations were used in the experiment:

P_1: The higher scoring parent
P_2: The lower scoring parent
F_1: $P_1 \times P_2$
F_2: F_1 selfed
B_1: $P_1 \times F_1$
B_2: $P_2 \times F_1$.

Extra hybridisations were made to produce the F_1, B_1 and B_2 generations. As comparisons would be made between generations produced by both hybridisation (i.e. clipped seed) and by selfing, clipped seed of the selfed generations was also produced for inclusion in the experiment. Fertile tillers of parental and F_1 plants were clipped at, or before, anthesis, bagged and allowed to self and develop in the same manner as hybridisations. A total of 69 families was produced for each pair cross studied. However, as already noted, only 19 F_2 families were included in the experiment for C×Y, bringing the total number of families to 342.

The experiment was sown with the NIAE spaced seeder on the 19th April 1978 at the Murrays Farm, Pathhead, East Lothian (map reference NT411662). The experimental design was a randomised complete block of four replicates. Within each block, each family was represented by a row of up to 20 seeds, sown at 5 cm spacings, with a wheat guard sown at each end of each row. Each row was spaced at 22.5 cm from its neighbour and each block consisted of six beds of 49 and one of 48 experimental rows with wheat guard rows at each end. The whole experiment was netted to prevent bird damage. Germination was monitored and, where plants failed to establish, either replacement plants or wheat guards were transplanted in their place to maintain a constant plant density. Unfortunately, weather conditions were dry and many transplants perished. As a number of plants failed to establish in a second F_2 family from C×Y, it was decided to omit its data from the TTC analysis, making a total of 18 F_2 families studied for this cross. The experiment was sprayed with a commercially available broad spectrum fungicide to prevent the development of any cereal foliar pathogens.

During the growing season, the following characters were scored on a single plant basis within rows. As there were approximately 27,000 single plants in the experiment, resources permitted only the first five plants in each row to be measured. The following variates are presented here:

H1: Height (cm) to the uppermost auricles of the tallest tiller measured 6 weeks after sowing
AE: Days from June 1st, until awns emerged from the flag leaf sheath of the main tiller
EE: Days from June 1st, until the ear was fully emerged from the flag leaf sheath of the main tiller (collar above the auricles)

H2: Height (cm) to the flag leaf auricles at ear emergence
H3: Height (cm) to the collar
NL: Neck length (cm) measured as the distance between the flag leaf auricles and the collar.

The three measurements of height were chosen to represent juvenile plant height (H1), overall height of the vegetative part of the plant (H2) and total plant height, excluding ear length, (H3). Awn emergence is taken as a measure of heading but this could be misleading in erectoides types which have reduced awn length (Persson and Hagberg 1969), so ear emergence was also measured. However, this could also be biased by neck length. The relationship between these characters and maturity was therefore of interest. In Scotland, resistance to head loss is an important agronomic character and short neck length is considered a form of resistance to loss. Little is known about the inheritance of this character.

The experiment was grown in blocks and the variance of a generation mean was the variance of the mean pooled over blocks, if the blocks effect was significant. If not, the pooled variance of the generation mean between and within blocks was used. Where no significant differences were detected between parents for a character, a model was not fitted. This was because lack of a significant [d] component may reflect gene dispersion and does not imply that there will not be other significant components, although both [i] and [j], whilst not necessarily non-significant, will also be affected by gene dispersion. The other estimates are subject to higher errors than [d] and models with non-significant [d] terms are consequently much more likely to apparent failure, and, from the point of view of future cross prediction, the only other parameter of interest would be [i].

Heritabilities were calculated as:

h^2_b(broad-sense heritability) = (1/2 D + 1/4H)/(1/2D + 1/4H + E′)

h^2_n(narrow-sense heritability) = 1/2D/(1/2D + 1/4H + E′).

For inbred lines, the narrow sense heritability is the more relevant statistic.

Results

Height Characters

The results from the TTC analysis (Table 1) show that much of the variation for these characters was under genetic control. Environmental effects accounted for a larger portion of the variation for H1 than for H2 or H3, where the relative amounts of environmental variation were similar. This was reflected in the estimated heritabilities for the characters, estimates of the

Table 1. TTC analysis – height characters, components of variation

		GP × M	U × M	GP × AR	BH4 × AR	C × Y
D	H1	9.23***	25.16***	6.52***	9.46***	131.51***
	H2	138.78***	78.11***	135.60***	82.11***	192.43***
	H3	146.58***	176.85***	112.41***	93.18***	126.20***
H	H1	11.33***	6.47***	3.81***	1.55 NS	85.94***
	H2	75.14***	26.49***	76.52***	35.59***	75.62***
	H3	112.46***	46.54***	50.51***	53.64***	25.00***
E′	H1	2.91	2.80	4.54	4.18	19.23
	H2	2.32	10.35	19.05	27.46	8.26
	H3	0.00	2.98	17.98	20.55	8.51
h^2_b	H1	0.72	0.84	0.48	0.53	0.82
	H2	0.97	0.82	0.82	0.65	0.93
	H3	1.00	0.97	0.79	0.75	0.89
h^2_n	H1	0.45	0.74	0.37	0.53	0.82
	H2	0.77	0.70	0.64	0.53	0.78
	H3	0.74	0.86	0.65	0.58	0.81
F	H1	−2.80 NS	4.69*	1.29 NS	1.99*	53.40***
	H2	50.41***	14.87*	45.35***	27.31***	−60.46***
	H3	66.80***	33.25**	40.30***	36.81***	−28.53***
$(H/D)^{1/2}$	H1	1.11	0.51	0.76	–	0.81
	H2	0.74	0.58	0.75	0.66	0.63
	H3	0.88	0.51	0.67	0.76	0.45
$[i]^2$	H1	NS	**	NS	***	***
	H2	NS	NS	*	NS	NS
	H3	NS	*	NS	NS	NS
J + L	H1	NS	NS	NS	NS	NS
	H2	NS	NS	NS	NS	NS
	H3	NS	*	NS	NS	NS

NS = P<0.10; + = P<0.10>0.05; * = P<0.05>0.01; ** = P<0.01>0.001; *** = P<0.001
Heritabilities and dominance ratios were not calculated when H and D were non-significant

broad-sense heritability (h_b^2) ranging from 0.84 to 0.48 for H1 and from 1.00 to 0.65 for H2 and H3. Estimates of the narrow sense heritability (h_n^2) ranging from 0.37 to 0.74 for H1 and from 0.86 to 0.53 for H2 and H3.

With the exception of the dominance component of H1 for BH4×AR, highly significant additive and dominance effects were detected for the height characters in all crosses. Dominance was found to be complete for H1 in GP×M but was found to be incomplete in all other cases, $(H/D)^{1/2}$ ranging from 0.88 to 0.40. Significant directional dominance for increased height was detected in U×M, BH4×AR and C×Y for H1. Whereas the results for U×M were consistent with the lower scoring parent (U) possessing a recessive dwarfing gene, the H1 results for BH4×AR can only be attributed to sampling error as F was significant but no significant dominance variation was detected. Considering C×Y, it can be seen that F was highly significant for all three characters but that it was positive for H1 and negative for H2 and H3. The results were consistent with the crosses, with the exception of C×Y, segregating for recessive dwarfing genes. From Table 2 it can be seen that the higher scoring parent was C for H1 but that Y scored higher for H2 and H3. Thus it appears that C possesses the majority of dominant alleles controlling height variation for H1, H2 and H3, although this could be the result of C possessing a dominant daylength insensitivity factor.

Some evidence for epistasis was found, mainly of the $[i]^2$ type interaction, especially for H1. Epistasis for H1 could reflect the differences of juvenile growth habit associated with the dwarfing genes present in the crosses, one conferring an erect and the other a semi-prostrate juvenile growth habit. It is interesting to note that where a truer measure of overall height was made, as for H2 and H3, very little epistasis was detected.

In general, the MF analysis results (Table 2), agreed with the TTC results. For H1, there were no significant differences between the parents of GP×M, GP×AR and BH4×AR. For C×Y, no significant dominance component was detected for H1, although a significant [i] type interaction was. The results for H2 and H3 agreed in that highly significant additive and dominance components were detected in all cases, except for the dominance component of the best model for H3 in C×Y. Where significant, the dominance component was in the same direction as that found from the TTC analysis. Epistasis was only detected in one other case, a significant [i] type interaction was detected in the best model for H2 in GP×AR. This result agrees with that of the TTC analysis and is of interest as it was in a decreasing direction. However, some caution should be

Table 2. MF analysis – height characters, components of means

		GP × M	U × M	GP × AR	BH4 × AR	C × Y
Best model	H1	#	m[d] [h]	#	#	m[d] [i]
	H2	m[d] [h]	m[d] [h]	m[d] [i]	m[d] [h]	m[d] [h]
	H3	m[d] [h]	m[d] [h]	m[d] [h]	m[d] [h]	m[d]
m	H1	–	16.29***	–	–	47.77***
	H2	68.81***	72.32***	81.89***	75.22***	67.03***
	H3	80.86***	84.23***	82.91***	81.63***	80.15***
[d]	H1	–	3.64***	–	–	12.51***
	H2	8.15***	2.49**	12.55***	10.53***	9.30***
	H3	10.03***	6.91***	12.11***	10.61***	11.54***
[h]	H1	–	3.25*	–	–	–
	H2	7.29***	3.29*	–	7.65***	−7.45***
	H3	10.41***	6.64***	12.47***	13.69***	–
[i]	H1	–	–	–	–	9.14***
	H2	–	–	−9.89***	–	–
	H3	–	–	–	–	–
Parental means						
H1	Female	22.50	12.98	23.93	22.15	49.95
	Male	23.18	21.90	22.40	21.85	25.55
H2	Female	60.03	67.20	59.73	63.15	55.63
	Male	76.73	76.10	83.33	85.12	77.23
H3	Female	70.75	75.73	71.13	70.68	67.15
	Male	91.75	92.60	93.10	93.50	89.63

= No significant differences between parents
*, **, *** see Table 1

exercised in interpretation of this result, as the effect was not apparent for H3.

Heading Characters

From the TTC analysis (Table 3), it can be seen that environmental effects controlled a greater part of the variation for these characters than was found for the height characters. However, in C×Y, a very high degree of genetic control was apparent for AE, h_b^2 and h_n^2 ranging from 0.65 and 0.27 and from 0.61 to 0.15 respectively.

Highly significant additive effects were found for both characters in all the crosses. Dominance effects were generally significant, the exceptions being AE in

Table 3. TTC analysis – heading characters, components of variation

		GP × M	U × M	GP × AR	BH4 × AR	C × Y
D	AE	7.67***	9.51***	19.95***	20.61***	77.29***
	EE	5.50***	34.49***	10.11***	18.97***	43.26***
H	AE	9.49***	1.17 NS	6.34***	2.85*	24.32***
	EE	9.39***	4.80***	4.76*	0.97 NS	59.36***
E′	AE	8.34	10.09	8.51	6.90	0.00
	EE	13.61	9.96	13.21	8.29	23.43
h_b^2	AE	0.43	0.32	0.58	0.61	1.00
	EE	0.27	0.65	0.32	0.53	0.61
h_n^2	AE	0.26	0.32	0.50	0.58	0.88
	EE	0.15	0.61	0.26	0.53	0.36
F	AE	3.04**	0.44 NS	1.90 NS	2.97 NS	22.16***
	EE	1.99 NS	−4.65*	0.73 NS	−0.09 NS	−15.79*
$(H/D)^{1/2}$	AE	1.11	–	0.56	0.37	0.56
	EE	1.31	0.37	0.69	–	1.17
$[i]^2$	AE	NS	NS	NS	***	NS
	EE	+	NS	NS	**	*
J + L	AE	**	NS	NS	NS	NS
	EE	***	NS	**	NS	NS

*, **, *** see Table 1

Table 4. MF analysis – heading characters, components of means

		GP × M	U × M	GP × AR	BH4 × AR	C × Y
Best model		#	#	m[d] [h]	m[d] [h]	m[d] [h]
		#	m[d] [h] [i] [l]	m[d]	#	m[d] [h]
m	AE	–	–	33.58***	35.00***	20.37***
	EE	–	30.15***	41.71***	–	33.06***
[d]	AE	–	–	5.48***	3.83***	7.04***
	EE	–	2.40***	4.29***	–	3.96*
[h]	AE	–	–	3.16**	−2.77*	−4.44***
	EE	–	25.79**	–	–	−8.04**
[i]	AE	–	–	–	–	–
	EE	–	9.57*	–	–	–
[l]	AE	–	–	–	–	–
	EE	–	−17.00**	–	–	–
Parental means						
AE	Female	27.53	31.23	27.15	28.90	13.25
	Male	27.68	27.80	38.78	38.28	28.95
EE	Female	35.90	45.00	37.20	43.55	31.63
	Male	36.35	35.70	45.23	45.28	38.15

*, **, *** see Table 1; # see Table 2

U×M and EE in BH4×AR. In C×Y, significant directional dominance for earliness was detected for AE and EE, again possibly due to the presence of the daylength insensitivity factor. Otherwise, little evidence of directional dominance was found, although F was significant in an increasing direction for AE in GP×M and in a decreasing direction for EE in U×M. Evidence of complete dominance was found for AE and EE in GP×M and also for EE in C×Y, otherwise dominance was found to be incomplete, $(H/D)^{1/2}$ ranging from 0.69 to 0.37.

Some evidence of epistasis was found for these characters, with significant $[i]^2$ type interactions being detected as frequently as J+L types. It may be worth noting that significant $[i]^2$ type interactions were found for both AE and EE in BH4×AR.

Results from the MF analysis (Table 4) were not as consistent as those obtained from the TTC analysis. No significant differences between the parents were detected for AE and EE in GP×M, for AE in U×M and for EE in BH4×AR. A significant additive component was detected in all crosses where models were fitted but the dominance component was not always significant. With the exception of EE in GP×AR, a significant dominance component was detected where significant dominance variation had been detected by the TTC analysis. Apart from EE in U×M, the direction of dominance was consistent with that found from the TTC analysis.

Neck Length

Although the variation for this character was under some genetic control (Table 5), the greater portion of the variation was environmental. With the exception of U×M, where $h_b^2=0.60$ and $h_n^2=0.54$, heritabilities were low, ranging from 0.33 to 0.10 and from 0.28 to 0.10 for h_b^2 and h_n^2 respectively. The additive effects were highly significant for all the crosses but the dominance effects were variable, being highly significant for U×M and BH4×AR and non-significant for the other crosses. No evidence of directional dominance was detected and, when significant, dominance was incomplete, $(H/D)^{1/2}$ ranging from 0.57 to 0.46. Some evidence of epistasis was detected, significant $[i]^2$ effects being detected for GP×AR and C×Y, although only borderline for the former, and significant J+L effects for GP×M.

Results from the MF analysis (Table 6) were in general agreement with those from the TTC analysis, although no significant differences were detected between the parents of GP×AR and BH4×AR, possibly reflecting the dispersion of genes in the parents. For the other crosses, significant additive and dominance components were found where significant variation for these components had been detected by the TTC analysis, the nature of the dominance component also being in agreement. No evidence of significant epistatic components was found.

Table 5. TTC analysis – NL. components of variation

	GP × M	U × M	GP × AR	BH4 × AR	C × Y
D	3.94***	17.26***	2.71***	5.10***	1.93*
H	0.61	3.61***	1.47 +	1.65**	1.18
E′	8.05	6.43	6.43	6.10	8.45
h_b^2	0.20	0.60	0.17	0.33	0.10
h_n^2	0.20	0.54	0.17	0.28	0.10
F	0.72	1.99	−0.17	0.69	−0.44
$(H/D)^{1/2}$	–	0.46	0.74	0.57	–
$[i]^2$	NS	NS	*	NS	**
J + L	**	+	NS	+	NS

+, *, **, *** see Table 1

Table 6. MF analysis – NL. components of means

	GP × M	U × M	GP × AR	BH4 × AR	C × Y
Best model	m[d]	m[d] [h]	#	#	m[d]
m	8.41***	6.68***	–	–	8.07***
[d]	3.10***	2.93***	–	–	1.62***
[h]	–	1.76*	–	–	–
Parental means					
Female	5.18	3.45	5.73	3.00	5.93
Male	10.73	10.25	4.95	5.45	8.48

*, *** see Table 1; # see Table 2

Discussion

The high heritabilities for the height characters are consistent with the results of other studies. Riggs and Hayter (1975) found additive and dominance effects controlling final height in a 13×13 half diallel of 6-row and 2-row barleys and also in the 9×9 2-row subset. Dominance was complete and, in the 2-row subset, strongly directional. Similarly, Singh et al. (1979) found significant additive and dominance effects controlling final height in four barley pair crosses analysed by the F_2 TTC, with dominance being complete in one of the four crosses and strongly directional in all four. The former study found no evidence of epistatic effects for height but the latter found some evidence, although only at a low frequency. We conclude that height in the crosses studied was consistent with four of the five crosses segregating for recessive dwarfing genes and was of high heritability.

The results for H1 were, however, inconsistent with those for H2 and H3. H1 was chosen to estimate the effect of the dwarfing genes upon juvenile plant height. It is noticeable that in crosses involving the erectoides dwarfing gene, i.e. GP×M, GP×AR and BH4×AR, there were no significant differences between the parents. Presumably the more erect stature of the plants containing the erectoides gene has compensated for any height reduction at this stage. However, in U×M, where segregation was for the Abed Denso dwarfing gene with semi-prostrate juvenile growth habit, the parents differed significantly. If all the height characters are considered together, these effects are apparent in the additive genetic correlations between them (Table 7).

U×M and C×Y were the only crosses to show any additive genetic correlation between H1 and H2 or H3. Interestingly, H1 is strongly negatively correlated with H2 and H3 for C×Y, the result of 'Clipper' being the higher scoring parent for H1 but the lower scoring parent for H2 and H3. However, H2 and H3 were strongly positively correlated and it should be possible for a breeder to select adequately for height at ear emergence. It should be borne in mind that h^2_n was slightly greater for H3 than for H2 in four of the five crosses studied, suggesting that selection may be slightly more effective for final height.

Persson and Hagberg (1969) report that the majority of the erectoides mutations that they studied were controlled by a single recessive gene. Similarly, Haahr and von Wettstein (1976) have shown that the Abed Denso gene is a single recessive mutation. Other workers have reported single major gene segregation for height in barley (Ali et al. 1978; Singh et al. 1981). From the results of our study, it can be surmised that whilst there is segregation of a single major gene for height, there is also considerable polygenic variation for height which can be exploited if required. Significant positive correlations between plant height and yield are frequently found in cultivated cereals such as wheat (Knott and Kumar 1975), barley (Riggs and Hayter 1975) and oats (Sampson 1971) and Law et al. (1978) proposed that when selection for high yielding short-strawed types is practised, 'tall dwarfs' should be selected.

Table 7. Additive genetic correlations between the height characters

Character		H1	H2
	Cross		
	GP × M	0.2248	
	U × M	0.6827**	
H2	GP × AR	0.2516	
	BH4 × AR	0.2408	
	C × Y	−0.9702***	
	GP × M	0.1255	0.9854***
	U × M	0.8352***	0.9653***
H3	GP × AR	0.1817	1.0049***
	BH4 × AR	0.3310	0.9455***
	C × Y	−1.0070***	1.0046***

, * see Table 1

Results from the heading characters were very variable. Generally, these characters were controlled by additive and dominance effects with some epistatic interactions also being found. However, the nature of the dominance effects were variable. In GP×M, where the parents did not differ significantly, dominance was complete. With one exception, dominance was otherwise found to be incomplete. Apart from the exotic cross C×Y, there was little evidence of directional dominance. When directional dominance was detected, it was in the direction of lateness for AE and earliness for EE. Riggs and Hayter (1972) found evidence of partial dominance in a diallel analysis of 6-row and 2-row barleys. On examining the 6-row and 2-row sub-groups, they found evidence of directional dominance for earliness in the 6-row genotypes but ambidirectional dominance in the 2-row genotypes. However, in diallel analysis of five winter barleys, Mersinkov and Breshkov (1979) found that heading was inherited with partial dominance in the direction of lateness. Paroda and Hayes (1971) analysed 10 spring barleys of varying origin and their F_1 habrids by diallel analysis in eight different environments. Over all environments, a large part of the variance was found to be additive but partial dominance in the direction of earliness was also found. They also reported changes in the expression and direction of dominance in different environments. It therefore appears that the nature of dominance effects for heading characters varies according to both the origin of a genotype and the environment in which it is grown.

For the heading characters, early generation selection should generally be worthwhile, although variable

dominance effects may cause some problems. Unless some information about the genetic control of the characters is available, breeders may select more reliably by discarding the worst lines, as suggested by Hanson et al. (1979). The narrow-sense heritability of AE was greater than EE in four of the five crosses studied, the exception being U×M where the parents did not differ significantly. AE would be the better character for early generation selection, despite possible complications arising from segregation for awn length.

The large part of the genetic variation for NL was found to be additive with some evidence of partial dominance. Significant epistatic effects were found more regularly than for the height or for the heading characters. However, the character was found to have low heritability in four of the five crosses studied. We can conclude that selection for this character would be possible but not recommended in the early generations of a breeding programme.

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