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Cross prediction studies on spring barley

3. Correlations between characters

W. T. B. Thomas [1] and C. R. Tapsell [2,*]

[1] Scottish Crop Research Institute (Pentlandfield), Roslin, Midlothian EH25 9RF, UK
[2] Department of Genetics, University of Birmingham, Birmingham B15 2TT, UK

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Summary. Additive genetic, dominance genetic and environmental correlations between pairs of agronomically important characters in five spring barley crosses were calculated from estimates of the components of variance and covariance, obtained by Triple Test Cross analysis. Phenotypic correlations were calculated from the Triple Test Cross family means and compared to the additive genetic correlations. Phenotypic correlations were generally lower than the additive genetic correlations and, occasionally, of different sign. The highest phenotypic correlations between single plant yield and its components were found with number of tillers whereas these were the lowest additive genetic correlations, thousand grain weight giving the highest. High dominance genetic correlations were found between single plant yield and both grain number and thousand grain weight thus indirect early generation selection for single plant yield using these two characters would be ineffective. Additive and dominance genetic correlations confirm association of the *erectoides* dwarfing gene with low thousand grain weight and plant yield.

Key words: Barley – Correlations – Agronomic characters – Selection

Introduction

In two previous papers, the genetical architecture of a number of characters of importance in five crosses in spring barley was presented (Thomas and Tapsell 1983; Tapsell and Thomas 1983). Knowledge of the genetic architecture of a character can be used to predict the value of a cross with respect to that character (Jinks and Pooni 1976). However, plant breeders generally select lines from a cross on the basis of more than one character. A knowledge, therefore, of the inter-relationship between important characters is necessary for effective selection.

For a plant breeder producing inbred lines, the additive genetic correlation is the relevant measure of the likely inter-relationship between pairs of characters in his final inbreds. Many reports of the phenotypic and genotypic correlations between characters have been published (e.g. Rasmusson and Cannell 1970; Riggs and Hayter 1975; Fejer and Fedak 1978). However, phenotypic correlations may not be a true reflection of genotypic correlations as they may also include different environmental correlations. Furthermore, the genotypic correlations may be distorted by different non-additive correlations and not, therefore, be a true reflection of the additive genetic correlation. This paper presents the phenotypic, additive genetic, dominance genetic and environmental correlations between a number of important characters in five crosses between seven spring barley varieties and examines the relationships between these correlations. The additive genetic correlation is a true measure of the effect of selection for one character upon another in inbred lines and the phenotypic correlation will only be an adequate substitute where it is in close agreement.

In the early segregating generations from a cross between two lines differing at a number of loci, selection will mainly be acting on heterozygotes. Therefore, where large dominance genetic and environmental correlations are found between pairs of characters, early generation selection of one character to indirectly select for another is unlikely to be effective.

Materials and methods

Since a detailed account of the experiment and abbreviations was given in Thomas and Tapsell (1983), they will not be

* Present address: Rosewarne EHS, Camborne, Cornwall TR14 0AB, England

presented in full here. The crosses studied were 'Golden Promise' × 'Mazurka' (GP × M), 'Universe' × 'Mazurka' (U × M), 'Golden Promise' × 'Ark Royal' (GP × AR), BH4/143/2 × 'Ark Royal' (BH4 × AR) and 'Clipper' × 'Ymer' (C × Y). Correlations were calculated for a subset of the characters measured – Final Height (H3), Neck Length (NL), Awn Emergence (AE), Number of Tillers (NT), Grain Number measured in the laboratory (GNL), Thousand Grain Weight (TGW) and Single Plant Yield (SPY). Phenotypic correlations were calculated using the Triple Test Cross (TTC) L1, L2 and L3 family means from each of the crosses studied. The degrees of freedom were large for all the correlation coefficients, the smallest being 214 for those calculated for characters from the cross C × Y, and the significances of the correlation coefficients were therefore tested using the formula

$$t = \frac{r}{\sqrt{1-r^2}} \cdot \sqrt{n-2}$$

(Snedecor and Cochran 1969).

Genetical and environmental correlations were calculated using the Triple Test Cross analysis of variances and covariances (Pooni and Jinks 1978). From this design, estimates of genetical (D_J and H_J) and environmental (E_J) components common to a pair of characters can be obtained using the same orthogonal comparisons as for the TTC (Jinks and Perkins 1970) but with the appropriate covariances replacing variances. As the covariances can be negative, normal variance ratio tests cannot be used to determine the significance of the covariance components. The genetical and environmental components of variance and covariance can be used to derive the additive and dominance genetical and the environmental correlation coefficients. For example the additive coefficient r_D between characters H3 and AE is derived as:

$$r_{D(H3,AE)} = \frac{D_{J(H3,AE)}}{\sqrt{D_{(H3)} \cdot D_{(AE)}}}.$$

Where a variance component was non-significant for either of a pair of characters, the correlation was not calculated. No significances were attached to the genetical correlations as there is no adequate test of significance for them (Jinks pers comm). Similarly, there is no adequate test for the environmental correlations as they were derived from the environmental components of variance and covariance estimated from the error term of the differences comparison of the TTC analysis (Tapsell 1984).

Results

Table 1 shows the phenotypic correlations between the characters. Most of them are highly significant, al-

Table 1. Phenotypic correlations between pairs of characters

		H3	NL	AE	NT	GNL	TGW
	GP × M	0.686*** [a]					
	U × M	0.787***					
NL	GP × AR	0.314***					
	BH4 × AR	0.401***					
	C × Y	0.348					
	GP × M	0.107 NS	0.086 NS				
	U × M	−0.199**	−0.242***				
AE	GP × AR	0.338***	−0.150*				
	BH4 × AR	0.420***	−0.021 NS				
	C × Y	0.868***	0.214**				
	GP × M	0.207**	0.084 NS	0.025 NS			
	U × M	−0.178**	−0.169**	0.017 NS			
NT	GP × AR	0.310***	0.056 NS	0.190**			
	BH4 × AR	0.215***	0.101 NS	0.079 NS			
	C × Y	0.116 NS	−0.125 NS	0.140*			
	GP × M	0.524***	0.435***	−0.196**	0.221***		
	U × M	0.260***	0.145*	−0.081 NS	0.113 NS		
GNL	GP × AR	0.342***	0.249***	0.249***	0.249***		
	BH4 × AR	0.322***	0.106 NS	0.144*	0.240***		
	C × Y	0.832***	0.180**	0.802***	0.232***		
	GP × M	0.700***	0.535***	0.131*	0.229***	0.478***	
	U × M	0.488***	0.512***	−0.069 NS	0.016 NS	0.313***	
TGW	GP × AR	0.631***	0.123 NS	0.267***	0.273***	0.366***	
	BH4 × AR	0.618***	0.241***	0.152*	0.298***	0.356***	
	C × Y	−0.113 NS	−0.075 NS	−0.036 NS	0.054 NS	−0.089 NS	
	GP × M	0.582***	0.352***	0.064 NS	0.764***	0.476***	0.670***
	U × M	0.105 NS	0.075 NS	−0.019 NS	0.806***	0.269***	0.435***
SPY	GP × AR	0.522***	0.092 NS	0.275***	0.832***	0.431***	0.595***
	BH4 × AR	0.503***	0.185**	0.197**	0.793***	0.426***	0.695***
	C × Y	0.516***	0.032 NS	0.543***	0.744***	0.619***	0.266***

[a] NS = Non-significant, + = $P < 0.1 > 0.05$; * = $P < 0.05 > 0.01$; ** = $P < 0.01 > 0.001$; *** = $P < 0.001$

Table 2. Additive genetic correlations between pairs of characters

		H3	NL	AE	NT	GNL	TGW
	GP×M	0.838					
	U×M	0.939					
NL	GP×AR	0.854					
	BH4×AR	0.842					
	C×Y	0.083					
	GP×M	0.563	0.774				
	U×M	−0.546	−0.615				
AE	GP×AR	0.342	−0.143				
	BH4×AR	−0.052	−0.465				
	C×Y	1.011	0.130				
	GP×M	0.180	−0.150	−0.468			
	U×M	–	–	–			
NT	GP×AR	0.329	0.175	−0.123			
	BH4×AR	–	–	–			
	C×Y	0.686	−0.259	0.746			
	GP×M	0.702	0.697	−0.003	0.402		
	U×M	–	–	–	–		
GNL	GP×AR	0.205	0.182	0.924	−0.728		
	BH4×AR	0.755	0.666	0.449	–		
	C×Y	1.011	0.010	0.997	0.728		
	GP×M	0.995	0.848	0.533	0.312	0.661	
	U×M	0.892	0.856	−0.636	–	–	
TGW	GP×AR	0.965	0.512	0.541	0.119	0.082	
	BH4×AR	0.919	0.744	−0.178	–	0.503	
	C×Y	0.828	−0.438	0.809	1.062	0.739	
	GP×M	0.745	0.440	0.165	0.639	0.664	0.848
	U×M	0.022	−0.227	−0.136	–	–	0.318
SPY	GP×AR	–	–	–	–	–	–
	BH4×AR	1.010	0.657	0.132	–	0.787	0.928
	C×Y	0.948	−0.122	0.959	0.909	0.940	0.944

though of the 105 individual correlations only nine are greater than 0.7. H3 generally showed highly significant positive correlations with the other characters. Values ranged from +0.868 for AE in C×Y to −0.199 for AE in U×M. With the exception of AE and GNL in C×Y, the correlations between both AE and NL and the other characters are fairly low. The components of yield (NT, GNL and TGW) generally showed highly significant correlations amongst themselves, only four of the fifteen being non-significant, but none of these were large. All were positive, apart from a small non-significant correlation between GNL and TGW in C×Y. For the correlations between SPY and its components, the highest values were found between NT and SPY in all five crosses. TGW showed quite high correlations with SPY in four crosses, whereas GNL did not correlate so highly.

The estimates of the additive genetic correlations generally were positive (Table 2). High correlations were most frequently found between H3 and the other characters. High positive correlations were found between H3 and TGW for all five crosses and between both H3 and SPY and H3 and GNL in three of the crosses. H3 also showed high positive correlations with NL in four of the five crosses. Apart from high positive correlations with TGW and H3, the correlations between NL and the other characters were generally low. Similarly, with the exception of H3, the correlations between AE and the other characters were mainly low. However, the correlations between AE and the other characters for C×Y were higher and positive except for that with NT. The components of yield all showed high positive correlations with SPY, apart from that between TGW and SPY in U×M, the highest values being found between TGW and SPY. However, there were few high positive correlations between the yield component characters themselves.

Most of the dominance correlations were positive and the few negative correlations were mainly low (Table 3). There were a number of higher correlations between H3 and the other characters, the most notable being those with TGW for GP×M, GP×AR and BH4×AR. H3 also showed high correlations with SPY for GP×M and GP×AR, with GNL for GP×AR, with

Table 3. Dominance genetic correlations between pairs of characters

		H3	NL	AE	NT	GNL	TGW
	GP×M	–					
	U×M	0.969					
NL	GP×AR	0.711					
	BH4×AR	0.379					
	C×Y	–					
	GP×M	0.301	–				
	U×M	–	–				
AE	GP×AR	0.368	−0.690				
	BH4×AR	0.526	0.332				
	C×Y	0.970	–				
	GP×M	–	–	–			
	U×M	–	–	–			
NT	GP×AR	–	–	–			
	BH4×AR	0.477	0.584	−0.803			
	C×Y	–	–	–			
	GP×M	0.586	–	−0.347	–		
	U×M	–	–	–	–		
GNL	GP×AR	1.018	0.890	0.256	0.814		
	BH4×AR	0.363	−0.001	−0.809	0.595		
	C×Y	–	–	–	–		
	GP×M	0.928	–	0.487	–	0.810	
	U×M	0.391	0.603	–	–	–	
TGW	GP×AR	1.057	0.798	0.112	–	0.772	
	BH4×AR	1.119	0.949	0.396	0.564	0.312	
	C×Y	–	–	–	–	–	
	GP×M	1.090	–	0.412	–	0.605	1.113
	U×M	–	–	–	–	–	–
SPY	GP×AR	0.977	0.827	−0.297	–	0.927	0.774
	BH4×AR	1.016	0.745	−0.406	0.824	0.650	0.988
	C×Y	–	–	–	–	–	–

AE for C×Y and with NL for U×M. All the seven correlations between SPY and the components of yield were high. There were some high correlations between the yield component characters themselves – between TGW and GNL for GP×M and GP×AR and NT and GNL for GP×AR. It is worth noting that all but two of the high dominance correlations were in crosses segregating for the *erectoides* dwarfing gene, although this might be a reflection of some discontinuity in the distribution of one of the characters. Furthermore, where there were both high additive and dominance correlations between pairs of characters in a cross the signs of the correlations were the same.

Very few of the environmental correlations were greater than 0.5 (Table 4). Except for H3 and NL in U×M, all of these high correlations were positive. There were high correlations in all five crosses for NT and SPY. The only other high correlations were between H3 and NT and H3 and SPY, both in U×M. Virtually all of the environmental correlations were less than their respective additive genetic correlations.

Discussion

From a plant breeding viewpoint, the most interesting correlations in the results are those involving SPY. In an earlier paper, Tapsell and Thomas (1983) found that SPY was not a suitable character for early generation selection for higher yielding inbred lines from a cross. As an alternative approach, highly heritable characters showing high correlations with SPY might be used to indirectly select for yield in early generations (Valentine 1979). However, in Tapsell (1984), evidence is presented that SPY can be used to predict the higher yielding crosses, allowing the breeder to concentrate on them and discard the lower yielding crosses.

Comparing the phenotypic and additive genetic correlations it can be seen that there is a higher frequency of correlations greater than 0.6 in the latter. A number of instances can be found where there is even a reversal in the sign of a correlation coefficient. The greatest discrepancy is found between H3 and TGW for C×Y, where the phenotypic correlation is

Table 4. Environmental correlations between pairs of characters

		H3	NL	AE	NT	GNL	TGW
	GP×M	–					
	U×M	−0.019					
NL	GP×AR	0.182					
	BH4×AR	0.162					
	C×Y	0.293					
	GP×M	–	−0.100				
	U×M	0.265	0.105				
AE	GP×AR	−0.359	0.020				
	BH4×AR	0.071	0.176				
	C×Y	–	–				
	GP×M	–	0.103	−0.001			
	U×M	0.572	0.212	−0.030			
NT	GP×AR	0.211	0.157	0.049			
	BH4×AR	0.178	0.018	−0.022			
	C×Y	0.237	0.039	–			
	GP×M	–	0.043	0.044	0.164		
	U×M	0.084	0.015	0.024	0.099		
GNL	GP×AR	0.026	0.014	−0.099	0.183		
	BH4×AR	0.196	0.015	−0.097	0.241		
	C×Y	−0.867	−0.074	–	0.211		
	GP×M	–	−0.033	−0.206	0.091	0.221	
	U×M	0.327	0.095	0.063	0.124	0.272	
TGW	GP×AR	0.379	0.123	−0.162	0.219	0.066	
	BH4×AR	0.401	−0.009	0.071	0.235	0.277	
	C×Y	−0.213	−0.065	–	0.077	0.206	
	GP×M	–	0.084	−0.088	0.889	0.215	0.191
	U×M	0.770	0.264	−0.042	0.831	0.231	0.315
SPY	GP×AR	0.278	0.173	−0.023	0.864	0.197	0.337
	BH4×AR	0.255	0.027	−0.011	0.874	0.332	0.394
	C×Y	−0.043	−0.001	–	0.833	0.138	0.231

−0.113 and the additive genetic is 0.828. Indeed, the whole group of additive genetic correlations between H3 and TGW are much larger than the phenotypic correlations. Further examination of the correlations shows that the highest phenotypic correlations of the components of yield (NT, GNL and TGW) and yield itself (SPY) were found between NT and SPY whereas they were the lowest additive genetic correlations for each cross, those between TGW and SPY being consistently the highest. The environmental correlations between NT and SPY are all high and these correlations are reflected in the high phenotypic correlations between this pair of characters. This emphasises the view that the use of phenotypic correlations can be very misleading when considering the relationship between a pair of characters. Considering the high additive genetic correlations between TGW and SPY, indirect selection for increased yield by selecting for increased thousand grain weight would appear possible in three of the five crosses studied. However, in two of the three crosses, there also are high dominance genetic correlations, thus rendering such a technique unreliable in the early generations of a breeding programme.

It is interesting to note that the three crosses showing high dominance correlations between TGW and SPY are GP×M, GP×AR and BH4×AR. Both BH4 and GP possess the same dwarfing gene which is associated with low thousand grain weight and also low single plant yield. Hence the dominance genetic correlations between SPY and TGW and between TGW and H3 could be due to the presence of the *erectoides* dwarfing gene in three of the crosses. High additive genetic correlations were also found between H3 and TGW for these three crosses and between TGW and SPY for GP×M and BH4×AR. All three crosses gave similar high dominance correlations between H3 and SPY. The results confirm an association of the *erectoides* dwarfing gene with low thousand grain weight and plant yield. This association could be due to close linkage or to pleiotropy. If close linkage is the cause, fixing of the dwarfing gene in an early generation would not be desirable. It would be better to delay

selection for height until a later generation to provide further opportunities for recombination between the genes concerned as suggested by Thomas et al. (1984).

The additive genetic correlations observed between AE and other characters in C×Y could be due to association with a daylength insensitivity factor, present in C. Apart from C×Y, there were no high phenotypic or additive genetic correlations between AE and SPY. It should therefore be possible to combine high yield with early awn emergence in four of the five crosses studied. Apart from C×Y, the additive genetic correlations observed between NL and characters other than H3 were of a similar pattern to but less than those between H3 and the characters.

The fact that dominance correlations were in the same direction as their respective additive correlations means that production of F1 hybrids will not lead to more desirable character associations than the utilisation of suitably selected inbred lines. Together with the lack of evidence of significant heterosis for the characters studied in these crosses (Tapsell 1984), production of F1 hybrids from the crosses does not appear worthwhile.

With high additive genetic and low environmental correlations, only two of the four possible phenotypic classes exceeding the parental range for both of a pair of characters (Pooni and Jinks 1978) will be found in recombinant inbred lines. Thus with high additive genetic correlations, either due to tight linkage or pleiotropy, improvement in some directions for both of a pair of characters may not be possible in some crosses. For example, the results suggest that there is little chance of producing recombinant inbred lines with short straw and high thousand grain weight.

The conclusions from this study are relevant to the effects of any character associations on early generation selection in the crosses studied, although there are some reports of a reduction or even a change in sign of correlations between characters measured in spaced plant and more dense populations (e.g. Adams 1967; Fejer and Fedak 1978). For whilst this experiment was space planted, the plant density was greater than that of F2 populations and similar to that of F3 populations in a number of breeding programmes. It is also worth noting that there is variation in the magnitude and, in some cases, the sign of correlations between a pair of characters in the five crosses studied, making it clear that no general rules can be applied. This effect could also have been present in other studies where the overall correlation may mask variation for that correlation amongst different crosses (e.g. Riggs and Hayter 1975). Variation amongst crosses for a particular correlation is also of relevance to the plant breeder, for, in the absence of any knowledge of any character associations, the breeder may be selecting against an agronomically important character by the early generation selection of another character.

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