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Competitive effects in monocultures and mixtures of spring barley (*Hordeum vulgare*)

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Summary. The presence of significant levels of intergenotypic competition amongst barley (*Hordeum vulgare*) genotypes has profound consequences for barley breeding programmes. Breeding programmes based on the pedigree system attempt to identify genotypes in genetically heterogeneous populations but the elite genotypes are grown in monoculture. Thus, to attain varietal status genotypes produced by this breeding strategy must perform well in mixtures as well as in pure stands. The effectiveness of early generation selection may be hampered by intergenotypic competition. To examine this problem in spring barley, a modified substitution experiment (Mather and Caligari 1981, 1983) was used and included genotypes sampled from a random set of inbred lines generated without conscious selection. This approach to the investigation of competitive effects in barley indicated the presence of significant levels of intergenotypic competition for a range of agronomic characters. The analyses allowed a distinction to be made between aggression (a) and response (r) with the component r displaying greater variation than a. The lack of correlation in the distribution of a and r suggested that they were under separate genetic control and hence adjustable by selection. The implications of these results for barley improvement, the use of varietal mixtures and mixed cropping are discussed.

Key words: *Hordeum vulgare* – Competition – Plant breeding – Monocultures – Mixtures

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Introduction

In autogamous crop species such as barley (*Hordeum vulgare*), the pedigree method of breeding predominates. During the early stages of pedigree breeding individuals are grown in genetically heterogeneous mixtures and the seed from single F_2 plants is grown in rows until, after several generations of selection and inbreeding, relatively homozygous plots are being assessed. The end products of such breeding schemes are true-breeding cultivars which are, almost universally, grown as pure stands, i.e., monocultures. To survive such schemes, genotypes must perform well both in genetically heterogeneous mixtures and in pure stands. Obvious questions raised by such breeding schemes are whether early generation selection results in the elimination of desirable genotypes because of their inability to grow and compete well in mixtures or equally whether facilitative effects introduce any biases.

The relationship between the performance of genotypes in mixture and monoculture is critical to the concept of the basic pedigree method of breeding. Numerous studies (reviewed by Spitters 1979) have been conducted into the effects of competition on the selection process in barley. Unfortunately, the main experimental material used in these studies consisted of commercial cultivars which were the products of pedigree breeding systems (Baker and Briggs 1984; Valentine 1979, 1982). The cultivars would have had to perform well in mixture and monoculture in order to attain commercial status. Hence, any observed correlations between performance in monoculture and mixture is likely to be biased by the previous artificial selection imposed on the experimental material.

Recent studies of competition in *Drosophila melanogaster* (Caligari 1980; Mather and Caligari 1981) and in *Lolium perenne* (Mather et al. 1982) have indicated the complexity of the interactions involved. Furthermore, the importance of intragenotypic competition has been established. Thus any quantitative analysis of competitive interactions must consider both intra and intergenotypic effects. Methods and analyses

have been developed by Mather and Caligari (1981, 1983) and allow the separation of intra and intergenotypic effects.

To achieve a more accurate assessment of the relative strengths of intergenotypic competition in mixtures of spring barley, an experiment was conducted with genotypes produced without conscious selection. In this paper the results from a modified substitution experiment involving six spring barley genotypes produced by single seed descent are reported.

Materials and methods

The genotypes were derived from two spring barley crosses by the technique of single seed descent (Brim 1966). Three lines were sampled from the cross BH4/143/2×'Ark Royal' (BDR 200) and three lines from 'Heriot'×'Rif' (TSR 131). The six genotypes sampled also represent three possible juvenile growth habits. Thus the six genotypes were:

Genotype	Code	Parentage	Juvenile growth habit
A	BDR 200/8	BH4/143/2×'Ark Royal'	tall
B	BDR 200/145	BH4/143/2×'Ark Royal'	erect
C	BDR 200/172	BH4/143/2×'Ark Royal'	erect
D	TSR 131/22	'Heriot'×'Rif'	tall
E	TSR 131/29	'Heriot'×'Rif'	prostrate
F	TSR 131/5	'Heriot'×'Rif'	prostrate

The experimental technique of Mather and Caligari (1981) involves growing each genotype in a series of monocultures and in duoculture mixtures with various frequencies of each component, but maintaining a total number N of plants (the reference density). In the present experiment it was only possible to grow two combinations of duocultures for each primary genotype and the structure of the experiment may be illustrated by reference to genotype A:

	Numbers of plants per plot					
Monoculture	A	10	15	30	45	60
Duoculture	A:B		15:45	30:30	45:15	
Duoculture	A:D		15:45	30:30	45:15	

The combinations actually grown were:

		Associate genotype					
		A	B	C	D	E	F
Primary/	A	M	D	–	D	–	–
Indicator	B	D	M	D	–	–	–
genotype	C	–	D	M	–	–	D
	D	D	–	–	M	D	–
	E	–	–	–	D	M	D
	F	–	–	D	–	D	M

[M = monoculture and D = duoculture]

The experimental design was a randomised complete block of two replicates. Each replicate consisted of 48 plots (it should be noted that each duoculture gives two D's in the above table i.e., AB and BA obviously come from the same duoculture). A maximum of 60 seeds per plot were sown by hand at a density of 388 plants per square metre. The experiment was netted to prevent bird damage and the perimeter of the experiment was sown with the cultivar 'Tweed' to reduce edge effects. The experiment was sprayed with a broad spectrum fungicide to prevent development of disease.

Data were collected for 11 traits. Four characters were scored on an individual plant basis seven weeks after planting: tiller number (TN1), plant width measured as the maximum width of plant rosette in cm (PW), height measured from the base of the plant to the tallest point in cm (Ht1) and percentage survival (Sv). During the growing season, awn emergence was also scored as days from the 1st June until awns emerged from the flag leaf sheath (AE). After harvest the following characters were scored: The weight of grain on the main stem in g (MSW), final plant height in cm (Ht2), number of grains on the main stem (GN), thousand grain weight (TGW), the number of fertile tillers per plant (TN2) and the total yield of grain per plant in g (SPY).

The growth habit of each of the plants was also recorded and this allowed the separation of the two components in a duoculture in most cases. However, juvenile growth habit did not differ for the following combinations. A with D, B with C, and E with F. Hence, for these combinations the position of each component in a plot was physically mapped at the time of sowing and individual plants tagged prior to harvest. For all plots the position of seed within a plot was allocated at random.

Results and analyses

The results from all plants of the same genotype within a plot were averaged to give the basic items of data and analysed using the methods proposed by Mather and Caligari (1981). In the present case the reference density [N] was 60 plants and estimates were obtained for the effect of changing numbers in the monocultures (b_m) and of substituting genotypes in the duocultures (b_d) on the assumption of linear relationships. As an example, the estimates for the character awn emergence are given in Table 1. Also presented in Table 1 are estimates of e, the expression of the character at the reference density, [N] of 60 plants. This parameter is the one referred to by Mather and Caligari (1983) who renamed the parameter of a Mather and Caligari (1981).

Obviously, the assumption of linear responses needs testing and this can be achieved, as described by Mather and Caligari, by the comparison of the residual variation after fitting the model with the appropriate replicate error variance obtained from the experiment. With 11 characters and 6 genotypes, each of which can be taken as the primary genotype, there were 66 such tests of which 58 proved to be non-significant. In other words, in 58 of the cases the amount of residual variation was no greater than would be expected from

Table 1. Estimates of the parameters e, b_m and b_d with their standard errors for the character awn emergence

	Primary/indicator					
Genotype	A	B	C	D	E	F
Parameter						
e	27.474±1.262	15.257±0.982	22.463±0.710	17.838±0.755	14.288±0.623	17.457±0.544
b_m	−0.024±0.041	−0.040±0.032	−0.037±0.023	−0.064±0.024	0.006±0.020	−0.011±0.017
b_{d1}	0.210±0.050	−0.121±0.039	0.089±0.028	−0.122±0.030	−0.042±0.247	−0.031±0.022
b_{d2}	0.180±0.050	−0.078±0.039	0.107±0.028	0.050±0.030	−0.033±0.025	0.010±0.022
Associate	1 B	A	B	A	D	C
genotype	2 D	C	F	E	F	E

Table 2. Estimates of the intra and intergenotypic competition effects

	MSW	Ht2	TN1	GN	TGW	SPY	TN2	AE	PW
c_{AA}	0.0119***	0.1197	0.1230***	0.1872***	0.0917*	0.2036***	0.1447***	0.0244	0.0303***
c_{AB}	0.0121***	0.2950**	0.1018**	0.1260	0.1427**	0.1851***	0.1114***	0.2341***	0.0383***
c_{AD}	0.0088*	0.2363**	0.1178***	0.1834*	0.0841	0.1827***	0.1267***	0.2040***	0.0307**
c_{BB}	0.0063***	0.0799	0.1201***	0.0814**	0.1399**	0.1805***	0.2103***	0.0403	0.0264*
c_{BA}	0.0049**	0.0289	0.1528***	0.0664*	0.1188**	0.1808***	0.2269***	0.0812*	0.0341**
c_{BC}	0.0037*	0.0932	0.1235***	0.0454	0.1067*	0.1430**	0.1866***	0.0380	0.0239*
c_{CC}	0.0105***	0.1082*	0.1524***	0.1346***	0.1544**	0.2292***	0.2066**	0.0375	0.0384***
c_{CB}	0.0089**	0.1658**	0.1520***	0.1284***	0.1115*	0.2195***	0.1979**	0.1269***	0.0407***
c_{CF}	0.0098**	0.1343*	0.1872***	0.2135***	0.1626***	0.2686***	0.2459**	0.1445***	0.0501***
c_{DD}	0.0081***	0.0586	0.1047***	0.0906***	0.1570***	0.1942***	0.1386***	0.0643*	0.0683***
c_{DA}	0.0032***	0.1282	0.0406*	0.0278*	0.0768**	0.0755**	0.0430*	0.0582	0.0441*
c_{DE}	0.0118***	0.0626	0.1175***	0.1442***	0.2064***	0.2073***	0.1075***	0.1145***	0.0623**
c_{EE}	0.0057**	0.0831	0.1302***	0.0646*	0.1391**	0.1641***	0.1546***	0.0062	0.1116***
c_{ED}	0.0030	0.0900	0.1045***	0.0108	0.1290**	0.1453***	0.1244***	0.0485*	0.0864**
c_{EF}	0.0038*	0.0029	0.1323***	0.0441*	0.0646	0.1481***	0.1462***	0.0397	0.1252***
c_{FF}	0.0077**	0.0474	0.0968***	0.0938**	0.1206*	0.1803**	0.1332***	0.0107	0.0654***
c_{FC}	0.0057*	0.0663	0.0566**	0.0612	0.1087*	0.1137**	0.0816**	0.0207	0.0448**
c_{FE}	0.0067**	0.1542**	0.0686**	0.0746*	0.1204*	0.1253**	0.0865***	0.0209	0.0389**

*$P<0.05$; ** P 0.01–0.001; *** $P<0.001$

the error variance of the experiment. Out of the remaining 8, 4 were significant at the 5% probability level, 3 at the 1% level and 1 at the 0.1% level. These significant probabilities appeared to be spread over the range of characters and genotypes considered except that 2 were present for SPY and 2 for survival. Overall, however, there was little evidence of specific non-linearity for the characters studied and the linear model was therefore considered to be adequate.

Since non-linearity has been shown not to be important in the present cases, the estimates of b_m and b_d can be used to estimate competitive values as described by Mather et al. (1982). In other words, $-b_m$ provides a measure of the competitive properties of like genotypes (intragenotypic competition) while $b_d - b_m$ gives an estimate of competition from a different genotype (intergenotypic competition). Thus, taking genotype A as the indicator provide the following estimates of c_{AA}, c_{AB}, c_{AD}:

$c_{AA} = -b_{mA}$ (the competitive properties of A with itself.);

$c_{AB} = b_{dAB} - b_{mA}$ (the competitive properties of A with B) and

$c_{AD} = b_{dAD} - b_{mA}$ (the competitive properties of A with D).

For each of the six primary genotypes and for each of the eleven characters, an estimate of the intragenotypic competition effect was obtained along with two estimates of intergenotypic effects. Two of the characters, Sv and Ht1, showed no significant intra- or intergenotypic effects for any of the genotypes and will not, therefore, be considered further. The estimates of c are given in Table 2 for the remaining nine characters.

To examine the relationship between intra and the average intergenotypic effects, correlations were calculated between these components, thus giving nine correlations, each based on six pairs of observations, as shown in Table 3. The correlations are presented in order of the size of the correlation coefficient and range from zero, for awn emergence to 0.97 for MSW and TN2. Of the characters examined, some are in common

Table 3. Estimates of the correlation coefficients and amount of variation accounted for when the relationship between intra- and intergenotypic effects are compared. The characters are given in order of the size correlation. Also shown are the categories into which Valentine (1982) placed the characters (see text)

Character	Correlation coefficient	% Variation accounted for	Category
TN2	0.974	94.9	B
MSW	0.968	93.7	A
TN1	0.935	87.5	B
PW	0.866	75.1	?
GN	0.855	73.1	A
SPY	0.844	71.3	C
Ht2	0.721	51.9	A
TGW	0.504	25.5	A
AE	0.082	0.7	?

with those of Valentine (1982). From his study he proposed separating the characters into three categories A, B and C which showed high, medium and low correspondence between monoculture and duoculture performance. Evidence from his experiment put the characters Ht2, GN, TGW and MSW into category A, i.e., highly positively related. The experiment reported here, however, using random inbred lines, shows a range of relationships for these characters and in particular TGW displays a relatively low correlation.

The competitive effects observed may be examined in a different way (Mather and Caligari 1983), in terms of mean competition, aggression, response and interaction. In the present experiment the genotypes were not grown in all possible combinations and hence methods of estimation were performed by taking genotypes in appropriate pairs; i.e., A with B, A with D, B with C, C with F, D with E and E with F. Using the combinations involving A as an example, the c values for TN2 are:

		Associate	
		A	B
Primary	A	c_{AA} (0.1447)	c_{AB} (0.1114)
	B	c_{BA} (0.2269)	c_{BB} (0.2103)

which can be written in terms of $\bar{c}$, the mean competitive value, a the difference in aggression between the two genotypes, r the difference in response and i the interaction between a and r as follows:

		Associate	
		A	B
Primary	A	$\bar{c}+a+r+i$ (1)	$\bar{c}-a+r-i$ (2)
	B	$\bar{c}+a-r-i$ (3)	$\bar{c}-a-r+i$ (4)

If it is assumed that there is an additive relation between a and r then the parameters can be estimated using the appropriate orthogonal functions, i.e.,

$\bar{c} = \frac{1}{4}[(1)+(2)+(3)+(4)] = 0.1733^{***}$
$a = \frac{1}{4}[(1)-(2)+(3)-(4)] = 0.0125$
$r = \frac{1}{4}[(1)+(2)-(3)-(4)] = -0.0453^{***}$
$i = \frac{1}{4}[(1)-(2)-(3)+(4)] = 0.0042$

If the assumption of an additive relationship holds then the estimate of i will not differ significantly from zero. Such orthogonal functions were applied to the six pairs of genotypes for each of the nine characters, giving 54 estimates of $\bar{c}$, a, r and i and these are given in Table 4. The significance of these estimates was tested against the appropriate standard error estimated in the manner described by Mather and Caligari (1983). Tests of significance showed that of the 54 $\bar{c}$ values 53 were significantly different from zero, whereas only 26 r, 12 a and 7 i values were. The 7 significant i values appear to be spread fairly randomly over the characters and genotypes except for two for MSW involving genotypes D with E and E with F and one for GN involving E with F. In these three cases, the estimates of a and r are both significant as well as i and, therefore, suggest a failure in the assumption of additivity in the action of a and r. However, taken overall there is little indication of the relationship between a and r being other than additive.

The first noticeable feature of the present results when compared to those of Mather and Caligari (1983) is the greater variation in r with respect to a. In the reports of the *Drosophila* and *Lolium* experiments more variation was detected in a than in r. This manifests itself in the number of combinations of genotype and characters in which the difference in r is significant compared with a. Also, the variances of the estimates of a and r over the six genotype pairs are given (Table 5). It was arbitrary which of the two genotypes of a pair was designated plus or minus for a and r, so the variances have been estimated between the absolute values of the parameters. The ratios of Vr/Va were calculated and are also given in Table 5. All the ratios are either very close to unity or greater than one, giving clear evidence for the greater variation in response differences (r) in comparison to aggression (a). The biological contrast between *Drosophila* and *Lolium* compared to *Hordeum* involves many variables, but the one obvious difference is in the breeding system. *Hordeum vulgare* inbreeds to a much greater extent than the other two species and this may have affected its response to natural selection for competitive characters. This must, however, be treated as purely speculative until further evidence from a wider range of species is available.

Table 4. Estimates of the mean competitive value ($\bar{c}$), the difference in aggression (a) between genotypes, the difference in response (r) and the interactions (i) between a and r for each of the six combinations

		MSW	Ht2	TN1	GN	TGW	SPY	TN2	AE	PW
A/B	$\bar{c}$ =	0.00748***	0.13088***	0.12443***	0.11525***	0.12328***	0.18750***	0.17333***	0.05440***	0.03228**
	a =	0.00092	−0.05658*	0.01348	0.01155	−0.01805	0.00470	0.01248	−0.0828***	−0.00008
	r =	0.00452**	0.07648**	−0.01203	0.04135	−0.00608	0.00685	−0.04528***	0.07485***	0.00203
	i =	−0.00102	−0.03108	−0.00288	0.01905	−0.00748	0.00455	0.00418	−0.02205	−0.00393
A/D	$\bar{c}$ =	0.00800***	0.10683***	0.09653***	0.11975***	0.10238***	0.16400***	0.11323***	0.05862***	0.04335***
	a =	−0.00045	−0.04058	−0.01473	−0.01475	−0.01813	−0.02445	−0.01943	−0.07553***	−0.00615
	r =	0.00235	0.07113	0.02388	0.06305	−0.01453	0.02915*	0.02248	0.05558***	−0.05140***
	i =	0.00200	−0.01768	0.01733	0.01665	0.02198	0.03490*	0.02843*	−0.01428	0.00595
B/C	$\bar{c}$ =	0.00603***	0.11175***	0.13700***	0.09748***	0.12810***	0.21108***	0.20035***	0.04165**	0.03233***
	a =	−0.00107	−0.01770	−0.00095	0.00748	−0.00245	0.02498	0.00593	0.04195**	0.00118
	r =	−0.00367***	−0.02525	−0.01520	−0.04983***	−0.00480	−0.04933***	0.00190	−0.04050**	−0.00718
	i =	−0.00027	−0.01770	−0.00075	0.01053	0.01905	−0.00623	0.00810	−0.0028	0.00008
C/F	$\bar{c}$ =	0.04365***	0.08905***	0.12337***	0.12700***	0.13658***	0.19795***	0.16683***	0.04298**	0.04365***
	a =	−0.01410***	−0.00180	−0.01875	−0.02910**	−0.0049	−0.026***	−0.02273	−0.03463*	−0.00353
	r =	0.00060	0.03220	0.04655***	−0.04950***	0.02193	0.05095***	0.05938***	0.04803***	0.00060
	r =	0.00825**	−0.01125	0.00135	−0.01280	0.00925	0.00680	0.00303	−0.01898	0.00825*
D/E	$\bar{c}$ =	0.08215***	0.07358***	0.11423***	0.07755***	0.15788***	0.17773***	0.13123***	0.03103*	0.08215***
	a =	−0.0048***	0.00073	−0.00963	−0.02685***	−0.01488	0.00143	0.00023	−0.02313	−0.00480
	r =	−0.01685***	−0.01298	−0.00313	0.03985***	0.02383	0.02303	−0.00823	0.05528***	−0.01685*
	i =	0.0053	−0.00273	0.00323	0.00005	−0.00983	0.00143	0.01533	−0.00198	−0.00780
E/F	$\bar{c}$ =	0.08527***	0.07188***	0.10697***	0.04723***	0.11118***	0.15445***	0.13013***	0.00360	0.08528***
	a =	−0.01003***	0.04678	−0.00758	0.02245*	0.01858	−0.00975	0.01378	0.01095	−0.01003
	r =	0.03313***	−0.02893	0.02428*	−0.03698***	−0.00933	0.00165	0.02028	0.01935	0.03313**
	i =	0.00323	−0.00663	0.00653	0.03198***	0.01868	0.01775	−0.01378	0.00580	0.00323

* $P<0.05$; ** P 0.01–0.001; *** $P<0.001$

Mather and Caligari (1983) suggested, particularly from their results with *Drosophila,* that there was evidence of two separable genetic systems controlling aggression and response. In the present study it is also possible to examine the relationship between aggression and response over the six pairs of genotypes. The correlations between a and r, for the nine characters, are given in Table 6. For these correlations the signs of a and r were taken into account as in this case the relationships are within a genotype pair and therefore the sign of the estimates relative to each other is relevant. The correlation coefficients ranged from –0.20 to 0.81 (Table 6). Although six genotype pairs were examined, there is a large range in the correlation coefficients and even the biggest coefficient is not very close to unity. Thus the present results must be taken as supporting Mather and Caligari's proposal of genetically separable characters.

A further set of relationships can also be examined, and these are the relations of aggression and response over the nine characters. In other words if the characters are taken in pairs it is possible to estimate the correlation of the a values over the six genotype pairs and similarly for r (Table 7). There is no general relationship between characters for either a or r. Amongst the highest correlations are those between TN1 and TN2 which are expressions of the same character at different stages of development and, therefore, could be expected to be high. Thus the results give little evidence for aggression or response being a reflection of gross phenotypic responses but being specific to each character studied.

The six genotypes examined were derived from two crosses and represent three different genotypes with

Table 5. Variances of the estimates of aggression and response over the 6 crosses for each of the 9 characters

	V_a	V_r	V_r/V_a
MSW	0.000065	0.000284	4.37
Ht2	0.002451	0.002717	1.11
TN1	0.000180	0.000742	4.12
GN	0.001477	0.002394	1.62
TGW	0.000250	0.000281	1.12
SPY	0.000409	0.001292	3.16
TN2	0.000255	0.001313	5.15
AE	0.003235	0.003213	0.99
PW	0.000033	0.000816	24.73

Table 6. Estimates of the correlations between aggression and response over the 6 pairs of lines for each of 9 characters

MSW	Ht2	TN1	GN	TGW	SPY	TN2	AE	PW
0.31	0.74	0.56	–0.20	–0.04	0.78	0.75	0.79	0.81*

* $0.05 > P > 0.01$

Table 7. Estimates of the correlation coefficients between characters for aggression (a) and response (r). The top figure in each box is the correlation coefficient for a, while the lower is for r

		MSW							
MSW									
	a	–0.74							
Ht2	r	–0.12	Ht2						
				TN1					
		0.64	–0.44						
TN1		0.36	0.13						
					GN				
		0.04	–0.12	0.25					
GN		–0.37	0.68	–0.15					
						TGW			
		–0.59	0.87*	–0.16	0.36				
TGW		–0.57	–0.23	0.20	–0.08				
							SPY		
		0.53	–0.13	0.69	–0.05	0.02			
SPY		–0.08	0.49	0.72	0.44	0.46			
								TN2	
		0.31	0.19	0.78	0.11	0.37	0.71		
TN2		0.18	–0.17	0.88*	–0.42	0.26	0.43		
									AE
		–0.28	0.65	–0.10	0.02	0.70	0.52	0.35	
AE		–0.10	0.70	0.25	0.77	0.21	0.81	–0.17	
		0.23	–0.60	0.35	0.11	–0.45	0.42	–0.11	–0.02
PW		0.63	–0.50	0.05	–0.67	0.06	–0.02	–0.02	–0.02

* $0.05 > P > 0.01$

Table 8. The groupings of genotypes based on the differences of a and r in the genotype pairs. (Genotypes with the same number within a character showed no significant differences). The question marks indicate that the results for those genotypes were not consistent over the pairs examined

	Code	A	B	C	D	E	F
(a)	G. habit	T	e	e	T	s.p.	s.p.
	MSW	1	1	1	1	2	3
	Ht2	?	?	2	2	2	2
	TN1	1	1	1	1	1	1
	GN	1	1	1	1	2	3
	TGW	1	1	1	1	1	1
	SPY	1	1	1	1	1	1
	TN2	1	1	?	1	1	?
	AE	1	2	3	4	4	4
	PW	1	1	1	1	1	1
(r)							
	MSW	1	1	2	3	4	2
	Ht2	1	2	2	2	2	2
	TN1	1	1	1	2	2	3
	GN	1	1	2	1	3	4
	TGW	1	1	1	1	1	1
	SPY	1	1	2	3	3	3
	TN2	1	2	2	1	1	1
	AE	1	2	3	4	5	5
	PW	1	1	1	2	3	1

respect to growth habit ("Materials and methods"). The estimates of aggression and response can be examined to determine whether there are particular patterns with respect to either cross or growth habit. Taking the results for aggression in character MSW as an example, it was found that there were no significant differences for A with B, A with D and B with C while there were for C with F, D with E and E with F. It can therefore be deduced that A=B=C=D while E and F differ from those as well as from each other. The results of grouping the genotypes in such a way are shown in Table 8 for a and r separately. Genotypes which did not show significant differences are given the same number, within a character. Only two cases, both for a, gave rise to ambiguity. These were the results for Ht2 and TN2 where only one pair of genotypes gave a significant difference and since each genotype appears twice the results appear inconsistent. No clear overall pattern emerges although for some characters there would appear certain relations (e.g., a for MSW). The talls and erects behave similarly while the semi-prostrates differ. For r the SPY results could be interpreted as differentiating the two crosses. More genotypes would need to be examined before it was possible to draw general conclusions about the role of the different growth habits in aggression and response. Nevertheless, this experiment does illustrate how this might be achieved. The present results also show that even though only two duocultures were grown for each primary genotype only two cases of ambiguity were detected and suggest that the technique produces consistent results.

Discussion and conclusions

The presence of significant levels of intergenotypic competition reduces the effectiveness of early generation selection, since selection is exercised in genetically heterogeneous stands whereas the selected genotypes are invariably grown in monoculture. Previous studies on the role of competition in the selection process in barley have concentrated on the use of finished varieties which in itself introduces a fundamental anomaly. Since the pedigree method of breeding predominates it is reasonable to conclude that the varieties used by Valentine (1982) and Baker and Briggs (1984) are the products of such a breeding strategy and therefore any observed relationships may simply have been a reflection of past selection methods. The experimental and analytical methods presented here allow a separation of the effects of intra and intergenotypic competition. An assessment of the effects of intragenotypic competition is necessary to allow a true measure of the relative magnitude of intergenotypic competition. The present study indicates that significant levels of intergenotypic competition exist for a number of characters of importance to barley breeders. This finding differs from the result of Baker and Briggs (1984) who suggest that intergenotypic competition is of little importance in barley breeding programmes. Clearly this conclusion must be questioned given the fact that "adapted" varieties were used and the role of intragenotypic competition may not have been fully assessed.

The present experiment does, however, illustrate an approach which may be used with finished varieties for a different objective. Wolfe (1978) advocates the use of cereal cultivar mixtures and the identification of favourable combinations of cultivars could be attained by the methods outlined in this paper. Indeed this analytical approach may have applications in the general area of mixed cropping. In many Third World Countries traditional agricultural systems are based on the growing of crops in mixtures. There is therefore a need not only to identify compatible mixtures of crops but also devise suitable breeding strategies to produce improved cultivars for growth in crop mixtures. In this context the genetics of aggression (a) and response (r) in crop plants needs further investigation.

From this study estimates of a and r were made and it would appear that there is more variation in r than in a. This is in contrast to previous results in *Drosophila* and *Lolium* (Mather and Caligari 1983) and may reflect differences in propagation methods or the fact that barley has been subjected to intense artificial selection.

The results also support previous evidence (Mather and Caligari 1983) that a and r are under separate genetic control and are therefore amenable to manipulation by the barley breeder. It was also shown that both aggression and response were features of particular characters and did not appear as a response of the whole phenotype.

The experiments presented here illustrate an approach to the assessment of competitive interactions which is flexible and applicable to a range of crop plants. However, the main objective of this study was to establish the extent of intergenotypic competition in populations of spring barley. The presence of such complicating factors suggest that alternative schemes to the traditional pedigree method, for example those involving the production of random inbred lines, should be considered in barley improvement programmes.

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