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DIALLEL ANALYSIS OF COMPETITION BETWEEN SOME BARLEY SPECIES AND THEIR HYBRIDS

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SUMMARY

Plants from four 'species' of barley, *H. agriocrithon*, *H. spontaneum*, *H. distichum*, *H. intermedium*, and their F_1 hybrids were grown together in a 'mechanical' diallel and competitive effects were investigated by the application of the diallel analysis technique of DURRANT (1965).

There was no evidence of hybrid vigour when the hybrids were grown as pure stands but in binary mixtures the hybrids, considered overall, were more vigorous than their parents. Although this relationship was not complete the hybrids grown with the parents formed the most productive class, exceeding by 24% the combined mean grain yield of the parents grown alone and in parental mixtures.

In the eight characters investigated there was a tendency for compensation to occur between the mixture components but this was far from complete (i.e. an increase in one component was not precisely balanced by a decrease in the other). Those genotypes with large pure stand values tended to become smaller and, in compensation, the smaller genotypes larger. Since, however, the compensation was not complete the mixture means tended to be lower than the mean of the components in pure stand. The converse was found to be true for yield of grain.

The principal response to competition is for each genotype to be either uniformly suppressed or enhanced in the presence of an associated genotype, the strength and direction of this response being given by the α value calculated for each genotype. The α values were negatively correlated with their pure stand values (e.g. plants with a high dry weight when grown alone were depressed more than plants with a low dry weight when grown alone, and vice-versa). There was, however, no correlation between the pure stand value and the α value in respect of yield and 100-seed weight.

Although both *H. agriocrithon* and *H. spontaneum* were found to be poor competitors, only those hybrids derived from crosses with *H. spontaneum* have this poor competitive ability transmitted: hybrids involving *H. agriocrithon* are intermediate in competitive ability between their parents. Again, the hybrid formed between the two advanced barleys *H. distichum* and *H. intermedium* produces a hybrid of lower competitive ability than either parent.

The poorer competitors tend to produce fewer tillers and, as a consequence have a lowered seed output per plant when associated with other genotypes in mixtures. Grown in pure stand the weak competitors tend to be multi-tillering and to have a high output of seeds.

The plastic responses of other characters associated with yield, together with those such as ear emergence and height are also discussed. One hybrid, (s $\times$ d), a cross between *H. spontaneum* and *H. distichum* is of particular interest in that although a poor competitor it is nevertheless very high yielding when grown in pure stand. Furthermore, its suppression in mixtures is not sufficiently great as to reduce its overall ranking compared with its associates when aggregate yield is considered. Analytical techniques such as those described here could be of use to the plant breeder in his search for high yielding, compatible genotypes, of low competitive ability. The technique may also be used to test breeding procedures.

INTRODUCTION

An earlier investigation (see Fig. 1) into the competitive properties of hybrids compared with their parental genotypes showed that when two barley varieties Cb814 (an American 6-rowed variety), Cb545 (Rika) and their hybrid were grown as pure stands, the hybrid showed no superiority in growth over the parental genotypes, yet in mixtures (hybrid/Cb814 and hybrid/Cb545) the hybrid displayed marked heterosis (NORRINGTON-DAVIES, unpubl.). The present work examines this relation between parents

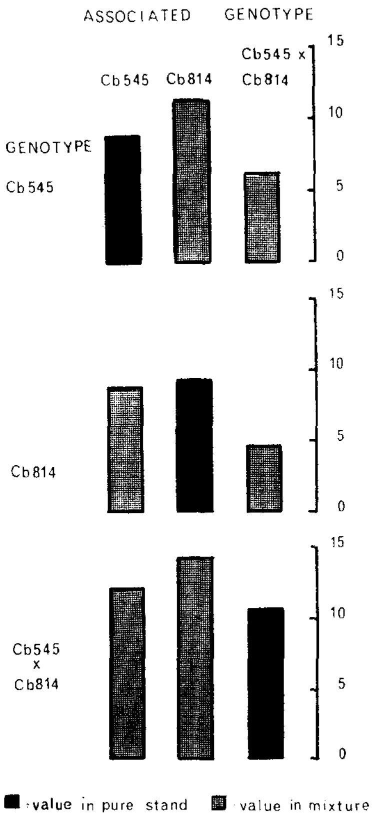

Fig. 1. Mean dry weight (g) of three genotypes of barley when grown in pure stands and in binary mixtures. D (Tukey's Confidence Interval) = 4.7 at $P<0.05$, and 5.8 at $P<0.01$

and hybrids in greater detail and makes use of four 'species' of barley and their six F_1 hybrids.

MATERIALS AND METHODS

A 'mechanical diallel', consisting of parental and F_1 seed of barley selected from a diallel cross made in the summer of 1963, was sown in April 1964.

The genotypes used are given in Table 1. The seeds were sown into 20-cm diameter composition pots filled with a standard John Innes Compost. Eight seeds were planted 5 cm apart in a circle 6.3 cm from the centre of the pot. In the mixture pots the seed of each genotype was sown alternately. Two replicates, each made up of 10 pure stand and 45 mixture pots, were randomised, grown for three weeks in a heated greenhouse, and subsequently placed on an outside terrace until maturity.

Hordeum agriocrithon and *H. spontaneum* carry genes causing brittle rachis. To avoid losses at harvest the heads of all crosses involving these two species were covered in cellophane bags after ear emergence.

Individual plants were measured for the characters listed in Table 2. The figures for dry weight per plant exclude root weight; yield refers to harvested grain and relative ear emergence to the number of days to heading from 12 June. All analyses, unless otherwise stated, were based on half-pot means, so that genotypes grown in pure stands may be compared directly with those grown in mixtures.

RESULTS

Pure stands

The data on pure stands and the results of the analyses of variance of the data are given in Table 2. From the analyses the following conclusions are drawn;

1. There is no significant difference in respect of any character scored between parents and hybrids (P–H) when the differences are tested against the variation among parents and among hybrids;

2. The test of significance of P–H (parents–hybrids) against the overall 'between pot'

Table 1. The genotypes used.

	Code number	
	in text	in Fig. 2
H. agriocrithon	a	1
H. spontaneum	s	2
H. distichum	d	3
H. intermedium	i	4
H. agriocrithon × *H. spontaneum*	(a × s)	5
H. agriocrithon × *H. distichum*	(a × d)	6
H. agriocrithon × *H. intermedium*	(a × i)	7
H. spontaneum × *H. distichum*	(s × d)	8
H. spontaneum × *H. intermedium*	(s × i)	9
H. distichum × *H. intermedium*	(d × i)	10

Table 2. Comparisons between the pure stand means of the ten genotypes represented in the mechanical diallel.

Character	Genotypes												Comparisons		
	a	s	d	$\bar{x}$	$\bar{x}$ parents	(a×s)	(a×d)	(a×i)	(s×d)	(s×i)	(d×i)	$\bar{x}$ hybrids	P-H	P	H
Av. dry weight per plant (g)	7.29	9.61	8.34	4.33	7.39	10.04	8.42	8.31	10.25	9.07	5.58	8.61	–	–	–
Av. yield per plant (g)	2.77	1.97	3.29	1.45	2.37	2.80	2.69	2.42	3.29	2.56	2.90	2.78	–	*	–
Av. number of fertile tillers per plant	3.30	5.19	4.04	2.75	3.82	3.63	2.81	3.06	6.69	6.88	3.56	4.44	–	–	***
Av. number of seeds per plant	85.65	64.05	69.15	33.65	63.13	68.55	52.60	57.65	85.75	73.45	57.15	68.86	–	*	–
Av. number of seeds per head	23.00	13.60	17.45	15.85	17.43	12.15	18.10	17.85	13.25	11.05	15.50	14.65	–	–	–
Av. weight per 100 seeds (g)	3.05	3.60	4.70	4.44	3.95	4.07	4.93	4.76	3.81	3.41	5.10	4.35	–	–	–
Relative ear emergence	17.40	12.94	20.31	6.00	14.16	6.63	16.37	10.46	4.69	5.75	13.13	9.51	–	***	***
Av. height (cm) of tallest fertile tiller per plant	65.29	91.56	82.56	77.09	79.13	89.81	87.19	83.25	72.25	80.00	88.37	83.48	–	*	–

P-H = comparisons between parents and hybrids; P = comparisons within parents; H = comparisons within hybrids. *$P<0.05$; **$P<0.01$; ***$P.<0.001$

error of the experiment ($P < 0.001$) revealed that some of the hybrids are significantly earlier to flower than their parents.

This indicates heterosis for *certain* of the crosses although on average, as is made clear from (1) above, the F_1's are not different from their parents. With regard to plant weight there is no significant difference between P and H when tested against the 'between pot' error for pure stands and mixtures combined. The difference is however significant when tested against pot error for pure stand alone ($P < 0.05$). There is therefore some slight indication of heterosis in respect of plant weight for some crosses It is worth noting that, on average, the F_1's do not display heterosis (SAKAI, 1955).

Comparisons between combinations of parents and hybrids

The results for the four combinations of plants, parents grown alone and in parental mixture (PP), parents grown with hybrids (PH), hybrids grown with parents (HP) and hybrids grown alone and with other hybrids (HH) are shown in Table 3. Analyses of variance of the differences between means (Table 3) show that:

a. The overall performance of the hybrids exceeds that of their parents in both dry

Table 3. Comparisons between the overall means of the four classes represented in the mechanical diallel.

Character	Class				Comparisons		
	PP	PH	HP	HH	parents against hybrid	competition effect	PP, HH, mixtures against PH, HP, mixtures
Av. dry weight per plant (g)	7.572	7.090	9.022	8.320	***	*	–
Av. yield per plant (g)	2.528	2.682	3.140	2.900	***	–	*
Av. number of fertile tillers per plant	4.274	4.328	4.646	4.550	*	–	–
Av. number of seeds per plant	65.700	65.300	68.540	62.660	–	–	–
Av. number of seeds per head	16.716	16.326	15.588	15.104	*	–	–
Av. weight per 100 seeds (g)	3.900	4.008	4.516	4.716	***	–	–
Relative ear emergence	13.714	11.822	9.006	9.154	***	**	**
Av. height in (cms) of tallest fertile tiller per plant	77.280	77.032	82.146	82.890	***	–	–

The comparisons made between the four classes, parents and parental mixtures (PP), parents grown with hybrids (PH), hybrids grown with parents (HP) and hybrids grown alone and in hybrid mixture (HH) were,

	PP	PH	HP	HH
Parents-hybrid	+	+	–	–
Competition effect	+	–	+	–
PP, HH, mixtures against PH, HP, mixtures	+	–	–	+

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

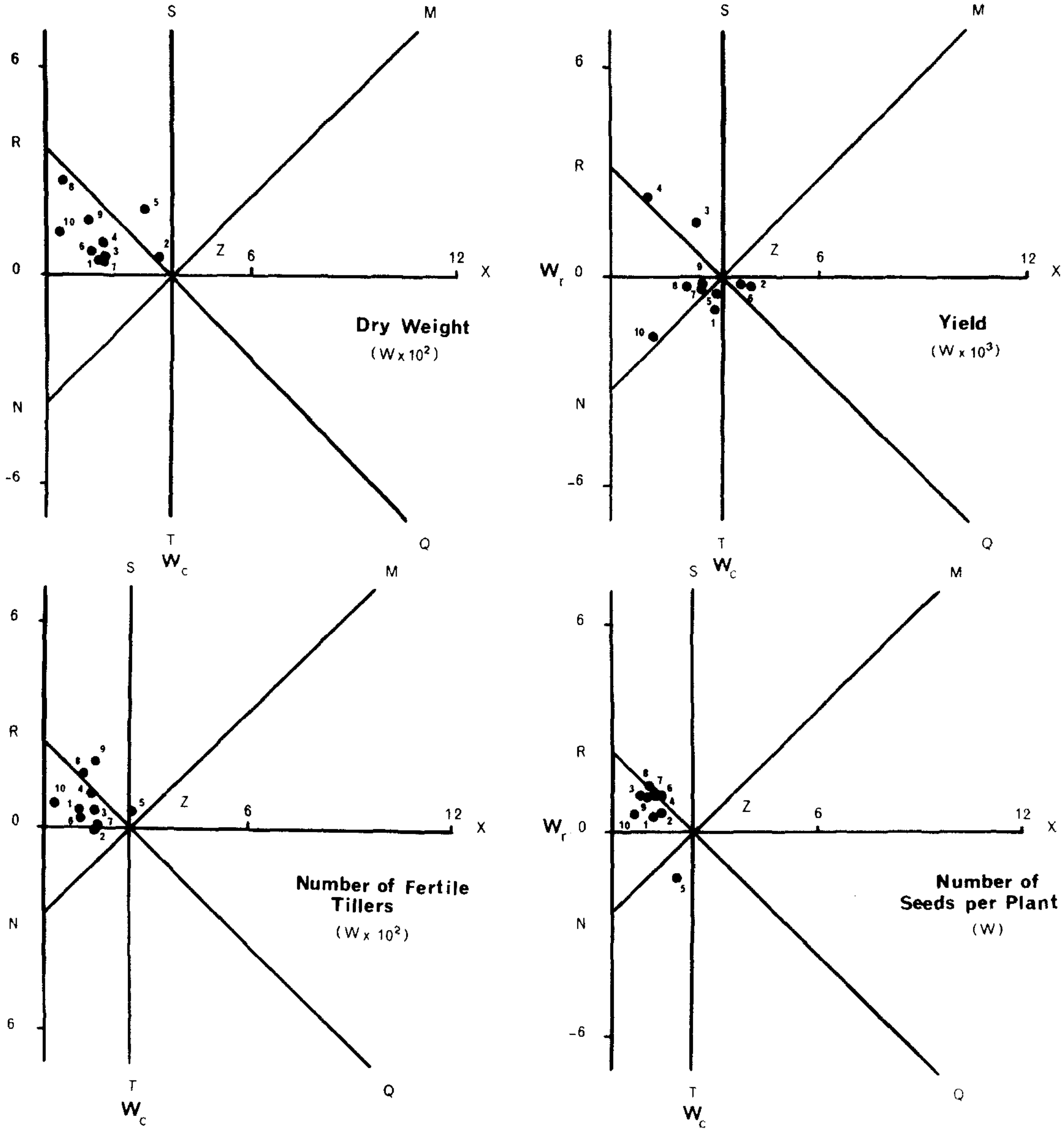

Fig. 2. Array covariances (W) for the summed replicates; 1 = *H. agriocrithon* (a); 2 = *H. spontaneum* (s); 3 = *H. distichum* (d); 4 = *H. intermedium* (i); 5 = (a × s); 6 = (a × d); 7 = (a × i); 8 = (s × d); 9 = (s × i); 10 = (d × i).

weight and yield. In achieving their superior yield they produce more fertile tillers which tend to carry fewer but heavier seeds. The hybrids are two to four days earlier to head than their parents and approximately 6 cm taller;

b. The hybrids grown with their parents (HP) are the most productive class, exceeding

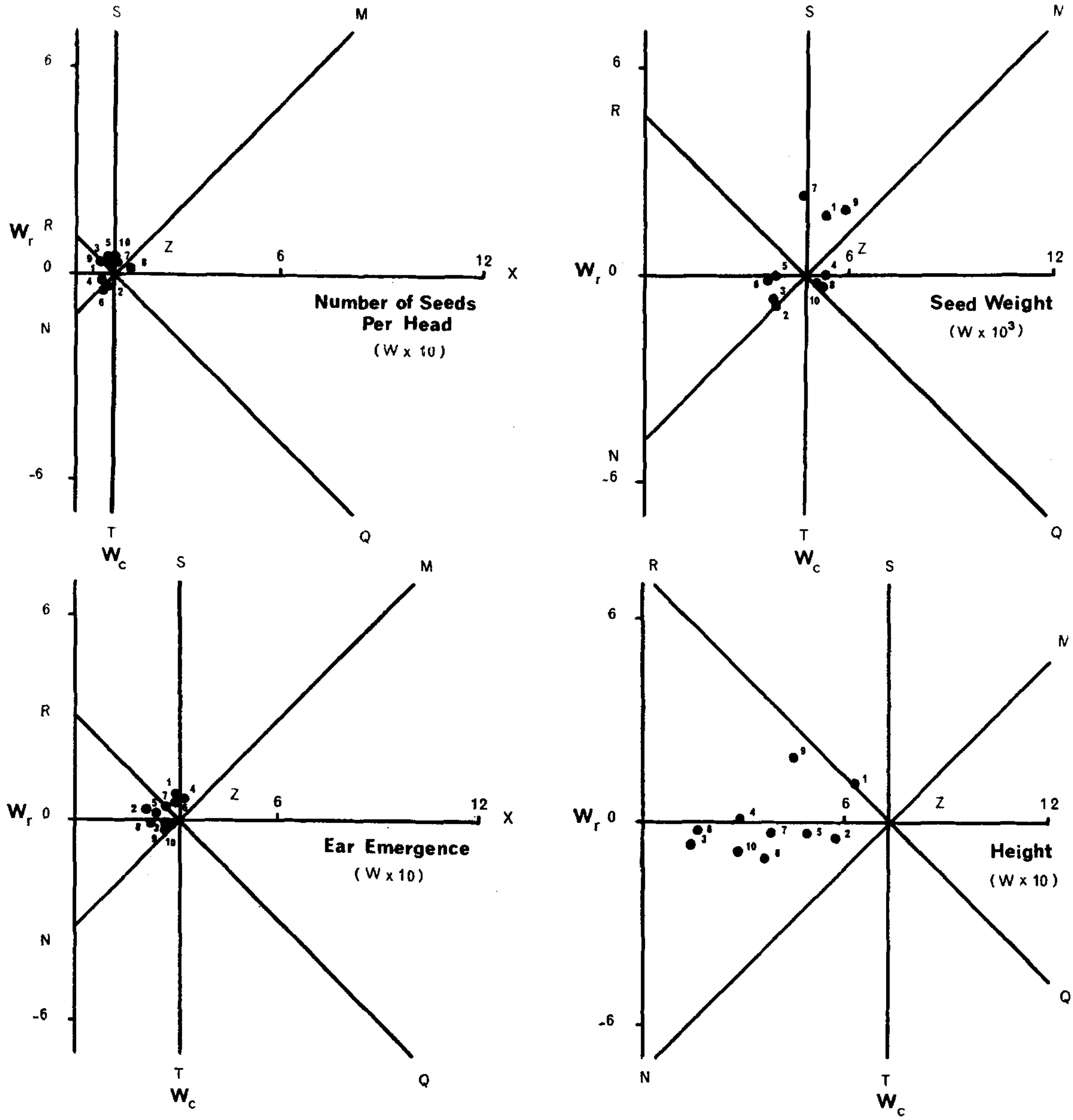

Fig. 2 (continued).

the combined mean yield of the parents grown alone and in parental mixtures (PP) by 24%;

c. Mixtures containing both hybrid and parental types (PH) (HP) are generally more productive than mixtures consisting of either parents (PP) or hybrids (HH) alone. Parents grown with hybrids yield 6% more than they yield in mixtures with other parents. Hybrids grown with parents yield 8% more than in mixtures of hybrids alone.

d. The vigour of the hybrids manifests itself in mixtures both of hybrids as well as of parental genotypes.

In order to examine further the competitive relationship between genotypes methods other than the analysis of variance are required (DURRANT, 1965; NORRINGTON-DAVIES 1967, 1968). The analyses are presented below.

Interpretations from the Wr/Wc graphs

The Wr/Wc graphs allow a provisional interpretation to be made of reciprocal means and reciprocal differences, considered as average effects over both column and row arrays (DURRANT, 1965). The features of the Wr/Wc graphs for all eight characters (Fig. 2) of immediate interest are:

1. The points tend in general to lie in the area of OZSR rather than ZXQT, which suggests that in mixtures genotypes with large pure stand values tend to become smaller;
2. There is a tendency for competition be to compensatory, i.e. as one component of the mixture increases in value the other component decreases. This follows from the distribution of points along the RQ axis. The compensation, however, is by no means complete as is made clear by the amount of scatter;
3. Although there is a general tendency for the points to be displaced from Z, along RQ, there is also a strong tendency for a lateral displacement from RQ parallel to MN. This suggests that the interaction between the genotypes is of the α type, i.e., where one of the components increases or decreases by a constant amount and/or its associate is decreased or increased by a constant amount (DURRANT, 1965; NORRINGTON-DAVIES, 1967, 1968). The differential displacement along RQ of the genotypes suggests that there may also be interactions of the β type whereby the competitive effects are a function of the difference between the genotypes grown in pure stand;
4. For each character measured, with the exception of yield, the mean displacement, $\bar{b}$, of the points from Z is positive. This confirms that there is an overall tendency for genotypes with lower values for a character to increase when grown with genotypes with a higher value for that character and/or for the genotype with higher values for a character to decrease when grown with a genotype with a smaller value for that character. The converse is true for yield. The magnitude of the competitive effect is appreciable for most characters, but weak for the number of seeds per head, mean seed weight and relative ear emergence;
5. *Hordeum spontaneum* and its three derived hybrids, (a × s) (s × d) and (s × i) on the one hand, and (d × i) on the other show a tendency to occupy peripheral postitions on the graphs indicating that they are, in general, more responsive to competition. *Hordeum spontaneum* and hybrids derived from *Hordeum spontaneum* are generally weak competitors, whereas (d × i) like its parents is a more vigorous competitor.

The location of the points in OZSR in the graph for dry weight indicates that genotypes with a high mean dry weight when grown in pure stand (*H. spontaneum* and its hybrid derivatives) decrease in weight when grown in mixtures, whereas those genotypes with a low mean dry weight when grown in pure stand, e.g. (d × i), increase in weight when grown in mixtures. On the same basis the derivatives of *Hordeum spontaneum* which have a high fertile tiller number, and are early to head in pure stand, produce fewer tillers and are later to head in mixtures.

The analysis of reciprocal differences

Analysis of variance of estimated values

The relative performance of mixture components may be examined on a qualitative and a quantitative basis by the analysis of their reciprocal differences. The result of such an anlysis is presented in Table 4. If it is assumed that only α competition occurs then it is seen that this component is highly significant for all characters other than for the average number of seeds per head, and even here it is significant at the 5% level, Table 4a.

If it is assumed that β competition only occurs then this component is significant for some, but not all of the characters (Table 4b).

α and β competition considered jointly, Table 4c shows again that with the exception of the average number of seeds per head this component is highly significant. To test which of the two competitive effects, α or β predominates, their individual sums of squares may be subtracted in turn from the joint sums of squares. The result of this test (Table 4d and 4e) shows that when α is removed from the joint sums of squares a negligible remainder sums of squares is left, whereas a highly significant remainder sums of squares is obtained after the removal of the β sums of squares. This confirms that the competitive interaction is largely of the α type.

The overall measure of competition, $\bar{b}$, can also be interpreted as α competition correlated with the pure stand values. This item is highly significant for five of the characters measured, the most notable expeption being yield.

The situation with regard to the type of competitive interaction is further clarified by the observation that where $\bar{b}$ is highly significant β competition is significant, and that where $\bar{b}$ is not significant β is not significant. The β sums of squares here then is due largely to the element of correlation between α and the pure stand values.

Other evidence in support of the interpretation comes from the correlation of the α values with their pure stand values (Table 4h). The majority of characters show a significant negative correlation. The notable exception once more is yield. The situation may be summarized as follows:

1. The competitive interactions are largely of the α type where the response is constant both in strength and direction for a given genotype;
2. The α values of the respective genotypes are negatively correlated with their pure stand values.

A more critical test for the significance of alpha competition takes into account the error mean square derived from the pure stand values, in addition to that from the mixture values, and may be expressed as $Ve_m + (n/2)\ Ve_p$ (McGilchrist, 1965). The two principal characters, dry weight and yield, remain significant when this test is applied but the remaining characters do not. However, in nearly every case, Table 4h and 4c, the significance of correlated α, a/P, and $\bar{b}$ support the original test for α competition.

Estimated values of α

The estimated values of alpha may be divided broadly into two main groups (Table 5): those values concerned with the estimates of dry weight, yield, tiller number and seed number on the one hand, and the rest.

Table 4. Analysis of variance of estimates, b values, and a/P correlations for the eight characters measured.

	d.f.	Av. dry wt per plant (g)		Av. yield per plant (g)		Av. number of fertile tillers per plant		Av. number of seeds per plant		Av. number of seeds per head		Av. wt. per 100 seeds (g)		Relative ear emergence		Av. wt. of tallest fertile tiller per plant	
		M.S.	V.R.	M.S.	V.R.	M.S.	V.R.	M.S.	V.R.	M.S.	V.R.	M.S.	V.R.	M.S.	V.R.	M.S.	V.R.
Total	45																
a. α competition	9	31.8	15.9***	2.7	11.9***	6.5	10.6***	1491	12.4***	16.0	2.4*	1.3	13.7***	11.4	5.2***	120	5.8***
Residual	36	1.9		0.2		0.6		120		6.8		0.1		2.2		21	
b. β competition	10	17.7	3.4**	1.1	1.7	5.2	6.2***	886	3.5**	9.0	1.1	0.5	2.0	10.6	4.9***	95	3.8**
Residual	35	5.1		0.6		0.8		254		8.5		0.2		2.2		24	
c. α and β competition	17	18.0	9.7***	1.6	6.6***	3.9	7.2***	838	6.7***	11.0	1.5	0.7	7.9***	7.0	3.1**	74	3.8**
$\bar{b}$	1	96.9	52.5***	0.9	3.9	29.4	54.8***	5855	47***	6.4	0.9	0.1	–	50.8	22.6***	882	45.0***
Residual	28	1.8		0.2		0.5		126		7.1		0.1		2.2		20	
d. α and β competition minus α competition	8	2.5	1.4	0.2	–	0.9	1.7	102	–	5.4	–	0.1	0.1	2.0	–	24	1.2
e. α and β competition minus β competition	7	18.5	9.9***	2.2	9.5***	2	3.8**	763	6***	13.9	1.9	0.9	10.7***	1.7		45	2.3
f. b calculated from α		0.427		0.038		0.307		0.400		0.098		0.041		0.095		0.209	
g. $\bar{b}$ calculated from α and β		0.382		–0.126		0.256		0.372		0.057		0.030		0.096		0.262	
h. r.a/P		–0.65*		–0.06		–0.85**		–0.71*		–0.38		–0.11		–0.71*		–0.73*	

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

Whilst the ten genotypes do not necessarily maintain the same rank order with regard to the magnitude of their α values they do maintain their sign, and at the same time show a tendency towards grouping in rank order.

Five of the genotypes bear a negative sign showing that in competition they are depressed uniformly, the extent of this depression being indicated by the magnitude of their α values.

H. agriocrithon (a) and *H. spontaneum* (s), the primitive barleys, are both very poor competitors, as are the hybrids (a $\times$ s) (s $\times$ d) and (s $\times$ i) derived from crosses involving *H. spontaneum*. The poor competitive ability of *H. spontaneum* is transmitted to its hybrids, but when *H. agriocrithon* is similarly crossed with either *H. distichum* or *H. intermedium*, the hybrids (a $\times$ d) and (a $\times$ i), intermediate in competitive ability between the primitive and advanced barleys are formed. The low competitive ability of *H. agriocrithon* has not been transmitted to the same extent. The hybrid (d $\times$ i), formed from a cross between the two advanced barleys is, rather surprisingly, not such a good competitor as either (a $\times$ d) or (a $\times$ i). Whilst successfully achieving a higher dry weight in competition than its associates it fails to make similar gains in tiller production, a character which has a considerable effect upon yielding ability (LUPTON et al., 1967).

When the estimated values of α for the number of seeds per head and the weight of seed are considered, a negative α value for either one of these characters is normally associated with a positive value for the other. This represents a compensatory interaction within the ear; a pattern from which the three hybrids involving crosses with *H. spontaneum* depart, (a $\times$ s) having a negative α value for both characters whilst (s $\times$ d) and (s $\times$ i) have positive α values. The reduced yield of these three hybrids in competition arises from a suppression of tillering. *H. agriocrithon* whose yield is affected adversely to a greater extent than any of the other types by competition produced not only fewer seeds per head, but also fewer tillers. *H. intermedium* the most favoured genotype in competition with regard to yield also produced fewer seeds per head but achieves its high yield by its capacity for increased tiller production under competitive stress.

The weak competitors all suffer alike in producing fewer seeds per plant, which in the case of *H. spontaneum* and (a $\times$ s) is accompanied also by a decrease in seed weight.

The Wr/Wc graph shows a tendency towards earlier flowering in mixtures. There is strong negative correlation ($r = -0.71$; $P < 0.05$), between the pure stand values of the genotypes and their estimated α values. Amongst the later heading genotypes *H. agriocrithon* flowers on average 5 days earlier when in competition, whereas *H. spontaneum*, *H. distichum* and (d $\times$ i) are, on average, a day earlier when grown in competition with other genotypes. Some of the earlier flowering genotypes in pure stand such as (s $\times$ d) and *H. intermedium* on the other hand flower later. Apart from the average effects it is found that certain genotypes tend to flower earlier in association with the later flowering types, for example, *H. agriocrithon*, *H. spontaneum* and (s $\times$ d) when grown with *H. distichum*. Other genotypes have a tendency to flower later in association with the earlier flowering genotypes, for example, (d $\times$ i) grown with either (s $\times$ d) or (s $\times$ i) behaves like this.

The behaviour of the genotypes with regard to height appears capricious. Of the weak competitors *H. spontaneum* decreases markedly in height when grown in compe-

Table 5. Estimated values of α

Genotype	Av. dry weight per plant (g)	Av. yield per plant (g)	Av. number of fertile tillers per plant	Av. number of seeds per plant	Av. number of seeds per head	Av. weight weight per 100 seeds (g)	Relative ear emergence	Av. height of tallest fertile tiller per plant
a = *H. agriocrithon*	–1.209	–1.055	–0.472	–30.150	–2.880	0.528	–3.536	6.200
s = *H. spontaneum*	–4.614	–0.787	–0.810	–7.140	0.540	–0.974	–0.812	–10.339
d = *H. distichum*	2.359	0.837	1.193	19.540	0.810	–0.030	–0.578	–3.014
i = *H. intermedium*	1.778	0.859	1.568	17.580	–3.020	0.157	0.637	5.648
(a × s)	–1.365	–0.646	–0.735	–10.610	–0.310	–0.146	1.131	–0.449
(a × d)	2.086	0.525	1.239	20.450	1.400	–0.587	–0.397	–3.877
(a × i)	0.240	0.584	0.455	0.510	–0.300	0.709	0.159	–0.287
(s × d)	–1.425	–0.169	–0.212	–7.060	0.010	0.407	2.017	2.472
(s × i)	–1.681	–0.665	–1.928	–16.530	1.080	0.093	0.481	1.053
(d × i)	3.831	0.517	0.402	13.410	2.670	–0.157	0.898	2.593

tition but this is not true of its hybrids. Of these, (a × s) decreases a little in height when grown in mixtures but (s × d) (s × i) actually increase in height in many mixtures. Other weak competitors such as *H. agriocrithon* are also increased in height in mixtures.

Strong competitors such as *H. intermedium* may also increase in height in mixtures, whilst other strong competitors such as (a × d) either themselves become shorter or tend to increase the height of their associates in competition. Clearly, the final height of plants in this experiment is not directly related to competitive ability.

Correlation between α and the pure stand values

It has already been noted that the α values calculated from the differences in growth between plants grown in mixtures may be correlated with their pure stand values.

In this particular experiment a significant negative correlation is shown between the α values and the pure stand values for five of the eight characters examined; dry weight number of fertile tillers, number of seeds per plant, relative ear emergence, and height. These correlation coefficients are shown in Table 4h and may be interpreted as follows;

a. In general, those genotypes which have a relatively high dry weight when grown in pure stands are reduced most in competition;

b. Weak competitors when grown in pure stand produce the highest number of tillers;

c. The greatest number of seeds per plant in pure stand are produced by the poorer competitors;

d. The later flowering genotypes in pure stand tend to flower earlier in mixtures, and the earlier flowering genotypes in pure stand tend to flower later in mixtures;

e. The taller growing genotypes in pure stand become shorter in mixtures, and the shorter growing genotypes in pure stand tend to become taller in mixtures. This confirms the conclusions reached from the Wr/Wc graphs where the points tend to lie in the area of OZSR.

It is intriguing to find that in so far as yield is concerned there is no correlation between the α values of the genotypes, and their pure stand values. The highest yielding genotype both when the pure stand value, and the aggregate yield in mixtures is considered in *H. distichum*. This genotype is both high yielding, and vigorous in competition. This contrasts with the hybrid (s × d) formed from the cross between *H. spontaneum* and *H. distichum* which is equal in yield to *H. distichum* when grown as a pure stand, is second to it when aggregate yield in mixtures is considered, but is undoubtedly a poor competitor where most characters are concerned. (s × d) maintains its high yield in mixtures because although the number of seed produced falls, its seed weight is increased, more than almost any other hybrid or parent; the exceptions are *H. agriocrithon* and (a × i). The increased seed weight of (s × d) in mixtures is more than sufficient to compensate for any fall in seed number.

In terms of mass, expressed as dry weight, (s × d) is as large as any genotype when grown in pure stand. In this respect (s × d) at the F_1 level seems to fulfil, in part at least, the criteria set out for the breeding of crop ideotypes by DONALD (1968).

Correlation coefficients between growth characters and between growth characters and yield

The correlation coefficients obtained when the values for both pure stands and mix-

Table 6. Correlation co-efficients between growth characters.

	Height	Ear emergence	100-seed wt	Seeds/head	Seeds/plant	Fertile tillers	Yield
Dry wt.	0.20	0.07	0.09	0.08	0.74***	0.52***	0.69***
Yield	0.13	0.27**	0.49***	0.32**	0.71***	0.23*	
Fertile tillers	–0.07	–0.42***	–0.32**	–0.58***	0.58***		
Seeds/plant	–0.08	0.15	–0.21*	0.24*			
Seed/head	0.00	0.55***	0.13				
Seed/wt. 100	0.32***	0.06					
Ear emergence	–0.07						

*P<0.05; **P<0.01; ***P<0.001.

tures are used are given in Table 6. In this experiment the most complete association is found between yield and the number of seeds per plant. The higher yielding genotypes produce a large number of seeds per plant. The number of seeds per plant in turn is closely correlated with the dry weight and the number of fertile tillers produced per plant. The greatest number of seeds per plant is produced by the multi-tillering genotypes. Yield is also strongly correlated with the 100-seed weight, high seed weight being associated with high yield. It is of interest to note that the only character having an association with height is seed weight, where a high seed weight is obtained by the taller growing genotypes. The strongest negative association is between number of fertile tillers and seeds borne by the tillers. The higher the tillering the fewer the seed per head. Finally, the later flowering genotypes tend to produce more seed per head.

Correlation coefficients may also be calculated between the alpha values, and this indicates those characters which respond in a similar way to competition. The results from this type of correlation are given in Table 7. In terms of this consistency of competition effect the principal components of yield are represented here by the number of fertile tillers and the number of seeds produced per plant. A strong correlation is also shown between the α competition effects of height and seed weight.

Estimates of $\bar{b}$ based on the α values

The estimates of $\bar{b}$ calculated from α where $\bar{b}$ gives the average effect over all genotypes are given in Table 4f. For each unit of difference between the genotypes when

Table 7. Correlation co-efficients between growth characters with estimates of α competition.

	Height	Ear emergence	100-seed wt	Seeds/head	Seeds/plant	Fertile tillers	Yield
Dry wt.	0.36	0.15	0.16	0.27	0.75*	0.76*	0.82**
Yield	0.07	0.31	0.09	0.18	0.92***	0.85**	
Fertile tillers	0.06	–0.07	–0.03	–0.11	0.83**		
Seeds/plant	–0.19	0.35	–0.30	0.34			
Seeds/head	–0.51	0.38	–0.47				
Seed/wt. 100	0.77**	0.00					
Ear emergence	0.00						

*P<0.05; **P<0.01; ***P<0.001.

grown in pure stand there is, on average, a difference of $2 \times \bar{b}$ when they are grown in mixtures. For example, in the case of dry weight this difference is 0.854 g/g. The greatest differences in terms of competitive effect are seen to have occurred within those characters most closely associated with yield, but yield itself shows little effect overall.

DISCUSSION

In seeking improved varieties the plant breeder is concerned principally with either the elimination of defects in currently available varieties, or in a process leading to selection for quality and higher yield. Variability is released by segregation following hybridisation, and selection pressures are then imposed from which higher yielding, agronomically uniform types are derived. The selection procedures may involve a simulation in part of the conditions under which the prospective variety is to perform. The physiological and morphological changes that may have occurred during the course of selection are not normally known. In bulk-population methods of breeding selection from the segregation populations occurs under conditions of high competitive stress. Genotypes superior to currently available commercial varieties may be produced in this way, but the full potential of the hybrid material may not have been realised. SUNESON (1956) demonstrated quite clearly that selections could be made from a bulked hybrid population (F24) which were capable of yields greatly in excess of the standard commercial variety from which they were in part derived, whereas only moderate increases were obtained under competitive natural selection.

Such evidence supports the view of DONALD (1963) who believes that the plant breeder must recognise the degree of independence that exists between yielding ability and competitive ability and distinguish between them.

SAKAI (1955) found, when comparing the performance of five inbred varieties of barley and their ten derived hybrids that the hybrids although superior to the parental varieties when grown in pure stand were generally inferior in competitive ability to the parents when grown with two tester varieties. There are two possible objections to these conclusions:

1. The assumption that to measure the competitive ability of a hybrid against a tester plant gives a more realistic measure of competitive ability than to test the hybrid against its parents;
2. The expectation that because the hybrids exceeded their parental average in plant weight, culm number, and weight of ears that they should be *ipso facto* strong competitors.

It is not unreasonable to suppose that hybrids which possess strong non-specific competitive ability will, when grown together, suppress each other to such an extent that their potential yield for a given density is not realised. When these strongly competitive hybrids are grown with their parents however hybrid vigour may then be expressed in terms of increased yield. Indications of this type of behaviour are evident in this experiment where the manifestations of hybrid vigour are seen in the performance of hybrids in mixtures both with the parental genotypes and other hybrids. Hybrids grown with their parents (HP) are 24% more productive than their parents grown alone and in parental mixtures (PP). That this competitive ability may be inherited is demonstrated by the performance of the hybrids (a × s), (s × d) and (s × i). Each of these hybrids is a poor competitor, and each in turn has *H. spontaneum*, itself a poor competitior, as a common parent. *H. agriocrithon* on the other hand, which may also be considered a poor competitor produces hybrids of intermediate competitive power.

The failure of (d $\times$ i), derived from the advanced barleys, to surpass the competitive ability of (a $\times$ d) and (a $\times$ i), derived from crosses involving *H. agriocrithon*, lies in the fact that not only is it a low tillering genotype in pure stand but also that it is unable to increase its tiller production substantially in competition.

It cannot be claimed that the relative competitive abilities demonstrated here represent an innate quality of competitiveness possessed by the genotypes examined but rather their competitiveness in relation to the conditions of this experiment. It is possible that under other conditions their relative competitive abilities might be changed (HARPER, 1964).

There is general agreement that increased density may result in the death of individuals within the plant population. Where less drastic density effects occur these may result in changes in the growth and reproductive capacity of the individual. In this experiment mortality effects were eliminated, and the study was confined to the plastic responses of the plants at a given density.

The estimates of alpha give both the degree and the direction of the plastic response to intergenotypic competition. Changes in tillering capacity are found to be of major importance in determining seed output, and hence yield. When grown in mixtures the poor competitors produce fewer tillers, which in turn leads to a lower output of seeds per plant. Some degree of compensation occurs between the number of seeds produced per head and the weight of this seed, whereby a negative α value for one of these characters is normally associated with a positive value for the other. This association does not hold in the case of the three *H. spontaneum* hybrids. The hybrid formed from the two primitive barleys has negative values for both seed number per head and seed weight, whilst (s $\times$ d) and (s $\times$ i) have positive α values for both characters. These two hybrids are affected mainly by suppression of tillering.

When grown in pure stand the weak competitors tend to be multi-tillering and to have a high output of seeds. The changes induced by competition in the components of the binary mixtures considered here cannot however be viewed in isolation but must be related to the performance of the components when grown in pure stand. When this is done it is seen that the hybrid (s $\times$ d) ranks high in dry weight, yield, number of fertile tillers, and the number of seeds produced per plant. It is these characters which are uniformly suppressed in competition with other genotypes. This suppression nevertheless is not so great in the mixtures as to reduce the aggregate position of (s $\times$ d), (i.e. summed over all mixtures), relative to its associates. In developing his ideas on the breeding of crop ideotypes DONALD (1968) has postulated that the successful, type will be a weak competitor relative to its mass, so that when grown in pure stand individual plants will compete with each other to a minimum degree. The hybrid (s $\times$ d) appears to have this attribute.

It is suggested that the application of such analytical techniques as have been demonstrated here would be of use to the plant breeder in evaluating both the methods of breeding that he employs and the value of the material that he selects.

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