The effects of competitive interactions on variances and on seed germination in spring barley (*Hordeum vulgare*)

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Competition in spring barley is shown to affect between plant variation and hence the observed heritability of characters. It is also shown that seed germination can be affected by the competitive interactions experienced by the parents. Both of these features point to the complications of attempting early-generation selection in barley breeding programmes as well as with many other crop species.

INTRODUCTION

The experimental and analytical methods developed by Mather and Caligari (1981, 1983) have been applied to six genotypes of spring barley in order to investigate the role of intergenotypic competition in the selection process for a number of characters of economic importance (Powell, Caligari, Goudappel and Thomas, 1986). Significant levels of intergenotypic competition were detected and such complicating factors can be expected to introduce bias during early-generation selection procedures. These analyses were based on mean performance. The present paper focuses attention on the effects of competitive interactions on the between plant variances for the same characters. Furthermore, the possible "carry over" effects of competition on germination in a subsequent generation are considered.

MATERIALS AND METHODS

The genotypes investigated and the experimental design employed are described in detail by Powell *et al.* (1986) and only a brief description is given here. The genotypes were derived by single seed descent from two crosses (Brim, 1966). Three lines (coded A, B and C) were sampled from the cross BH4/143/2 × Ark Royal and three (D, E and F) from Heriot × Rif.

The experimental design employed was as described by Mather and Caligari (1981) and in-

cluded growing each genotype in a series of monocultures and in duocultures with various frequencies of each component, but maintaining a total number N (in this case 60) plants in each plot giving a modified substitution experiment. The structure of the experiment may be illustrated by reference to genotype A:

Number 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	

As shown above, it was practicable to grow only two combinations of duoculture for each of the six primary genotypes, but the combination of A with B can be regarded as one with A as the primary genotype as well as one with B as primary. Thus the combinations were:

A:B, A:D, B:C, C:F, D:E and E:F

The experiment was set up as a randomised complete block of two replicates. Each replicate consisted of 48 plots. A maximum of 60 seeds per plot was sown by hand at a density of 388 plants per square metre in the field at the Murrays Farm, East Lothian, in 1984. The experiment was netted to prevent bird damage and the perimeter was sown with the cultivar Tweed to reduce edge effects. The experiment was sprayed with a broad spectrum fungicide to prevent disease development.

After harvest the following characters were scored: the weight of grain on the main stem in g (MSW), final plant height in cm (Ht), number of

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grains on the main stem (GN), thousand grain weight (TGW), number of fertile tillers per plant (TN) and the total yield of grain per plant in g (SPY). The germination of the seed produced was assessed 11 months after harvest by placing 100 seeds of each genotype from each plot on moist filter paper in a petri-dish at $20 \pm 2^\circ\text{C}$. After five days the number of seeds that had germinated were counted, giving the percentage germination which was converted into angles.

RESULTS AND ANALYSES

The results from all the plants of the same genotype within a plot were used to obtain the variance between plants. The square roots of such variances were analysed using the methods proposed by Mather and Caligari (1981). The model, assuming a linear relationship between the square root of the variance for a character and the number of plants per plot, was fitted for the 7 characters. Only one of the characters, GN, showed any evidence of non-linearity in that the residual variation around the fitted line was significantly greater than the replicate error variance at the 5 per cent probability level. As this was the only character which showed a departure from linearity and, moreover it was only just formally significant, it was taken that the linear relationships were adequate. From the estimates of the regression slopes for monocul-

tures and duoculture, the intra- and intergenotypic competition effects (c values) were obtained (Mather, Hill and Caligari, 1982) and are given in table 1. From these values, following Mather and Caligari (1983), estimates of $\bar{c}$ (the overall competitive effect), r (the response), a (the aggression) and i (the interaction) were obtained for the six pairs of genotypes as described by Powell *et al.* (1986), and are presented in table 2.

Two of the characters, MSW and Ht, have significant i effects for some of the pairs and indicate that a multiplicative model, rather than the additive one used to estimate r and a , might have been more appropriate. Nevertheless, the results indicate that competition is having an effect. With TN there is clear evidence that competition is present in 4 of the 6 pairs of genotypes, with genotype C differing in response from the other genotypes. The other 3 characters, namely GN, TGW and SPY, give evidence of competition having an effect but with no particular pattern of aggression or response between the genotypes. It should be noted that in table 1 some of the intragenotypic competition effects are negative, which could be taken as indicative of "auto-facilitation", but only one (c_{AA} for Ht) is significant. Also in table 2 some of the $\bar{c}$ values are negative and significant, again this would suggest facilitation if the mean expression of the characters was being considered. However, in the present case the negative $\bar{c}$ values indicate that the variances (or

Table 1 Estimates of the intra- and intergenotypic competition effects based on the square root of the variances for six agronomic characters

	MSW ($\times 10^3$)	Ht ($\times 10^2$)	TN ($\times 10^2$)	GN ($\times 10^2$)	TGW ($\times 10^2$)	SPY ($\times 10^2$)
c_{AA}	-0.80	-5.16*	3.79	0.54	-0.33	4.45
c_{AB}	-3.19**	-12.90***	2.99	-4.38	-9.71***	4.03
c_{AD}	-4.00***	-6.72*	1.98	-9.53***	-3.47	1.96
c_{BB}	0.29	-1.93	-1.17	-2.58	-4.16	2.12
c_{BA}	-1.32	-12.19**	7.01*	-1.70	-4.24	5.86*
c_{BC}	-2.79**	-8.24*	3.99	-3.90	-10.47***	0.94
c_{CC}	-1.43	1.99	13.14*	-3.71	-2.54	8.78**
c_{CB}	-2.48*	-3.22	9.12	-14.17***	-6.00*	9.68**
c_{CF}	-3.31***	-6.59*	15.83*	-5.46*	-8.38**	11.81***
c_{DD}	-0.94	3.53	8.58*	-1.76	-5.21	8.07**
c_{DA}	-1.89**	-4.79	-0.93	-1.06	-5.70	1.23
c_{DE}	1.55	-4.48	-2.47	0.37	0.13	11.78
c_{EE}	-0.28	-3.27	4.85*	-2.06	-0.80	6.50**
c_{ED}	0.49	7.29*	6.27*	1.38	0.72	6.54**
c_{EF}	-1.16	-14.97**	4.58	-2.05	-1.18	4.05
c_{FF}	-0.72	-4.64	6.44*	-2.70	-0.74	8.71**
c_{FC}	-0.04	-3.61	3.78	-1.10	0.14	6.04*
c_{FE}	-0.87	-4.64	-0.19	-1.50	-2.28	1.49

* $P = 0.05 - 0.01$, ** $P = 0.01 - 0.001$, *** $P = < 0.001$

Table 2 Estimates of the mean competitive value ($\bar{c}$), the difference in response (r) between genotypes, the difference in aggression (a) and the interaction (i) between r and a for the variances of the characters in each of the six combinations

	MSW ($\times 10^3$)	Ht ($\times 10^2$)	TN ($\times 10^2$)	GN ($\times 10^2$)	TGW ($\times 10^2$)	SPY ($\times 10^2$)
A/B $\bar{c}$	-1.25**	-8.04***	3.15	-2.03	-4.61***	4.12**
r	-0.74	-1.00	0.23	0.11	-0.41	0.12
a	0.19	-0.63	2.24	1.45	2.32	1.04
i	1.00	4.50**	-1.84	1.01	2.36	-0.83
A/D $\bar{c}$	-1.91**	-3.29*	3.35	-2.95	-3.68**	3.93*
r	-0.49	-2.65	-0.47	-1.54	1.78	-0.72
a	0.56	-1.69	-1.92	2.69	0.66	-1.09
i	1.04	2.47	2.83	2.34	0.91	2.33
B/C $\bar{c}$	-1.60***	-2.85*	6.27***	-6.09***	-5.79***	5.38***
r	0.35	-2.23	-4.86*	2.85	-1.52	-3.85*
a	0.51	2.75	-2.29	-2.28	0.71	0.52
i	1.03*	2.88*	-0.28	2.94	2.44	0.07
C/F $\bar{c}$	-1.37**	-3.21*	9.80***	-3.24	-2.88*	8.84***
r	-1.00*	0.91	4.69*	-1.34	-2.58*	1.46
a	0.64	2.40	-1.34	0.84	1.68	-1.43
i	0.30	1.89	-0.01	0.04	1.24	0.09
D/E $\bar{c}$	0.21	0.77	4.31*	-0.52	-1.00	8.22***
r	0.10	-1.24	-1.25	-0.02	-0.95	1.70
a	-0.43	4.64**	3.12	0.33	-1.25	-0.92
i	-0.81	-0.64	2.41	-1.39	-2.01	-0.94
E/F $\bar{c}$	-0.76	-4.88***	3.92*	-2.08	-1.25	5.19***
r	0.04	-4.24**	0.79	0.02	0.26	0.09
a	0.18	-4.92***	-1.59	0.30	-0.29	-1.19
i	0.26	-0.93	1.72	-0.30	0.48	2.42

* $P = 0.05 - 0.01$, ** $P = 0.01 - 0.001$, *** $P = < 0.001$

more strictly the square roots of the variances) are increasing with increasing competition, *i.e.*, as competition increases so the phenotypic expression of a given genotype becomes more variable.

The same analysis was carried out for the percent mean germination (transformed to angles) and the competitive values are presented in table 3, while the $\bar{c}$, r , a and i values are given in table 4. There are fewer significant estimates for percent germination than for the within family variances but they show that genotype F responds differently from the other 5 genotypes to the effects of compe-

tition. Interestingly, the only significant $\bar{c}$ value is negative and thus points to genotype F showing increased germination with increasing competition, *i.e.*, facilitation. Thus the next generation shows the effects of competitive interactions experienced by the parents. Germination was not measured under field conditions but assuming that similar effects would occur it is likely that other aspects of plant phenotype would be subsequently affected (Harper 1977).

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

A/B $\bar{c} = 0.017$	A/D $\bar{c} = 0.015$	B/C $\bar{c} = 0.073$
$r = -0.017$	$r = 0.004$	$r = 0.063$
$a = -0.020$	$a = 0.000$	$a = -0.025$
$i = 0.075$	$i = 0.035$	$i = 0.019$
C/F $\bar{c} = -0.062$	D/E $\bar{c} = 0.014$	E/F $\bar{c} = -0.101^*$
$r = 0.090^*$	$r = 0.023$	$r = 0.085^*$
$a = 0.035$	$a = 0.027$	$a = -0.014$
$i = 0.009$	$i = -0.017$	$i = -0.024$

* $P = 0.05 - 0.01$ **Table 3** Estimates of the intra and intergenotypic competitive effects for percent germination (in angles)

$c_{AA} = 0.055$	$c_{BB} = 0.129$	$c_{CC} = 0.054$
$c_{AB} = -0.055$	$c_{BA} = -0.061$	$c_{CB} = -0.035$
$c_{AD} = -0.016$	$c_{BC} = 0.143$	$c_{CF} = 0.002$
$c_{DD} = 0.046$	$c_{EE} = -0.053$	$c_{FF} = -0.196^{***}$
$c_{DA} = -0.024$	$c_{ED} = 0.035$	$c_{FC} = -0.109$
$c_{DE} = 0.028$	$c_{EF} = 0.022$	$c_{FE} = -0.175^{**}$

** $P = 0.01 - 0.001$, *** $P = < 0.001$

DISCUSSION AND CONCLUSIONS

The separation of the effects of intra- and intergenotypic competition allows the relative magnitude of intergenotypic competition to be assessed. Such analyses based on mean performance (Powell *et al.*, 1986) have indicated the presence of significant levels of intergenotypic competition in barley. Consequently selection for monoculture performance under conditions which display intergenotypic competition may result in a bias being introduced. The present study using the same material demonstrates that competition between genotypes of barley can also affect second degree statistics, *i.e.*, the between plant variances. Thus estimates of heritability and hence the efficiency of selection will vary depending on the competitive pressure exerted by individuals within a population. These two features of intergenotypic competition obviously complicate and confound methods used for early-generation selection in many crop species.

The effect of competition on characters in subsequent generations has also been investigated. Seed germination in this experiment was affected by the competitive pressure experienced by the parental genotypes. Such an effect will have profound implications for many characters since differential germination can influence establishment and survival. As stated by Harper (1977), "The advantage which an early emerging seedling gains is far greater than can be accounted for merely by the greater time that it has been allowed to grow".

The results presented here reinforce the general theme that early-generation selection should be avoided in barley breeding programmes. Intergenotypic competition has previously been shown

to affect the means of agronomic characters in spring barley (Powell *et al.*, 1986). In the present paper the variances of such characters are also shown to be affected and, in addition, it has been demonstrated that seed germination can be influenced by the competitive pressures experienced by the parents. Thus it is clear that if selection is practiced in early generations when genotypes are present in heterogeneous mixtures its effects will be confounded with the effects of competition in its broadest sense. This argument may be extended to other crop species where the procedures of early-generation selection are practiced.

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