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Frequency - Dependent Advantage in Wheat

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Summary. The effect of frequency-dependent advantage in wheat was investigated by growing F_1 hybrid seeds of the crosses (Warimek × Halberd) and (Wariquam × Halberd) in a stand of Halberd at 5 frequencies: 4%, 6.25%, 11.11%, 25% and 50%. A reduction of 35% to 40% in grain yield of individual plants was observed with both hybrids as their frequencies changed from 4% to 50%. A similar trend with frequency was noted for several other plant characteristics, including total grain number, particularly with those measured towards the end of the growing season. Halberd plants did not show a corresponding increase as their frequency declined from 96% to 50%. - The following season, 76 F_4 lines from the cross (Warimek × Halberd) and 70 F_4 lines from (Wariquam × Gabo) were grown at frequencies of 6.25% and 18.75% in machine sown stands of Wariquam and Halberd, respectively. Again grain yield decreased as genotypic frequency increased. Furthermore, there was a positive correlation between frequency-dependent advantage and relative grain yield, suggesting that high yielding genotypes show a greater advantage at low frequencies than lower yielding ones.

Introduction

Frequency-dependent advantage is a term used by us for the phenomenon where a genotype at a low frequency in a population has a higher fitness or a higher yield than it has when present at a high frequency. This phenomenon if demonstrated may have important consequences for selection within the segregating populations grown by plant breeders.

The isolation of superior genotypes from segregating populations and the persistence of off-type genotypes in a variety during several generations of seed multiplication are problems inherent in the breeding of self-pollinated cereals. In the former, the frequency-dependent effect may reduce the efficiency of single-plant selection, and in the latter it could result in a change in the properties of a variety during multiplication.

A breeder of a self pollinated crop would like to select effectively in the F_2 generation of a cross since the frequency of genotypes with all the desired alleles is highest in that generation (Shebeski 1967). However, for wheat and barley, selection for yield in the F_2 on a single plant basis is considered by many authors to be ineffective (Allard 1960; Bell 1963). The main reasons usually advanced are that single plant performance is confounded by genotype-environment interaction and inter-plant competition, and Allard and Adams (1969) and Sakai (1961) have shown that the performance of an individual in a mixture is often affected by its neighbours.

More specifically, it is possible that the performance of a genotype in a mixture is influenced by the frequency of like or similar genotypes in the population. Allard, Jain and Workman (1968) and Harding, Allard and Smeltzer (1966) found that, in populations of lima bean, the frequencies of the heterozygotes in a population were higher than could be accounted for by heterozygote advantage and out-crossing and that their fitness increased as they became rare. They ascribed this to frequency-dependent selection. Frequency dependence of reproductive values was also reported for wheat (Khalifa and Qualset 1974); but was not evident in barley, even when strong competition was demonstrated (Early and Qualset 1971). Experiments with insects (Kojima and Yarbrough 1967; Tobari and Kojima 1967) have also shown that the fitnesses of different karyotypes were frequency-dependent and Ehrman (1968) has indicated that the rare genotypes were more successful in securing mates.

An extensive literature now exists (for example McGinnis and Shebeski 1968; Knott 1972) which suggests that there is usually a low or insignificant correlation when the performance of genotypes grown in a mixture as spaced plants is compared to their performance in pure stands as crops or swards. These inconsistencies can be due to either variations attributable to changes in densities, or to differences arising from interactions with neighbouring genotypes. In a cereal breeding program it is possible to ignore the former by growing the segregating generations at commercial densities, but this may exacerbate the latter. The work reported here is part of a project investigating the feasibility of single plant selection at commercial plant densities.

A segregating population resulting from the intercrossing of diverse parents consists of a large number of different genotypes. Among these many of the individuals are similar, genetically; others rare and quite different from the majority. If selection is practised in these circumstances, it is possible that the choice of genotypes will be influenced by their frequency. If a genotype performs well in a mixture because it is rare, this advantage will not persist when it is selected and propagated in a pure stand. Selection would then be ineffective and many potentially high yielding genotypes might have been overlooked.

This paper reports the results from two experiments designed to demonstrate the existence and measure the magnitude of frequency-dependent advantage in wheat as a prelude to further investigations of its operation in segregating populations. In the first, two F_1 hybrids were grown at five different frequencies in a stand of one of the parent varieties to determine both the frequencies at which the effect could be measured and the mean response of a hybrid grown in a parent. The second was aimed at measuring the magnitude and variation of the effect in F_2 derived lines, and to compare these to the F_1s and their parents.

Materials and Methods

Experiment 1

Experiment 1 consisted of two sub-experiments of the same design. In Experiment 1A, F_1 plants of the cross (Warimek × Halberd), subsequently abbreviated as (Wm × H), were grown in a mixed stand with Halberd at five frequencies 4%, 6.25%, 11.11%, 25% and 50%. In Experiment 1B, (Wariquam × Halberd) F_1s subsequently abbreviated as (Wq × H), were grown in Halberd at the same 5 frequencies. There were four replicates in each experiment. To reduce the numbers of hybrid seeds required, each replicate was planted with the frequencies in ascending order. Hence 4% was always on the outside, the intermediate frequencies were bordered by lower and higher frequencies and the 50% was adjoined by the 50% of the adjacent replicate. The five frequencies of the hybrids could be regarded as consisting of 1 hybrid in successive stands of 5 × 5 plants, 4 × 4, 3 × 3, 2 × 2 and 1 × 2 with Halberd, respectively. Each replicate was surrounded on three sides by four rows of Halberd. The experiments were grown in 1972 at Roseworthy Agricultural College, South Australia. Halberd ≡ ((Scimitar × Kenya C6042 × Bobin) × Insignia 49), used in this experiment as a background stand of plants, is the major commercial variety in South Australia. It is an early maturing variety, of medium height (average 75 cm), with good tillering habit and semi-erect leaves. Warimek ≡ (Mexico-120 × Koda) and Wariquam ≡ (Mexico-120 × Quadrat) are breeders' lines, developed at the Waite Agricultural Research Institute, South Australia. Both of these lines are short (average height 65 cm), erect, with medium tillering habit and early maturing. The F_1s, (Wm × H) and (Wq × H), are of the same height as Halberd, early maturing and with good tillering capactiy. The hybrid seeds were produced in a glasshouse in 1971.

Seeds were sown every 6.7 cm. The distance between rows was also 6.7 cm, giving a density of approximately 222 plants per square metre, which is similar to that used commercially. The positions of the hybrids were marked by small wooden sticks to enable observation of their development from emergence to harvest. At each frequency in each replicate, eight hybrids were chosen at random for observation, except at the lowest frequency, where all the hybrids were recorded. The same number of Halberd plants immediately adjacent to the selected hybrids were also recorded, as it was thought these plants might show an inverse response to frequencies, as compared with the hybrids. At the two lower frequencies, 4% and 6.25%, the Halberd plants at the second position away from the hybrids were also measured to determine the extent of competition of the hybrids.

Experiment 2

During 1972 and 1973, a number of lines from the crosses (Warimek × Halberd) and (Wariquam × Gabo) subsequently abbreviated to (Wm × H) and (Wq × G) respectively, were advanced from F_1 to F_4 by single-seed-descent. At the start of the 1973 season sufficient seeds were obtained from 76 F_4 lines of the cross (Wm × H) and 70 F_4 lines of the cross (Wq × G) to be used in Experiments 2A and 2B, respectively. The F_4 lines, together with the F_1s of both crosses and the four parents were grown at two frequencies, 6.25% and 18.75%, at Roseworthy Agricultural College. Each experiment was a split-plot design, with genotypes as main plots and frequencies as subplots.

Due to the large area of the experiment, 70 × 30 m, it could not be hand sown; instead the seeds were mixed at the relevant frequencies and sown with a cone seeder. The genotype to provide the background stand of plants, Wariquam or Halberd, was chosen to be sufficiently distinct from the hybrid material for it to be identified at maturity.

The distinguishing features were:

(Wm × H) hybrid	: tall, tip-awned, brown heads.
Wariquam background	: short, strongly-awned, white heads.
(Wq × G) hybrid	: medium height, strongly-awned, white heads.
Halberd background	: tall, tip-awned, brown heads.

There were 3 replicates in each experiment. Each 2.50 m plot consisted of 12 rows 10 cm apart. The commercial rate of seeding (70 kg/ha) was used. The cone seeder was constructed to sow two rows from each cell of a seed magazine. In each plot, the 4 outer rows (rows 1, 2 and 11, 12) were borders and consisted of only the background genotype. Two of the remaining 8 rows were sown at the high frequency, 18.75%, and consisted of 15 hybrid plants and 65 background plants. The position of the high frequency was randomized between the 2 pairs of the middle rows (rows 5, 6 or 7, 8). The remaining 6 rows were sown with the hybrid at the low frequency, 6.25%. Each of these 2 rows consisted of 5 hybrid plants and 75 background plants. Fifteen plants per line (F_4 or F_1), per frequency and per replicate were harvested and bulked together.

Results

Experiment 1

Regression analyses of different characters on frequency percentages were performed for the F_1 and adjacent background plants. The mean yield of eight plants per frequency per replicate was used in the regression on frequency.

(i) Experiment 1A: (Wm × H) in Halberd

The results for grain yield per plant of the F_1 and Halberd are shown in Fig.1; and a summary of other characters in Table 1.

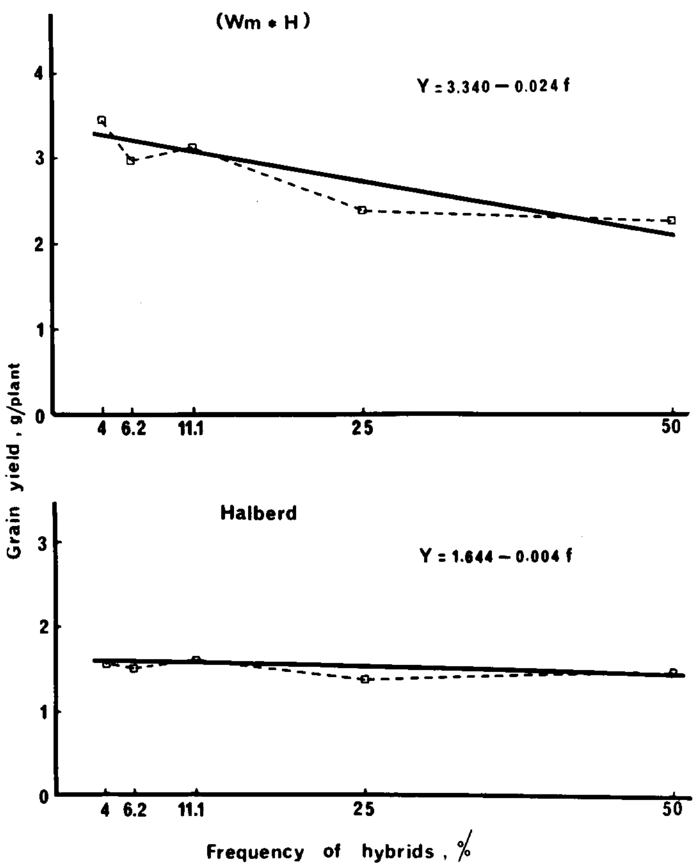

Fig.1. Relation between grain yield per plant of (Warimek × Halberd) F_1 and adjacent Halberd plants with frequency of the hybrid

It was found that hybrid plants at low frequencies yielded more grain than those at high frequencies, thus exhibiting frequency-dependent advantage (f.d.a.). The mean yield was 3.55 g/plant at 4% frequency and 2.26 g/plant at 50% frequency, a reduction of about 36%. Other characters related to grain yield also showed significant reductions with increasing frequencies; notably, number of grains per plant and spike weight per plant.

Figure 1 and Table 1 also show the relationships between morphological characters and frequencies for the Halberd background plants immediately adjacent to the hybrids. It can be seen that none of the regressions was significant and that Halberd plants had similar yields at all frequencies. The mean yield only varied from 1.65 g/plant at the lowest frequency of the hybrid neighbour to 1.45 g/plant at the highest frequency of the neighbour.

(ii) Experiment 1B: (Wq × H) in Halberd

In this experiment, one of the 4 replicates was severely damaged by waterlogging and has been excluded. Again, a significant negative linear regression of yields on frequencies was observed (Fig.2). The regression coefficients for grain yield and other characters for varying frequency are summarized in Table 2.

Grain yield was reduced from 3.54 g/plant at 4% frequency to 2.22 g/plant at 50% frequency, a reduction of 37%. Most of the other characters also showed a significant regression with frequency; especially those measured late in the growth of the plants, including flag leaf area at anthesis, total weight, spike weight, number of spikes, number of spikelets and number of grains per plant.

The Halberd plants as neighbours, again, did not differ significantly with different frequencies of the hybrid; varying only between 1.94 g/plant at the lowest frequency to 1.67 g/plant at the highest frequency of the neighbour. Nor did they show any significant change in other characters with changing frequencies.

Both hybrids were significantly higher yielding than adjacent Halberd plants, especially at the low frequencies. Tables 3 and 4 show the mean performance of each genotype at frequency, 50%. At this frequency, the differences between Halberd and hybrids

Tables 1 and 2. Regression coefficients of (Wm × H) and Halberd, and (Wq × H) and Halberd at 5 frequencies

Character	Table 1 $(Wm \times H) F_1$	Halberd	Table 2 $(Wq \times H) F_1$	Halberd
No. of tillers (8 wks)	-0.006	-0.005	-0.007	0.001
No. of tillers (10 wks)	-0.021	-0.001	-0.019	0.008
Tiller length (8 wks)	-0.025	0.005	-0.020	0.044
Flag leaf area (anthesis)	-0.138	-0.091	-0.092*	-0.041
Total height (maturity)	-0.103	-0.005	-0.070	-0.015
No. of spikes	-0.015	-0.001	-0.018**	0.002
No. of spikelets	-0.276	-0.032	-0.328**	0.024
No. of grains	-0.716*(a)	-0.182	-0.869**	0.009
Total weight	-0.053	-0.009	-0.071**	0.009
Spike weight	-0.030*	-0.004	-0.038**	0.003
Grain weight	-0.024*	-0.004	-0.031**	0.002
Weight per grain	-0.004	0.028	0.019	-0.002

(a)*, **, *** denote significance ($b \neq 0$) at 5%, 1% and 0.1% probability levels, respectively. This notation for statistical significance is used for all tables.

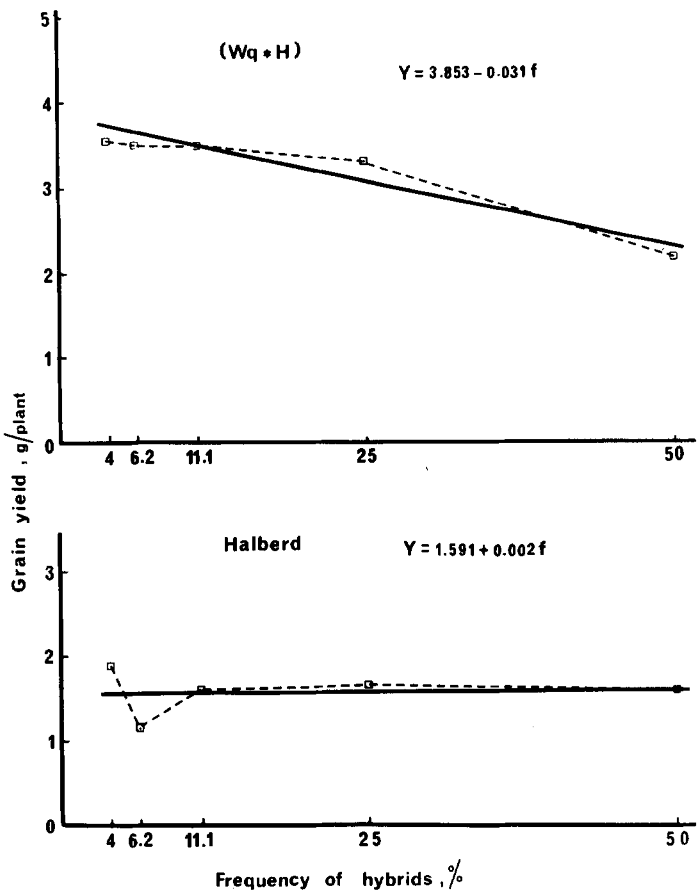

Fig.2. Relation between grain yield per plant of (Wariquam × Halberd) F_1 and adjacent Halberd plants with frequency of the hybrid

were due to genetic effects rather than to any frequency effect, since they occurred in equal proportions. For most of the characteristics, (Wm×H) was significantly different from Halberd at this frequency but (Wq×H) was only different in height at maturity and weight per grain.

Experiment 2

(i) Experiment 2A: (Wm × H) in Wariquam

The analyses for several characters are presented in Table 5. Seventy six F_4 lines of (Wm × H) all showed f.d.a. when grown in a stand of Wariquam. They had higher yields at the low than at the high frequency (Fig.3). The mean yield per line was 41.15 g/plot at the low frequency compared to 25.57 g/plot at the high frequency. This reduction of 38% was comparable to that found in Experiments 1A and 1B although the range between frequencies was less in this experiment (6.25% to 18.75% compared to 4% to 50%). The results in Table 5 indicate that high yield of the hybrids at the low frequency was associated with a greater height, more spikes per plant and a greater total weight.

F.d.a. is also evident in Fig.3 for the parents, Warimek and Halberd, and their F_1. The parents yielded about the same as the mean of the F_4s, whereas the F_1 was among the top 5% of the F_4 lines. The distribution for height of the F_4s, Warimek, Halberd and their F_1 is shown in Fig.4.

The F_4 lines had positive skew distributions for all characters, except height which had a negative skew. Skew distributions of this nature occur commonly in plant competition, especially at high densities (Koyama and Kira 1956). There was also a highly significant correlation between the f.d.a. and the re-

Tables 3 and 4. Comparisons between (Wm × H) and Halberd, and (Wq × H) and Halberd for various plant characters at the 50 % frequency

Character		Table 3 Genotype means $(Wm \times H)\,F_1$	Table 3 Genotype means Halberd	Table 3 Genotypic difference	Table 4 Genotype means $(Wq \times H)\,F_1$	Table 4 Genotype means Halberd	Table 4 Genotypic difference
No. of tillers (8 wks)		3.20	3.20	NS	3.20	3.10	NS
No. of tillers (10 wks)		4.50	5.20	NS	4.30	4.90	NS
Tiller length (8 wks)	cm	18.90	18.20	NS	19.90	19.10	NS
Flag leaf area (anthesis)	cm^2	21.23	24.28	NS	22.32	24.49	NS
Total height (maturity)	cm	76.56	69.92	**	77.16	69.61	**
No. of spikes		2.50	2.00	*	2.37	1.91	NS
No. of spikelets		38.06	27.66	**	33.21	27.09	NS
No. of grains		67.47	46.03	**	61.46	49.04	NS
Total weight	g	5.62	3.89	**	5.23	4.32	NS
Spike weight	g	2.98	1.96	**	2.94	2.21	NS
Grain weight	g	2.26	1.45	**	2.22	1.67	NS
Weight per grain	mg	33.25	31.80	NS	35.82	31.96	*

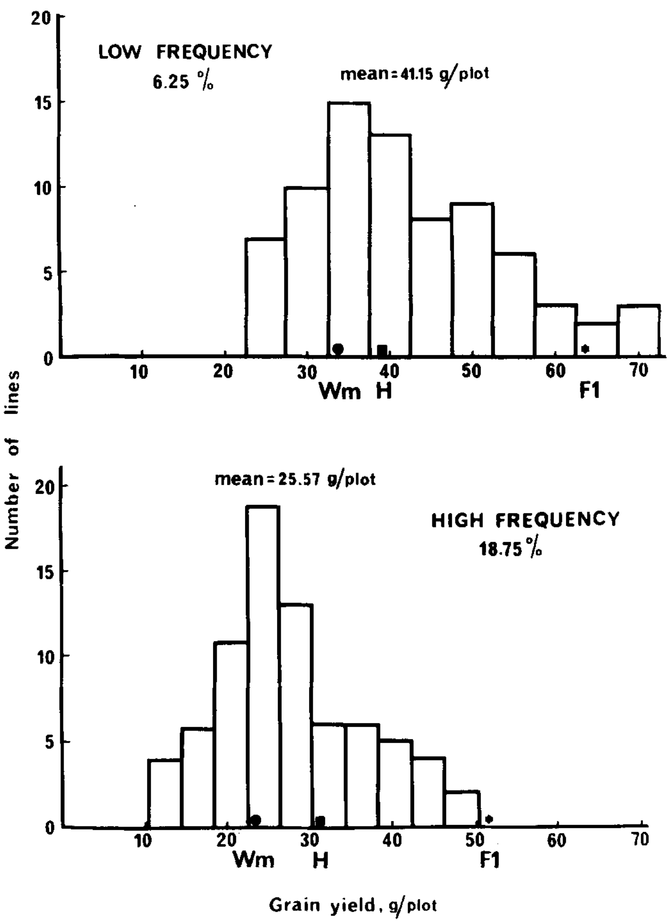

Fig.3. Distribution of 76 F_4 lines of (Wm × H) the two parents and the F_1 at 2 frequencies in a stand of Wariquam. Grain yield per line

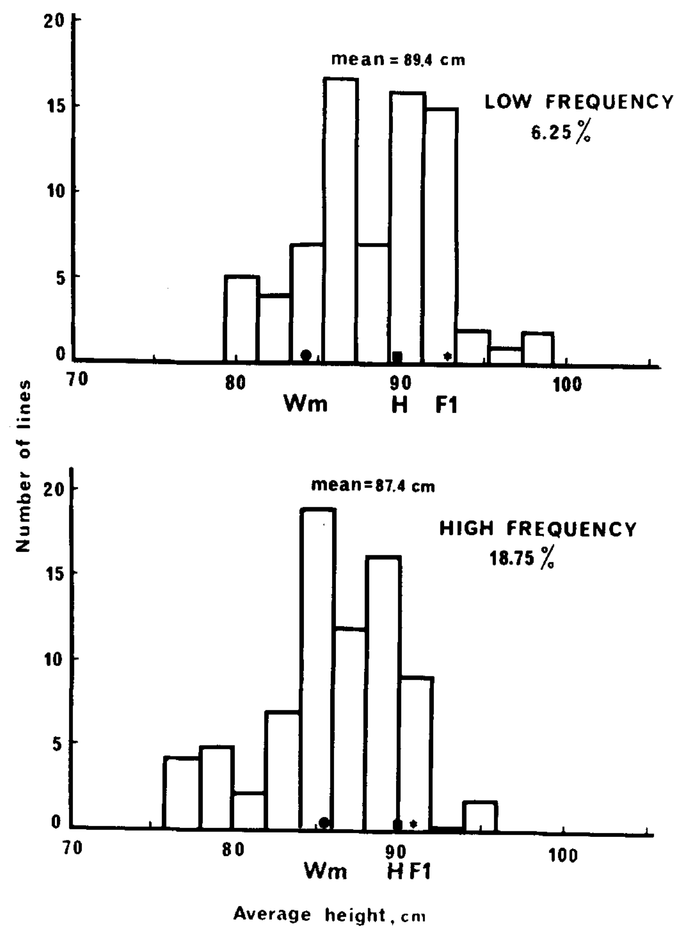

Fig.4. Distribution of 76 F_4 lines of (Wm × H) the two parents and the F_1 at 2 frequencies in a stand of Wariquam. Average height per line

lative competitive ability of these lines. The f.d.a. was estimated by the difference between the yield at low and high frequency, for each line. Competitive ability was assessed as the arithmetic mean of the yields at the 2 frequencies, for each line. This estimation was made because all 76 F_4 lines were competing against the same background, Wariquam. Hence, their mean yields reflected their relative competitive

Table 5. Mean squares for the comparisons of 76 F_4 lines of (Wm × H) grown in Wariquam at 2 frequencies

Source of variation	df	Character				
		Average height	No. of spikes	Total weight	Spike weight	Grain weight
Replicates	2	284.70	2123.60	11229.40	2108.20	321.21
Lines	75	101.89**	893.64***	6871.90***	1430.90***	487.42***
R×L (Error a)	150	56.04	265.28	2159.50	385.38	119.77
Frequencies	1	448.03***	69190.10***	514833.00**	101493.00***	26683.20***
Frequencies×Lines	75	17.25	167.28	1215.40	234.10	68.64
R×F×L (Error b)	152	17.40	163.94	1284.10	253.97	78.83

Table 6. Mean squares for the comparisons of 70 F_4 lines of (Wq × G) grown in Halberd at 2 frequencies

Source of variation	df	Character				
		Average height	No. of spikes	Total weight	Spike weight	Grain weight
Replicates	2	190.39	13.95	20.81	25.26	14.75
Lines	69	214.11***	180.81***	635.58***	87.81**	39.00**
R×L (Error a)	138	102.06	91.38	356.56	51.96	22.92
Frequencies	1	1030.40***	1113.90***	5589.60***	679.62***	270.71***
Frequencies×Lines	69	55.49	41.99	159.91	20.69	8.77
R×F×L (Error b)	140	63.01	48.00	172.81	24.50	11.38

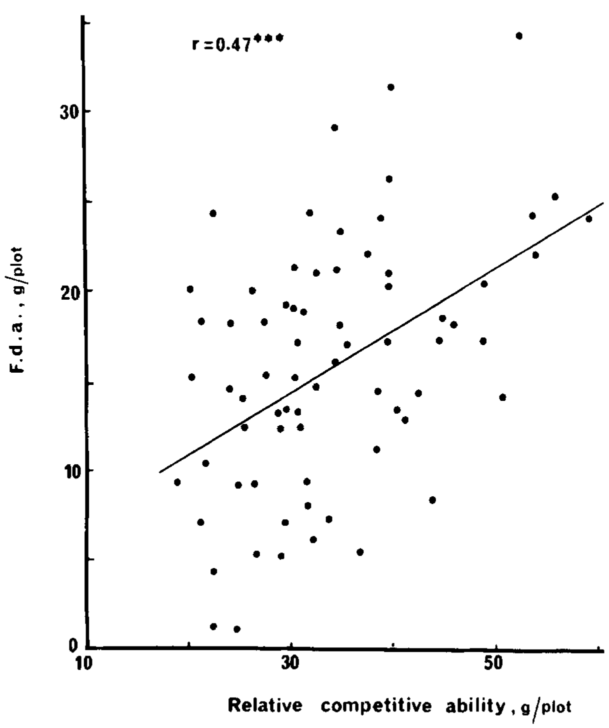

Fig.5. Relationship between f.d.a. (yield at low frequency - yield at high frequency) and relative competitive ability (mean of the yield at 2 frequencies) of 76 F_4 lines of (Wm × H) when grown in Wariquam at 2 frequencies. Y = 4.004 + (0.349) X

abilities. The correlation coefficient was 0.47 and was significant at the 0.1% level (Fig.5). The positive correlation suggests that highly competitive genotypes tended to be more likely to exhibit f.d.a.

(ii) Experiment 2B: (Wq × G) in Halberd

The results in Experiment 2B were similarly analysed (Table 6). Most of the F_4 lines of (Wq × G) had higher yields at the low frequency than at the high frequency (Fig.6). F.d.a. was also expressed by the parents, Wariquam and Gabo, and their F_1. Wariquam was slightly better than the F_1 and both were among the 25% highest yielding F_4s. Gabo was among the lower 30% of the F_4 lines. The higher yield at the low frequency was associated with a higher expression of other characters at this frequency.

The distribution for height (Fig.7) had a significant negative skew, whereas the distribution for other characters had a strong positive skew.

The F_4 lines showed very low yields, averaging 6.16 g/plot and 4.43 g/plot for the low and the high frequencies, respectively; and many plants failed to survive to maturity. One explanation is that in 1973 the variety, Halberd, was heavily infected with rust (*Puccinia graminis* f.sp. *tritici*). Some of the F_4 lines grown in this stand were severely infected, resulting in a large number of low yielding lines. The reduction in yield in this experiment from the low to the high frequency was about 28%.

The correlation coefficient between f.d.a. and competitive ability was 0.38 and was significant at 1% level (Fig.8). Although the analysis of variances indicated that the 70 lines had higher yields at the

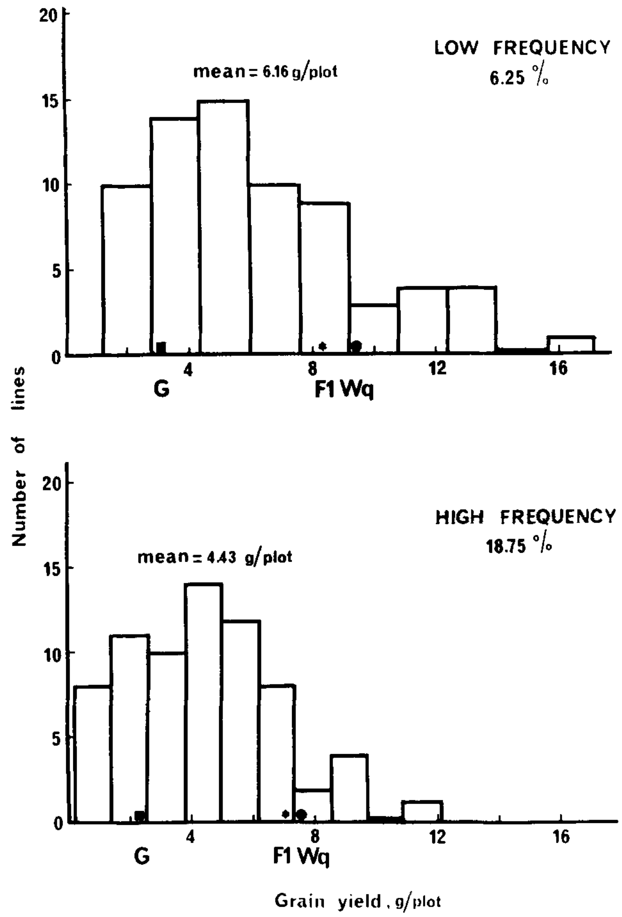

Fig.6. Distribution of 70 F_4 lines of (Wq × G) the two parents and the F_1 at 2 frequencies in a stand of Halberd. Grain yield per line

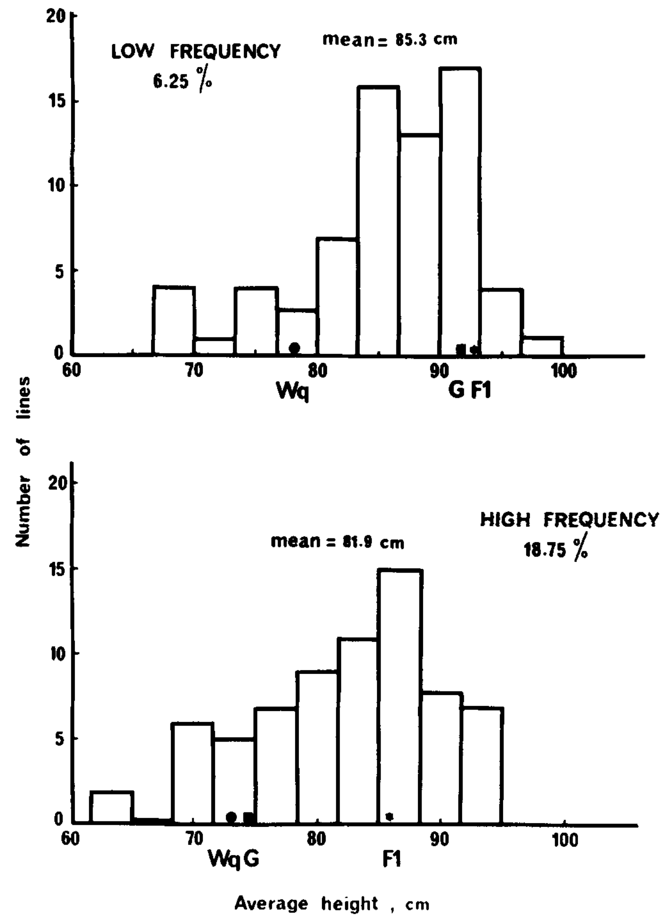

Fig.7. Distribution of 70 F_4 lines of (Wq × G) the two parents and the F_1 at 2 frequencies in a stand of Halberd. Average height per line

low frequency, the interactions between frequencies and lines were non-significant (Table 6). Figure 8 shows that some of these lines did have higher yields at the high frequency.

Discussion

Both of the present experiments were designed to determine if growing a genotype at different frequencies in a mixture resulted in differences in the yield of single plants of that genotype. In all four cases, frequency-dependent advantage was demonstrated, and increasing the frequency of the genotype from a low (4% or 6.25%) to a moderate frequency (50% or 18.75%) was associated with a reduction in grain yields ranging from 28% to 38%. As the response from 50% to 4% was linear, it is likely that at even lower frequencies the advantage would be greater.

That the occurrence of f.d.a. might be common is supported by the fact that it was obtained under different conditions. The seasons, 1972 and 1973, were quite different. The former had a below average rainfall and a relatively short period of crop growth, during the latter rainfall was appreciably above average. Also, Experiment 1 was grown as spaced plants in small plots, whereas Experiment 2 involved a large number of genotypes grown in large contiguous plots resembling a commercial crop. Although each experiment was conducted in only one environment, a similar response to frequency was observed for the (Wm × H) F_1 in both years, over different ranges of frequencies and in different mixtures, suggesting a consistency of the results. Furthermore, the same cross, (Wm × H), was used again in a third trial in 1974 during the investigations of the role of f.d.a. in single plant performance in a simulated F_2. In this latter season, a mean reduction of 19% was measured with 25 F_5 lines as the frequency increased from 4% to 16%. (This work is being prepared for publication.)

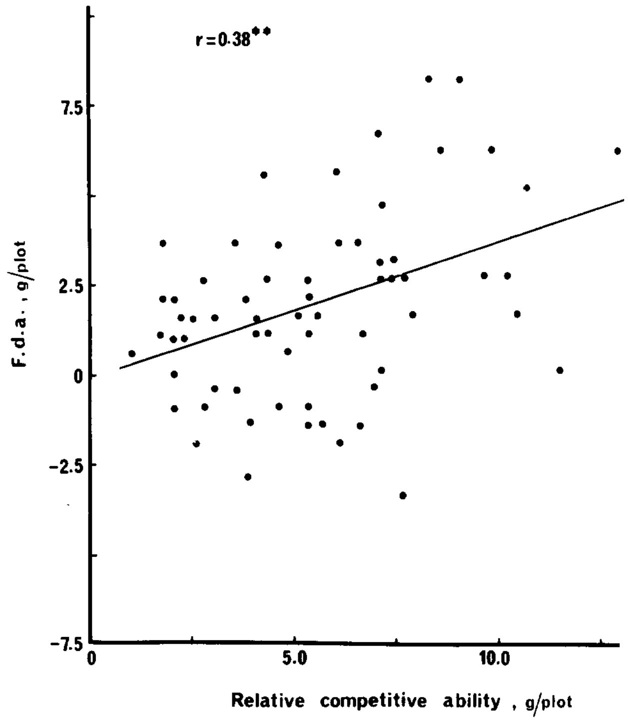

Fig.8. Relationship between f.d.a. (yield at low frequency - yield at high frequency) and relative competitive ability (mean of the yield at 2 frequencies) of 70 F_4 lines of (Wq × G) when grown in Halberd at 2 frequencies. Y = -0.135 + (0.346) X

Two other crosses (Warimek × Timgalen) and (Wariquam × Gabo), were grown in an adjacent experiment in 1972 and a significant f.d.a. was measured with the former but not the latter. Thus, on the grounds of the data presented here, and those subsidiary unpublished results, it would seem reasonable to conclude that f.d.a. is a common but not universal factor in the growth of mixtures of wheat in South Australia.

One major restriction of using hybrid seeds was that they were available in limited numbers. Hence, it was not possible to allocate the different frequencies (Experiment 1) in a completely randomized design as this would have required considerably more hybrid seeds for the borders, especially at high frequencies. This was overcome by growing the frequencies in ascending order, although one criticism of such a design was that the differences in yield of the hybrids at different frequencies could have been a systematic effect if there had been a fertility trend in the same direction as frequencies. However, the non-significant regression of the Halberd plants (Tables 1 and 2) with frequency indicated that this was not a factor. Furthermore, the results for each replicate separately showed that the hybrids had higher yields at the low than at the high frequency. It was unlikely that a similar trend in soil fertility occurred in all 4 replicates.

Since grain size did not change with frequency (Tables 1 and 2), the changes in grain yield were associated closely with changes in the number of grains per plant, which, in an agricultural population, is the factor most commonly influencing the fitness of the genotype (Palmer 1952; Suneson 1949). Hence, the f.d.a. represents the action of frequency-dependent selection in a single generation.

The results of Harding, Allard and Smeltzer (1966) for lima bean were much more pronounced than for the work reported here. In mixtures of hybrids and parents, the test genotype, a hybrid, had a yield reduction of 66.7 % as their frequency increased from 2 % to 16 %. At the latter frequency, it was found that the fitness of the hybrids was equal to those of the parents. Khalifa and Qualset (1974) found that when two genotypes of wheat were mixed in all combinations at 12.5 % frequency increments, grain yield of the stronger competitor was reduced from a relative value of 1.33 at 12.5 % frequency to 0.80 in pure stand, a reduction of 39.8 % which is comparable to the present findings. However, its yield in pure stand was lower than that of the poorer competitor by 20 % (reproductive value = 1.00).

As a marked f.d.a. effect was evident in Experiment 1, it was expected that the neighbouring background plants might show an inverse effect; that is a reduced yield when neighbouring a plant at low frequency. In fact, the plants showed no significant trend. An explanation is that the Halberd plants were not grown at low frequencies but between 50 % and 96 %; hence, they were almost always in competition with like genotypes at all frequencies of the test plant. This was evident by the non-significant difference in the yield of the Halberd immediately adjacent and in one position removed at the two lower frequencies of the hybrid. The mean yields were 1.73 and 1.80 g/plant respectively for the (Wm × H) experiment, and 1.70 and 1.66 g/plant for the (Wq × H).

During the growth of plants in Experiment 1, measurements were made of plant characters which can be used as indicators of vigour. Besides yield, yield components, and mature plant height, all the other measurements (Tables 1 and 2) had regression coefficients with the same sign as that for grain yield. In the later stages of growth these measurements were statistically significant. Thus, the f.d.a. would appear to result from a gradual amplification of an early advantage gained by the genotype at low frequency.

It is unlikely that either final plant height or time of maturity is a major factor in f.d.a. Differences in plant height are only expressed after stem elongation, and in a Mediterranean type of climate, where there is ample illumination in the latter part of the season, any advantage through additional light interception is likely to be negligible. Also, the f.d.a. was nearly as large in Experiment 2B, where most of the hybrids were shorter than the background Halberd, as it was in Experiment 2A, where the hybrids were taller than Wariquam. Furthermore, in the same experiment, consistent differences in maturity were absent.

The highly significant correlations between the mean yield and the f.d.a. of the lines in Experiment 2 are notable, (Figs. 5 and 8). The estimates of f.d.a. for practically all the lines were positive, despite the relatively small range in frequencies (effectively 12.5%). The highly consistent increase in yield associated with the lower frequency resulted in the very highly significant variance ratios for frequency in Tables 5 and 6. The absence of any significant interaction in the same tables supports the generality of the conclusion that f.d.a. is widespread in wheat.

Acknowledgements

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