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Grain yield in Composite Cross Five of barley: effects of natural selection

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SUMMARY

A range of three generations from each of three populations of Cambridge Composite Cross Five of barley spanning a period of 18 years of cultivation in Cambridge was evaluated for grain yield over 2 years in the field in 1991 and 1992. The design of the experiment was a randomized complete block with two replications. In 1991, the yield of the best composite cross generation was 78% that of Atem, a commercial variety bred for N.W. European conditions. In the drought-affected year, 1992, three of the composite cross generations performed better than Atem. It is suggested that composite cross populations may be useful in deriving lines for low-input agriculture.

INTRODUCTION

Ever since composite cross breeding was advocated as a cheap and efficient plant breeding method (Allard & Hansche 1964), plant breeders have exploited the method in several environments to investigate its applicability in breeding programmes. Bulk breeding assumes that natural selection will, over time, evolve superior genotypes of self-pollinated plants (Harlan & Martini 1929; Suneson 1956; Allard 1960). The procedure allows natural selection to increase the frequency of genotypes well adapted to prevailing conditions at the expense of poorly adapted kinds. The rate at which this proceeds, depends on the degree of selection pressure applied, the consistency of that pressure, and the heritability of the trait, or traits, under selection. In annual species, the most highly adapted genotype is defined as the one that produces the most seeds per unit of time (Quinsenberry *et al*. 1978). This, however, is not generally true. According to Endler (1986), there are problems in defining precisely what adaptedness is so that it can be measured. He argues that one solution is to define it in the sense of absolute fitness. Adaptedness, therefore, is a measure of the average absolute contribution to the breeding population by a phenotype or a class of phenotypes. The primary assumption underlying the use of bulk population breeding is that the most competitive genotypes in the bulk will be the most productive in pure stands. However, tests of this assumption have produced varied results (Suneson & Wiebe 1942; Adair & Jones 1946, Mumaw & Weber 1957; Jennings & Aquino 1968; Tucker & Webster 1970). Consequently, many plant breeders focusing on techniques for improving the efficiency of selection and testing have neglected, or overlooked, composite crosses as exploitable populations.

Genetically uniform cultivars produced from simple crosses in barley, wheat and many cultivars of self-pollinated species, give both high and stable yields, and such cultivars dominate commercial production (Soliman & Allard 1991). However, these cultivars are not high yielding by themselves. They are high yielding only in certain environmental conditions and under particular agronomic practices. The socio-economic pressures that have created the move towards intensive agriculture has led to serious environmental problems such as water, soil and air pollution, soil erosion and restriction of animal welfare and loss of rural communities. A major problem with monoculture is the persistent difficulty in the control of important plant diseases (Wolfe 1992).

There are a number of breeders who still exploit the bulk breeding method because they work in environments where bulk breeding provides a suitable alternative, if not a better way of producing crop varieties (Hensleigh *et al*. 1992). A number of issues, however, remain unclear about these populations, especially with respect to their yielding ability. Although a number of studies have demonstrated

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yield increases with time in composite cross populations, others have postulated that there is a limit beyond which composite cross populations will not improve for yield and that the diversity of the base population determines this limit. There are still others who believe that most of these populations regress towards weed-like types (Grafius 1971), however, this is not a universal observation.

In any environment, it is essential that the changes occurring with time are investigated to evaluate the strengths and weaknesses of this method. Although the desire for uniformity makes composite cross populations unacceptable in many commercial systems, there are several places where uniformity is not the most important criterion for example, in many farming systems in the tropics where stability of yield may be more important. These populations could, therefore, play an important role in many agricultural systems. Wide diversity in base populations allows specific environments to select suitable genotypes.

The objective of this study was to determine whether yield has improved in Composite Cross Five (CCV) of barley grown at Cambridge after 18 years of cultivation.

MATERIALS AND METHODS

CCV of barley was developed between 1937 and 1940 by hierarchical crossing of 30 diverse accessions from the USDA collection of barley (Suneson 1956). The bulk hybrid seeds were designated F_1 and subsequent generations have been grown at Davis, California since 1941. The material has been maintained as discrete generations in large populations with no conscious selection (Jain & Allard 1960). In 1974, large samples of seed from F_{10}, F_{20} and F_{30} generations of Californian CCV were used to establish three parallel populations in Cambridge, UK. These populations are referred to as Populations 1, 2 and 3 of Cambridge CCV (CCCV) respectively (Luckett & Sharif 1987; Ibrahim *et al.* 1996).

The plant material used in this study were F_{12}, F_{18} and F_{24} for Population 1, F_{22}, F_{28} and F_{34} for Population 2 and F_{32}, F_{38} and F_{44} for Population 3. Atem, a variety on the UK National List at the time of the experiment, was included as a check variety. Two experiments were carried out in the summers of 1991 and 1992. The experimental design in both cases was a randomized complete block with two replicates. Each block comprised 20 plots. Plots consisted of six rows, which were 50·8 cm apart. Spacing between plots was 60 cm. The nine generations and Atem were randomly assigned to plots within blocks. Thirty seeds were sown per row at 3·8 cm spacing giving a total of 180 seeds of each treatment per plot. The plots were protected with a net supported on steel poles. No fertilizers and chemical were applied. At maturity, the number of plants surviving to reproductive age was counted. The entire plot was harvested and plot yield kept separately. Threshing was done by machine (Almaco, US).

Data analysis

Analysis of variance was first used to evaluate total grain yield. A mixed model was assumed with sowing year (year experiment was sown) and blocks as random and generations and Atem considered as fixed effects. In a second analysis, the number of plants per plot was used as a covariate in the analysis of variance. Orthogonal polynomials were also calculated to determine the type of relationship that existed among populations and the interaction of these relationships with years and environment. Where the F values indicated significant differences, means were compared to determine where the differences lay.

RESULTS AND DISCUSSION

The analysis of variance for total plot yield is shown in Table 1. The analysis showed that sowing year (syear), Atem *v.* CCCV, syear × (Atem and CCCV), generation year (year bulk was grown in Cambridge (gen)), populations (pop), syear × gen, syear × pop, syear × gen × pop were all significant sources of variation. The significant interaction terms involving sowing year and the main effects indicate the presence of G × E interactions. This was confirmed by the different rankings of the generations and Atem in the two environments. These results suggest that genetic, environmental and G × E effects are important in seed yield which is not unexpected.

Significant differences between Atem and the mean of the nine generations and the significant effect of populations suggested genetic differences. However, grain yield was based on different numbers of surviving individuals. It was, therefore, possible that differences in yield could be due to the correlation between the number of individuals surviving and grain yield. Analysis of covariance was used to adjust seed yield for differences in the number of plants surviving to reproductive age (Table 2). When this was done, the F value for environment was not significant indicating that covariance composes a very large proportion of the previously significant effect of the year in which the experiment was sown. This suggests that the differences in yield between Experiments 1 and 2 were mainly due to differences in the number of surviving plants. The F values for gen, syear × gen, syear × pop remain significant but at the 5% level. It is, however, clear that covariance adjustment did not appear to remove the significant effects associated with Atem *v.* CCCV generations, syear × Atem and CCCV generations, population and the interaction of syear × gen × pop.

Table 1. *Analysis of variance of total grain yield of the nine generations and Atem over 2 years*

Source	D.F.	MS
Sowing year (Syear)	1	2002357·0**
Residual	2	20849·0
Atem *v.* CCCV	1	405550·0***
Syear (Atem & CCCV)	1	202814·0***
Generation year (Gen)	2	36470·0***
Population	2	177865·0***
Syear × Gen	2	23544·0**
Syear × Population	2	25097·0**
Gen × Population	4	5196·0
Syear × Gen × Population	4	20729·0**
Residual	18	3792·0

, * Significant at the 0·01 and 0·001 probability levels respectively.

Table 2. *Analysis of covariance of total grain yield of the nine generations and Atem over 2 years*

Source	D.F.	MS	Covariate efficiency
Sowing year (Syear)	1	882913·0	0·56
Covariate	1	30606·0	
Residual	1	11091·0	1·88
Atem *v.* CCCV	1	105161·0***	0·27
Syear × Atem & CCCV	1	178876·0***	0·89
Generation year (Gen)	2	21105·0*	0·48
Population (Pop)	2	92313·0***	0·69
Syear × Gen	2	17276·0*	0·86
Syear × Pop	2	22655·0*	0·93
Gen × Pop	4	3857·0	0·91
Syear × Gen × Pop	4	20494·0**	0·80
Covariate	1	44·0	
Residual	17	4013·0	0·95

*, **, *** Significant at the 0·05, 0·01 and 0·001 probability levels respectively.

The analysis was taken a stage further by calculating orthogonal polynomials to determine the type of relationships that existed between the interaction of populations, years and environment. It is interesting to note that only the linear × population × gen × syear interaction was significant (Table 3). This interaction was caused by differences in the relative magnitudes of the generation means. Although there are a few changes in the mean ranking among generations, the main source of interaction is, probably, differences in response of the generations to the different years.

The data on grain yield (g/plot) of the nine generations and Atem are shown in Table 4. Yields varied considerably between the two years. For example, the yield of Atem (which was the highest in 1991) was 2466·1 g per plot. In 1992, the yield was as low as 716·7 g per plot and was the fourth in ranking after IIIF_{44}, IIIF_{32} and IF_{12}. Mean yield over the 2-year period between Atem and the mean of the CCCV generations differed significantly according to LSD. All of the CCCV generations and Atem gave better yields in 1991 than 1992 indicating that 1991 was generally a better year for grain yield. Changes in yield over time within the three populations did not reveal steady increases. There was a marked decline in yield between the earlier generations for all three populations followed by an increase in yield in the advanced generations. This trend was not correlated with the number of surviving plants.

The study revealed that, on average, the control variety out-yielded the composite cross generations over the 2-year period in the Cambridge environment. The highest yielding composite cross generation over the period of the experiment was the advanced generation of population III, F_{44} which was only 78% of the yield of Atem. It is interesting to note that in the 1992 season three of the composite cross generations performed better than Atem. These were

Table 3. *Analysis of variance of total grain yield of the nine generations showing linear and quadratic effects*

Source	D.F.	MS
Sowing year (Syear)	1	1440044·0**
Residual	2	14920·0
Population	2	177865·0***
Generation year (Gen)	2	36470·0**
Syear × Population	2	25097·0**
Syear × Gen	2	23544·0*
Population × Gen	4	5196·0
Linear	2	2745·0
Quadratic	2	7648·0
Syear × Pop × Gen	4	20379·0**
Linear	2	28296·0**
Quadratic	2	13162·0
Residual	16	3988·0

*, **, *** Significant at the 0·05, 0·01 and 0·001 probability levels respectively.

Table 4. *Mean grain yield (g/plot) of Atem and a range of generations from three CCCV populations grown in the field over 2 years*

Cultivar/CCCV	1991	1992	2-year Mean	% of Atem
Atem	2466·1	716·8	1591·4	100·0
IF_{12}	945·2	722·9	834·1	52·4
IF_{18}	928·9	102·6	515·8	32·4
IF_{24}	1184·5	451·5	817·9	51·4
IIF_{22}	1247·7	393·9	820·8	51·6
IIF_{28}	1240·4	301·3	770·9	48·4
IIF_{34}	1463·8	426·9	945·4	59·4
$IIIF_{32}$	1678·8	785·5	1232·2	77·4
$IIIF_{38}$	1712·8	483·9	1098·3	69·1
$IIIF_{44}$	1479·2	1012·7	1245·9	78·3
Mean of CCCV	1320·1	520·1	920·1	57·8

$IIIF_{44}$, $IIIF_{32}$ and IF_{12} (Table 3). This change in ranking was probably due to environmental conditions during the 1992 season. There was a long period of drought, which may have affected Atem more than the composite cross populations. Atem is a cultivar selected for high input systems so the poor yield during the 1992 season was not unexpected and any interpretations must be made with caution. However, the observations agree with reports in the literature, which indicate that composite crosses are in general more stable than most commercial cultivars (Soliman & Allard 1991) evaluated 11 composite cross generations and a commercial variety, Sutter in California and found that none of the composite cross generations out-yielded Sutter. Hockett *et al.* (1983) however, provided evidence that the best contemporary varieties at Bozeman and Moccassin did not out-yield the best CCII populations developed at those places.

The trends in yield of the three populations were the same. Yields of the early generations were higher than the middle generations, which were in turn lower yielding than the advanced generations. The trend appeared to be uncorrelated with the number of surviving plants. These results appear to contradict the marked steady increase in yield reported for composite crosses over time (Jain & Qualset 1975; Lohani 1975; Mak & Harvey 1982). A number of reasons can account for this. It is possible that the 1981 year of seed production was an exceptionally poor year and this may have led to very poor seed yield. Luckett (1982) also raised this possibility when he recorded that yields of his 1981 experiments were poorer than the 1982 experiments. It is possible that the age of the seed used in the experiments could have affected plant vigour or establishment. The early generations were rejuvenated seed in 1989 and the advanced generations were from 1988 seed. It is, therefore, possible that the 1981 middle generations were too old and this may have affected seedling vigour and establishment adversely. Rejuvenation of the early generations could also have led to intense selection leading to higher yielding genotypes, but it is questionable how one year of selection could possibly lead to an effect comparable to 13 years of selection. 1989 could also have been an exceptionally good year and, therefore, could have led to very good seed. Another possibility is that all of the three populations declined in yield following introduction from California during the first 6 years of acclimatization at Cambridge and, thereafter, began to increase in yield. All of these reasons are possible but none completely explain the data.

It is the general belief that genetic diversity often leads to stability under varying environmental conditions. Relatively little yield improvement, however, has been realized in later generations of most composite cross populations (Soliman & Allard 1991). If genetic variability remains in the advanced generations of such populations, it should be possible to select high-performance homozygous genotypes from composite crosses. Harlan *et al*. (1940) purified lines from CCII at F_8 generation and found them equal to lines developed from the parents of CCII by the pedigree method. At least 19 barley cultivars have already been selected from composite crosses (Eslick 1977). Barley is, however, cultivated in several low input areas in many developing countries and composites could still serve a useful purpose where objectives such as yield stability and disease resistance are more important than yield per se. In high input areas, breeders could exploit composite crosses by selection of individual lines from advanced generations and evaluation of such lines in breeding programmes for low-yielding environments. Futhermore, breeders could upgrade existing composites by continually incorporating modern elite material by hybridizations, perhaps utilizing male sterility.

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