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Genetic and environmental contributions to bread-wheat flour quality using the SDS sedimentation test as an index

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Abstract. The contribution of a locus to the genotypic variance depends not only on the effects of its genes but also on their frequency and on the genetic background in which it segregates. In two synthetic populations, involving common cultivars of our collection, estimates were made of the contributions of alleles at the homoeologous high-molecular-weight glutenin (HMW) loci, *Glu-A1*, *Glu-B1*, and *Glu-D1*, to the variation in flour quality using SDS sedimentation as an index. These estimates were of the magnitude of the contributions relative to each other, relative to the residual genetic variance, and relative to the environmental variance. The first population was a synthetic formed from ten bread-wheat cultivars known for their good quality, and selected under forced random mating for high SDS sedimentation. The second was the selfed progeny of a cross of Ribereño, a very poor quality bread-wheat of genotype (Null, 7–8, 2–12), with line 7681, a very good quality bread-wheat with the genotype (2*, 7–9, 5–10). Slightly over one-half of the phenotypic variance is under genetic control and over one-half of this was accounted for by HMW contributions. The initial response to selection was very rapid, as is expected when genes with large effects are involved. In addition, the frequencies of good HMW alleles increased so quickly that their contribution to the genetic variance was exhausted by the fourth generation of selection. If our estimates are correct, over one-half of the maximum possible advance in quality in heterogeneous populations similar to ours can easily be achieved in 2 years, or less, of marker-assisted selection.

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Introduction

Recently a considerable number of significant positive associations between wheat flour quality indices and endosperm proteins have been reported. The majority of these have involved high-molecular-weight (HMW) glutenin subunits and flour quality indices such as Zeleny, SDS sedimentation, loaf volume and alveograph, farinograph and extensograph measurements.

Three main types of materials have been used most frequently in studies of this sort: (1) segregating populations of varying degrees of inbreeding, F_2–F_8, obtained through self fertilization of a cross of two cultivars usually of contrasting qualities (Payne et al. 1979, 1981, 1984, 1987; Moonen et al. 1982, 1983; Lorenzo et al. 1987; Gupta and Shepherd 1987; Lagudah et al. 1988; Carrillo et al. 1990); (2) collections, of variable size, of homozygous and homogeneous cultivars (Payne et al. 1979; Bournof and Bouriquet 1980; Moonen et al. 1982, 1983; Branlard and Dardevet 1985a, b; Lawrence et al. 1987), and (3) populations obtained through more sophisticated techniques such as random mating, or else near-isogenic lines, chromosomal substitution lines, or interspecific crosses (Lagudah et al. 1987; Payne et al. 1987; Zemetra et al. 1987; Dong et al. 1991).

In most cases, after genotyping and scoring for the index used, the materials have been repeatedly grouped into two sets, each with a specific genotype. The differences between the mean scores of the two sets are then tested statistically for significance. Using these

methods, it has been possible within each HMW locus to establish rankings of alleles based on their contributions to flour quality. Several different quality indices have been used, and the consistency of some rankings reflect the positive correlations between indices. Some of the rankings reported are:

(1) *Glu-A1* locus. 1 > Null (Payne et al. 1981, 1987; Lagudah et al. 1988; Carrillo et al. 1990); 2* > 1 > Null (Moonen et al. 1982, 1983); 2* = 1 > Null (Payne et al. 1984; Branlard and Dardevet, 1985a, b); 1 ≧ 2* (Lorenzo et al. 1987); 2* = 1 = Null (Dong et al. 1991).
(2) *Glu-B1* locus. 7–8 = 17–18 = 13–16 > 7–9 > 7 ≧ 6–8 (Payne et al. 1984); 7–8 > 17–18 (Lorenzo et al. 1987; Lagudah et al. 1988; Carrillo et al. 1990); 7–8 > 13–19 (Lorenzo et al. 1987).
(3) *Glu-D1* locus. 5–10 > 2–12 (Payne et al. 1981, 1984; Moonen et al. 1982, 1983; Branlard and Dardevet, 1985b; Lagudah et al. 1987, 1988; Lawrence et al. 1987; Lorenzo et al. 1987; Carrillo et al. 1990).

The inconsistencies of some of the rankings reported are most likely due to either different genetic backgrounds, epistasis, genotype-environment interactions, or simply to very small differences.

With only two exceptions, the authors referred to above do not provide rankings or explicit comparisons between the contributions of alleles at different HMW loci, or estimates of how much of the genetic control of flour quality, if any, is not accounted for by HMW loci.

Carrillo et al. (1990) used a set of F_8 highly-inbred recombinant lines derived from the bread-wheat cross Anza (Null, 17–18, 2–21) × Cajeme (1, 7–8, 5–10), which are recognized as poor and good quality bread-wheats respectively. Their results were expressed at the linear level with HMW gene effects α_i, rather than $\Sigma\alpha_i^2$ or variances. Using the ratio $\Sigma\alpha_i/\delta$ of the sum of gene effects of the best genotype (222 in their notation) over the difference between the parents, they obtained SDS sedimentation ratios of 0.18 for all the effects, and 0.32 for the main effects only. They conclude that the portion of the total genetic variability accounted for by HMW loci is relatively small. However, since $\Sigma\alpha_i$ is the deviation of the best genotype from the mean of all genotypes, it could be argued that it would be more correct to divide $\Sigma\alpha_i$ by $\delta/2$, one-half the difference between the parents, rather than by δ the entire difference. Calculating these ratios in this way, gives 0.36 and 0.64, which are considered significantly large estimates by breeding standards. Carrillo et al. (1990) report significant epistatic interactions between all three HMW loci.

No estimates of the environmental contribution to quality were reported because, working at the linear level of gene effects, the environment is assumed to be a random effect, and it is impossible to estimate its contribution to quality. As breeders design their breeding strategy, it is critical to know whether quality is under strong genetic control, under strong environmental control, or somewhere in between.

Dong et al. (1991) used a synthetic population obtained from the random mating of an original collection of 85 cucltivars. Three quality indices were used, and an analysis of the total variance showed highly significant contributions of the *Glu-B1* and *Glu-D1* loci, an interaction of the *Glu-A1* and *Glu-B1* loci, and a residual genetic component. Estimates were not reported of the magnitude of these contributions or of how much of the total genetic variance is accounted for by HMW loci, or by the environment.

The present paper reports that using two synthetic populations, the environmental and genetic contributions to quality can be separated, and the genetic contribution can be divided between HMW and residual genetic components. This was accomplished by first selecting for quality within a forced random-mating synthetic population and estimating changes in HMW allelic frequencies, and then subsequently, by analysing the phenotypic variance of a completely balanced inbred population that was the progeny of a cross of two cultivars of extreme contrasting qualities. Zeleny and SDS sedimentation analyses were used as quality indices.

Materials and methods

Outbred population

The names, origins and genotypes of the 11 cultivars selected for the basic synthetic population are given in Table 1.

Starting with this collection the synthetic outbred population was developed at follows:

1975. Two cycles of random mating without selection.
1976–1979. Four cycles of selection. Spring: 400 kernels planted, a single kernel to a hill. Summer: Zeleny sedimentation anaylsis of the progenies and selection of the best 40. Fall: random crosses in the Greenhouse of the 40 selections (sib kernels) to obtain 400 kernels for the next generation.
1980–1991. Cycles of selfing without selection. Planting one head to a hill and harvesting a single head per hill.

All cultivars were selected because of their good quality except in the case of Siete Cerros, which was selected because of its excellent yielding ability. Spring generations were grown outdoors in Aranjuez (Madrid, Spain) and Fall generations either in the greenhouse in Madrid or outdoors in Illora (Granada, Spain).

A total of 39 lines and two samples of each line were scored for SDS sedimentation in 1988 and 1990.

Inbred population

Ribereño (Null, 7–8, 2–12), a cultivar known as an extremely poor quality bread-wheat, was crossed in 1985 to Line 7681 (2*, 7–9, 5–10) which had shown the highest SDS sedimentation

Table 1. Parents of the outbred population. Origins, genotypes and allelic frequencies

Cultivar	Origin	Genotype									
		Glu-A1			*Glu-B1*					*Glu-D1*	
		1	2*	Null	7	7–8	7–9	13–16	17–18	5–10	2–12
Inia 66	Mexico	+						+	+		
Jaral	Mexico	+				+					+
Ciano	Mexico	+							+	+	
Cajeme	Mexico	+							+	+	
Noroeste	Mexico	+							+	+	
Siete Cerros	Mexico		+						+		+
Ariana	Spain		+				+			+	
3048	Spain		+			+				+	
Compadre	Spain			+	+					+	
Chris	USA		+				+			+	
Kafue	Rhodesia		+						+	+	
Allelic frequencies:		0.46	0.46	0.09	0.09	0.18	0.18	0.09	0.46	0.82	0.18

value in the outbred population in 1984. All F_2 kernels were planted, one kernel to a hill, in the fall of 1985. Four more cycles of selfing during 1986–1987 were accomplished. A single head from each hill was planted, one head to a hill. In 1988, eight lines homozygous for each of the eight possible recombinant genotypes were selected. Homozygosity was determined by examining ten kernels of each line. The 64 selected lines, each coming from a different F_2 kernel, were maintained one head to a hill in 1988, 1989, 1990, 1991 with outdoor Spring planting, and each year two samples of each of the lines were scored for SDS sedimentation.

Flour quality

The standard A.A.C.C. Zeleny sedimentation index was used for selections in the outbred population. From 1984 onwards we used a modified SDS sedimentation index involving:

(1) Whole grain meal obtained by grinding the sample in a UDY mill with a 1.00 mm sieve.
(2) A water solution of lactic acid and SDS as in Axford et al. (1979).
(3) Six hundred milligrams of meal mixed with 10 ml of solution in a 10 ml cylinder. Using this method a single head can be scored and sufficient remnant seed is available for crosses, increases, etc. Graduated cylinder readings were scroed and expressed in ml $\times 10^2$.
(4) Soaking period, the mixture was left soaking overnight.
(5) Shaking period, 10 min in a mechanical shaker.
(6) Resting period, 15 min.
(7) Sedimentation volume scored.

In the conventional SDS index the soaking period is only 20 min. We extended it overnight because we noticed that, in a test conducted in 1984 using a 20-min soaking period, Ribereño demonstrated an SDS sedimentation value very near to that of line 7681. This was not consistent with Ribereño's known quality. Subsequently, shaking and resting periods were repeated with the same samples but with 1-h intervals between readings, and the sedimentation values scored. The results are shown in Table 2.

The data suggest that extended soaking periods result in more accurate determinations of quality differences between lines.

Statistical analysis

The design used for the outbred population was:

Factor	Year	Lines	Repicates
Symbol	Y	L	R
Type	Fixed	Random	Random
Levels	2	39	2

That is, the model Y, L, R (YL) with the replicates nested within Y, L.

For the inbred population the design was:

Factor	Year	*Glu-A1*	*Glu-B1*	*Glu-D1*	Lines	Replicates
Symbol	Y	A	B	D	L	R
Type	Fixed	Fixed	Fixed	Fixed	Random	Random
Levels	4	2	2	2	8	2

That is, the model Y, A, B, D, L (ABD), R (LY) with the lines nested within A, B, D and replicates within Y, L.

The analysis corresponding to the inbred population is given to illustrate the corrections made to obtain the estimates of the variance components.

Source	Error term	Expected mean square	Source	Error term	Expected mean square
1 Y	YL(ABD)	128(1) + 2(17) + (18)	10 YA	YL(ABD)	64(10) + 2(17) + (18)
2 A	L(ABD)	256(2) + 8(9) + (18)	11 YB	YL(ABD)	64(11) + 2(17) + (18)
3 B	L(ABD)	256(3) + 8(9) + (18)	12 YD	YL(ABD)	64(12) + 2(17) + (18)
4 D	L(ABD)	256(4) + 8(9) + (18)	13 YAB	YL(ABD)	32(13) + 2(17) + (18)
5 AB	L(ABD)	128(5) + 8(9) + (18)	14 YAD	YL(ABD)	32(14) + 2(17) + (18)
6 AD	L(ABD)	128(6) + 8(9) + (18)	15 YBD	YL(ABD)	32(15) + 2(17) + (18)
7 BD	L(ABD)	128(7) + 8(9) + (18)	16 YABD	YL(ABD)	16(16) + 2(17) + (18)
8 ABD	L(ABD)	64(8) + 8(9) + (18)	17 YL(ABD)	R(YLABD)	2(17) + (18)
9 L(ABD)	R(YLABD)	8(9) + (18)	18 R(YLABD)		(18)

If the main effects of a fixed factor with I levels are designated as α_i, the contribution of that factor to the total variance is $\frac{1}{I}\Sigma\alpha_i^2$. In the expected mean squares, however, the component due to that factor is $\frac{1}{I-1}\Sigma\alpha_i^2$ (Sheffé 1959). Adjustments were made whenever needed to take account of this fact.

Results and discussion

Synthetic outbred population

The 39 lines of the outbred population were maintained under selfing from 1980. They were not analyzed until 1987 by which time the lines were essentially homozygous.

The frequencies of genotypes and alleles determined in 1988 are given in Tables 3 and 4 respectively. Changes in allelic frequencies were larger than expected for only four generations of selection and are consistent with the rankings reported in the literature. The 2* allele at locus *Glu-A1*, as well as 7–8 and 7–9 at locus *Glu-B1* and 5–10 at locus *Glu-D1*, all increased their frequency at the expense of the others. The frequency of allele 5–10 was high in the original population probably because it is the allele with the greatest effect on quality, and all but one of the original cultivars were selected for good quality.

If the independence of allelic distributions at the three HMW loci is tested by comparing observed and expected frequencies of genotypes, a $\chi^2 = 18.60$ is obtained with 15 *df* and a probability P (higher χ^2) = 0.23. This suggested that possible linkage disequilibrium generated by selection and large gene effects or epistasis, if present, was not very important.

Average SDS sedimentation indices and standard deviations of the parents and the 39 progenies in 1987 and 1988 were:

Year	Parents	Progenies
1987	576±90	685±119
1988	758±95	814±113

The response to four generations of selection is approximately one original standard deviation. The analysis of variance of SDS sedimentation indices of the 39 progeny lines, using two replicates of each, is given in Table 5. We ignored the variance component between years because differences between years are identical for all lines and do not affect selection. The variance component between lines, an estimate of the genetic variance, accounts for 61% of the total variance, significantly greater than expected. This may be due to inbreeding which would release the potential

Table 2. SDS sedimentation volumes in ml × 10^2 of Ribereño and line 7681 with increasingly longer soaking periods

Soaking (h)	Ribereño	7681	Soaking (h)	Ribereñõ	7681
0	950	1020	6	550	1020
1	770	1020	7	530	1010
2	680	1020	8	510	1010
3	650	1020	9	500	1010
4	600	1020	10	480	1010
5	560	1020	24	470	1010

Table 3. Frequencies of genotypes in the outbred population

Genotype			Number of lines
2*	7–8	5–10	15
2*	7–9	5–10	13
2*	17–18	5–10	3
1	7–8	5–10	3
1	13–16	5–10	2
2*	7–8	2–12	1
2*	7–9	2–12	1
1	7–8	2–12	1

Table 4. Allelic frequencies in the outbred population

Locus	Allele	Original frequency	Final frequency	Change
Glu-A1	2*	0.46	0.85	+0.39
	1	0.46	0.15	−0.31
	Null	0.09	0.00	−0.09
Glu-B1	7–8	0.18	0.51	+0.33
	7–9	0.18	0.36	+0.18
	13–16	0.09	0.05	−0.04
	17–18	0.46	0.08	−0.38
	7	0.09	0.00	−0.09
Glu-D1	5–10	0.82	0.92	+0.10
	2–12	0.18	0.08	−0.10

Table 5. Analysis of variance of SDS sedimentation indices of 39 progeny lines of the synthetic outbred population in 1988 and 1991

Source	SS	*df*	MS	F	*P*	EC	%
Y	64294	1	64294	32.23	0.000	399	2
L	1636909	38	43077	21.59	0.000	10007	59
YL	783863	38	20628	10.34	0.000	4538	27
R(YL)	155609	78	1995			1995	12

P, probability of higher F. EC, estimate of variance component corresponding to the source

Table 6. Analysis of variance of SDS sedimentation indices of 64 progeny inbred lines in 1988, 1989, 1990 and 1991

Source	SS	*df*	MS	F	*P*	EC	%
Y	3.326E+6	3	1108754	36.30	0.000	8408	18
A	1.044E+6	1	1043561	16.83	0.000	3839	8
B	1.068E+5	1	106809	1.72	0.195	–	–
D	1.803E+6	1	1803219	29.09	0.000	6806	14
YA	9.963E+4	3	33208	1.09	0.356	–	–
YB	2.477E+5	3	82555	2.70	0.047	–	–
AB	2.962E+5	1	296209	4.78	0.033	1839	4
YD	3.334E+5	3	111145	3.64	0.014	1229	3
AD	3.946E+4	1	39462	0.66	0.428	–	–
BD	1.871E+4	1	18709	0.30	0.585	–	–
YAB	2.785E+5	3	92823	3.04	0.031	1886	4
YAD	2.385E+5	3	79489	2.60	0.054	–	–
YBD	1.048E+5	3	34951	1.14	0.333	–	–
ABD	9.496E+3	1	9496	0.15	0.697	–	–
L(ABD)	3.472E+6	56	61993	115.94	0.000	7529	16
YABD	1.222E+5	3	40717	1.33	0.265	–	–
YL(ABD)	5.131E+6	168	30544	57.12	0.000	15973	33
R(YABDL)	1.369E+5	256	535			535	1

P, probability of higher F. EC, estimate of variance component corresponding to the source

variance from heterozygous loci. In additive models, this amounts to a final two-fold increase in total genetic variance, and could be even larger if interactions were present.

The sum of squares for lines may be partitioned further into components between and within genotypes as follows:

Item	SS	*df*	MS	F
Between genotypes	263.081	7	37.583	0.85
Within genotypes	1.373.829	31	44.317	
Lines	1.636.909	38		

The F test is not significant, which suggests that the genotypic variance component between genotypes, the component due to HMW loci, is negligible among the 39 lines.

An unusually large initial response to selection reflects the presence of genes of large effect controlling the character (Robertson 1960; Silvela 1980). The favourable alleles are rapidly fixed and the variance expressed by them is readily exhausted. Response to selection thereafter will be slow.

In our study a large initial response to four generations of selection, a simultaneous increase in HMW allelic frequencies, and the concomitant exhaustion of their contribution to genetic variance, suggest that these HMW alleles should be recognized as genes with a large effect. The magnitude of these effects relative to each other, relative to the residual genetic variance, and relative to the environmental variance, is analyzed in the next section.

Synthetic inbred population

Two replicates of the 64 progeny inbred lines were scored for SDS sedimentation indices in 1988, 1989, 1990 and 1991. In the analysis of variance, sums of squares and degrees of freedom, corresponding to non-significant F tests, were pooled into the corresponding errors. The analysis is given in Table 6 and confirms that HMW genes indeed express large effects. Ignoring the between-years component which does not affect selection, the difference in contributions between alleles 5–10 and 2–12 at the *Glu-D1* locus accounts for 17% of the total phenotypic variance and for 34% of the total genetic variance. This agrees with previous results and confirms that this locus is the one with the largest effects. At the *Glu-A1* locus the difference in contributions of the 2* and Null alleles accounts for 10% and 19% of the total phenotypic and genetic variances respectively. The competing alleles at the *Glu-B1* locus,

7–9 and 7–8, do not make a significant contribution to variances, as would be expected from previously published results. The portion of the variance attributed to epistasis was significant, but very small, and was noted only for the AB interaction. It was highly significant in 1988 but not significant in the other 3 years (data not shown). The HMW loci account for 32% of the total phenotypic variance and for 62% of the total genetic variance. It is assumed that these contributions would be larger with two alleles of more contrasting effects at the *Glu-B1* locus such as 7–8, on the one hand, and 17–18 or just 7, on the other hand.

These results are significant from a breeding point of view. In any heterogeneous population, the desired alleles, or an epistatic combination of alleles, can be easily fixed in two or three generations by making the appropriate crosses and determining the genotype of single kernels without destroying them. This is done by using the distal part of the endosperm for SDS-PAGE. More than one-half of the total possible advnace would be successfully achieved in 2 years or less by using marker-assisted selection.

The residual genetic variance accounts for 19% of the total phenotypic variance in this experiment and for 61% in the synthetic outbred population. Clearly-defined loci contributing to this component have not been reported. Candidates for such studies include low-molecular-weight glutenins (Gupta and Shepperd 1988), gliadins (Sozinov and Poperelya 1980), and lipids (Morrison et al. 1989). It is not known whether genes with large effects that are easy to manipulate are involved. More experiments are needed to test this.

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