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AN INHERITANCE STUDY OF SEDIMENTATION VALUES
IN THREE WINTER WHEAT CROSSES

by

Douglas J. Baker

A thesis submitted in partial fulfillment
of the requirements for the degree

of

MASTER OF SCIENCE

in

Plant Breeding

UTAH STATE UNIVERSITY
Logan, Utah

1969

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I would like to express my sincerest thanks to Dr. Wade G. Dewey, my major professor, for supplying the material used in this thesis, and for his friendship, help and encouragement while working with him. He has taught me much about the plant breeding profession, for which I am very grateful.

To Dr. Orson Cannon and Dr. DeVere McAllister, members of my committee, I express my thanks for their friendship and help. A special thanks goes to Dr. McAllister for his encouragement during my undergraduate work here at Utah State University.

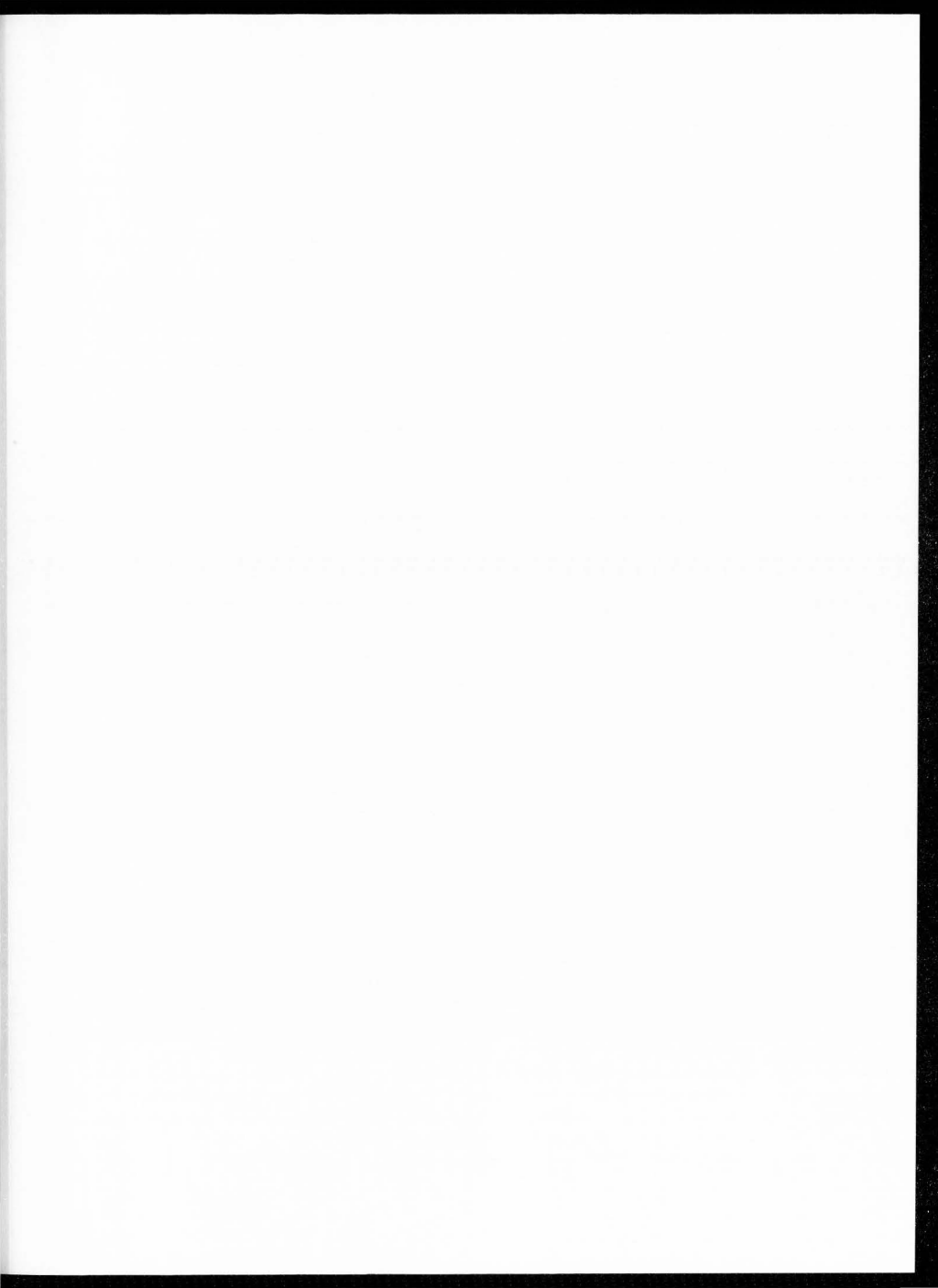
To my wife, Lois--who helped harvest the wheat and run the sedimentation tests, and who gave encouragement, love and understanding--I owe much credit.

Douglas J. Baker

Douglas J. Baker

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ABSTRACT

An Inheritance Study of Sedimentation Values

In Three Winter Wheat Crosses

by

Douglas J. Baker, Master of Science

Utah State University, 1969

Major Professor: Dr. Wade G. Dewey
Department: Plant Science

Three crosses were used to study the inheritance of the sedimentation properties in hard red winter wheat. The parents of the three crosses were the variety Delmar, and the breeding lines 217-61-7-14 and 217-19-5. Delmar has high sedimentation properties, 217-61-7-14 is intermediate, and 217-19-5 has very poor sedimentation qualities.

Sedimentation tests were run on five replications of the parents and 300 samples of the F_3 populations in each cross. A semi-micro sedimentation test (a one-fourth scale test) was run on 200 F_2 plants and the F_1 's from each cross. The distributions from each cross were analyzed and the type of gene action and possible number of genes involved were estimated.

There were two general trends apparent in the progeny of all three crosses. (1) In the F_2 generation there were more low parental types than high parental types recovered. This situation was reversed in each of the F_3 populations where more high parental types were recovered than the low parental types. (2) All three F_3 means

were about 10 units higher than their respective F_2 means.

The type of gene action appeared to be mainly additive but with some partial dominance for the high parent in each cross. Depending on the cross, from one to three genes were estimated to be functioning in the determination of the sedimentation properties.

(54 pages)

INTRODUCTION

In recent years quality has become an important factor in wheat breeding programs. However, breeders have been hampered by the lack of simple, quick tests which will accurately measure the baking potential of their breeding lines. The only sure tests that will show the actual baking quality of wheat are the mixing and baking tests themselves. It would facilitate breeding for quality if the bread-making characteristics of breeding lines could be determined in early generations; however, at this stage there is usually not enough wheat to perform the actual mixing and baking tests.

The sedimentation test has been suggested as a quick test to estimate bread-making quality. This test is based on measuring the volume of a sediment resulting from acidulating a water-flour mixture. Since it requires a relatively small amount of wheat, it is particularly useful for estimating quality in early generations. There has been considerable research done on the sedimentation test itself and how well it correlates with actual mixing and baking tests, but little is known about the inheritance of the factor or factors that determine the sedimentation properties.

There are two main reasons why the inheritance of the factor or factors regulating the sedimentation properties of wheat needs to be investigated. The first is that there is little known about the inheritance of the factors involved. The second is that this knowledge would be of practical use to wheat breeders in crossing and selection programs involving parents with different sedimentation properties.

REVIEW OF LITERATURE

There have been many tests developed throughout the years by cereal chemists and wheat breeders to help determine wheat and flour quality. Miller and Johnson (1954) and Hehn and Barmore (1965) discuss several of these tests. Some of them are the protein, farinograph, loaf volume, mixograph, and wheat meal fermentation time tests. No one of these tests has yet proven to be a panacea. Each has weak points in that they require elaborate and expensive equipment, highly trained personnel, too much wheat, or some other undesirable features.

The sedimentation test was developed by Zeleny (1947) as a quick test for estimating the bread-baking and gluten qualities of wheat flour without expensive machinery or trained personnel. The test is based on the rate of sedimentation of the solid phase from an acidulated suspension of flour in water. The rate of sedimentation is dependent on the rate and amount of hydration of the glutens in the flour. Gortner and Doherty (1918) found that glutens from strong flours have more rapid rates of hydration and higher hydration capacities than do glutens from weak flours. Rapid settling of the solid phase has been found to be associated with poor gluten quality, because of less and slower hydration, while slow settling is associated with good gluten quality because of greater and faster hydration.

Several researchers have indicated that the original test can

be modified and still obtain similar results. Pinckney, Greenaway, and Zeleny (1957) modified the test to make it applicable to soft as well as hard wheat. Preliminary tests by Zeleny et al. (1960) indicate that two grams of wheat can be used in a semi-micro test by reducing the amount of flour and all reagents to one-tenth and by using a 10 ml graduated cylinder instead of the 100 ml cylinder used in the standard test, then by multiplying the sedimentation values by ten. The values thus obtained closely approximated the values obtained by the standard procedure.

Wise, Sneed, and Pope (1965) used five grams of wheat in a micro test. They also reduced their amount of flour and reagents one-tenth and used the 10 ml cylinder. After multiplying the values by ten, the values correlated closely with the standard test but were slightly lower.

Wise, Sunderman, and Sneed (1966) compared the accuracy of macro, semi-micro and micro sedimentation tests. The standard test was designated as the macro test. The semi-micro test was performed by reducing the amount of flour and reagents by one-fourth and by using 25 ml stoppered graduated cylinders. The micro test was a one-tenth scale test using 10 ml cylinders.

In using the standard test, Dewey (1963) reduced the amount of wheat from 200 grams to 40 grams. The sedimentation values obtained when using 40 grams averaged 4.3 points lower than when 200 grams were used.

In August 1961, the U. S. Department of Agriculture announced that, starting with the 1962 crop, sedimentation value rather than

protein content would be used as a basis for premiums in connection with the government's wheat price support program. This announcement started a widespread and keen interest in the sedimentation test. Many researchers immediately began extensive studies to see if the sedimentation test provided a valid estimate of the baking quality of wheat.

Many opinions were formed--some in favor of the test, others strongly opposed. Findley (1962), Pratt, Thornby, and Schlesinger (1962), and Sibbitt and Gilles (1962a) indicated, from their studies, that the protein test is a better indicator of loaf volume and that the sedimentation test appears to add nothing above that provided by the protein test.

Harris and Sibbitt (1956) said that sedimentation values gave closer correlation with loaf volume than did expansion volume or protein content. Zeleny (1962) published a large review supporting the sedimentation test.

Great concern arose when wheat was found to have lower sedimentation values after it had been in storage for extended periods. Matern (1967) indicated that the protein particles in wheat occur as single particles attached to starch. There are more single particles soon after harvest than there are after a storage period. After storage the larger particles, protein plus starch, do not all go through the sifter; consequently, they all do not get into the sedimentation test. Studies by Austin and Jhamb (1961) showed that the gluten was not affected during the first 13 weeks of storage. Zeleny (1963) found a loss of 1.4 units in six months. He considered this

to be a small and almost negligible change. Greenaway et al. (1963) found changes of three units but considered them not significant because they were within the experimental error of the test. They also pointed out that a large increase in fat acidity or a large decrease in viability will ordinarily also result in a decrease in sedimentation value.

Because of all the controversy about whether the sedimentation test was sufficiently stable, and whether it actually represented an improvement over previously used quality tests, it was dropped from the price support program in 1965. Today the sedimentation test is used mainly by wheat breeders as a rapid, simple method of screening breeding selections.

Literature relating directly to the inheritance of the sedimentation properties is rather scarce. Zeleny et al. (1960) studied the sedimentation values of 159 samples of hard red spring wheat representing F_3 generation lines. These lines were obtained from a cross between Conley, a strong gluten variety, and P. I. 56219-12, a weak gluten strain. Sedimentation values of Conley and P. I. 56219-12 were 69 and 26, respectively, and all but one of the F_3 generation lines had values intermediate between the parents. The values of the F_3 lines tended toward a bimodal distribution. A large peak occurred between 35 and 44 units and a smaller peak at 60-64 units. Lebsock et al. (1964) reported further on this cross grown from F_3 through F_6 . Heritability values for sedimentation values were 56 percent for F_3 vs F_5 and 60 percent for F_3 vs F_6 .

Kaul and Sosulski (1964) studied the variation in sedimentation

values in segregating populations of the cross Selkirk x Gabo. They found from the P_1 , P_2 , F_1 , F_2 , BC_1 , and BC_2 populations that high sedimentation value was partially dominant, though the F_2 distribution indicated a 1:2:1 segregation. They calculated that two genes were responsible for the determination of sedimentation. The heritability of this quality character ranged from 79.68 percent to 92.15 percent, depending on the method of calculation.

Sosulski and Kaul (1966) found a partial dominance for high sedimentation value in a Conley x Ceres cross. The heritability of this cross figured from the variance of the F_2 and backcross populations was 50.2 percent. The heritability values obtained from the Conley x Ceres cross and the Selkirk x Gabo cross indicate the presence of considerable genetic variability for this quality test.

In a related inheritance test, Worzella (1934) determined the gluten strength by the wheat-meal fermentation time test. The distribution of the F_2 population indicated partial dominance of strong gluten. He indicated that there were probably more than three factor pairs involved in the inheritance of quality.

Heyne and Finney (1965) disagreed with Worzella. They concluded, by the use of the wheat meal fermentation time test, that quality of the poor parent appeared to be partially dominant.

METHODS OF PROCEDURE

Parents and source of seed

Three parents were used in this study. These were crossed in all possible combinations in 1965. The three parents were the variety Delmar, and the breeding lines 217-61-7-14 and 217-19-5. All three are hard red winter wheats. Delmar is a strong sedimentation type, 217-61-7-14 is intermediate and 217-19-5 has very weak sedimentation properties. Figure 1 shows the approximate sedimentation levels of the three parents. The cross Delmar x 217-19-5 was designated as cross number 849. Delmar x 217-61-7-14 was designated as cross number 848 and the cross 217-61-7-14 x 217-19-5 as number 847. The two selections from cross 217 have the pedigree (Ridit x Relief) x (Orfed x Elgin).

Field procedure

The parents, F_1 's, F_2 's and F_3 's, were all grown on the Evans Experimental Farm during the 1967-68 winter wheat crop year. The nurseries were planted in mid-October 1967 with a 4-row V-belt seeder. The parents and 300 F_3 's from each cross were planted in 5-foot headrows. The parents were replicated five times. Three hundred F_2 plants were space planted approximately 1 foot apart in order to obtain adequate seed for sedimentation testing on a single plant basis. The F_1 's were also space planted. A border row was planted on both sides of the F_3 nursery to eliminate possible border effects.

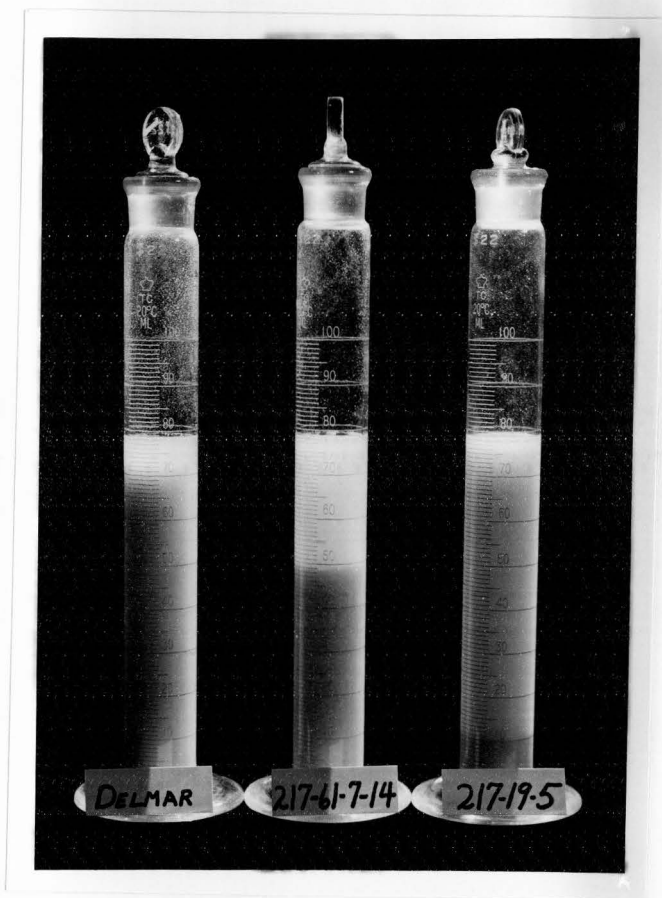


Figure 1. Graduated cylinders showing the approximate amount of sediment of each parent.

The following spring about 70 pounds of nitrogen per acre were applied as a side dressing to make sure the protein content of the wheat would be adequate for meaningful sedimentation tests. (If the protein level falls below approximately 11 to 12 percent, sedimentation values are often erratic.)

Each headrow was harvested separately by hand with a sickle and tied in a bundle. These bundles were later threshed individually and about 200 grams of seed were put in an envelope to be used for the sedimentation test. Two hundred of the largest F_2 plants were individually pulled, threshed and put in separate envelopes. Each replication of the parents was harvested, threshed, and put in separate envelopes. The F_1 plants with enough seed for a separate sedimentation test were kept separate; the others were combined to get sufficient seed for the test.

The sedimentation test

The procedures, reagents, and equipment outlined for the standard sedimentation test by American Association of Cereal Chemists (1962) (see Appendix 1) were followed as closely as possible with the following exceptions. None of the sedimentation values were corrected to 14 percent moisture, but were used directly as read from the cylinders. This was done because of insufficient wheat in the F_1 and F_2 samples for the moisture test. The author also felt that to take an average moisture percentage and apply to all samples would introduce more errors. The moisture percentage was determined on several F_3 samples. The moisture percentage varied by only 2 percent in all samples. Sibbitt and Gilles (1962b) indicated, from their

studies concerning the moisture correction factor, that in general the values used as read showed smaller deviation from the mean value than did the corrected or 14 percent moisture basis expression. They suggested a re-evaluation of the accuracy of the moisture correction factors.

The amount of wheat used for the standard test was 60 grams instead of 200. The author felt justified in doing this because all the F_3 rows did not produce 200 grams. Also, this would leave some wheat for correlation tests and repeated tests, if necessary. Dewey (1963) indicated that the sedimentation values obtained when using 40 grams averaged 4.3 units lower than when using 200 grams, but that the values from replicates of the 40 gram samples were as consistent as values from the replicated 200 gram samples.

To show the segregation patterns, F_2 plants were tested individually. Semi-micro tests, as described by Wise, Sunderman, and Sneed (1966), were used on these F_2 plants because of insufficient wheat produced by each plant for the standard test to be used. One-fourth the amount of flour and reagents was used and put in 25 ml cylinders. Figure 2 shows the cylinders used for the standard and for the semi-micro sedimentation tests.

Special refilling pipettes were used to dispense the water and acid-alcohol solutions for the semi-micro tests. These pipettes were used because they could be calibrated to dispense a fraction of an ml needed in the semi-micro tests with very little error. Figure 3 shows this apparatus.

The F_1 procedure was the same as the F_2 except the amount of

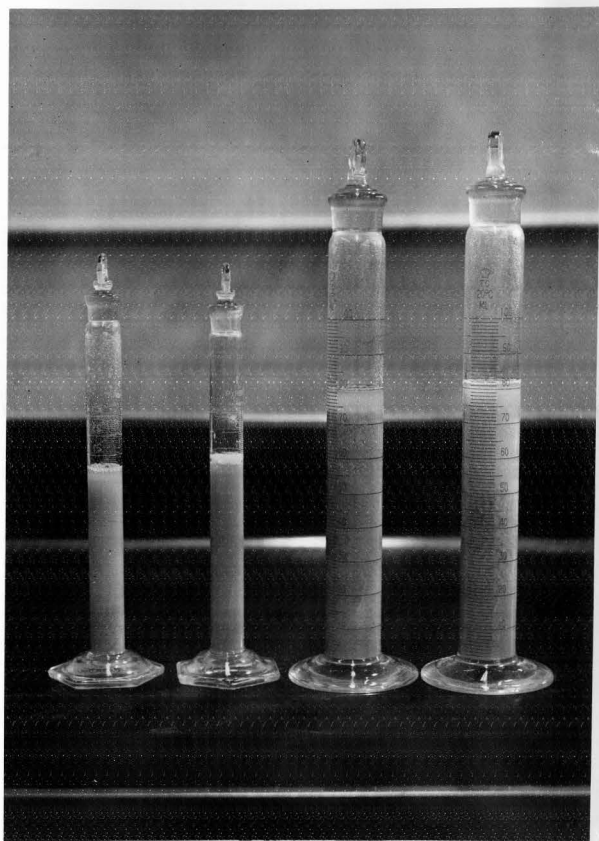


Figure 2. Small cylinders used for the semi-micro test shown in contrast with the regular cylinders used for the standard test.

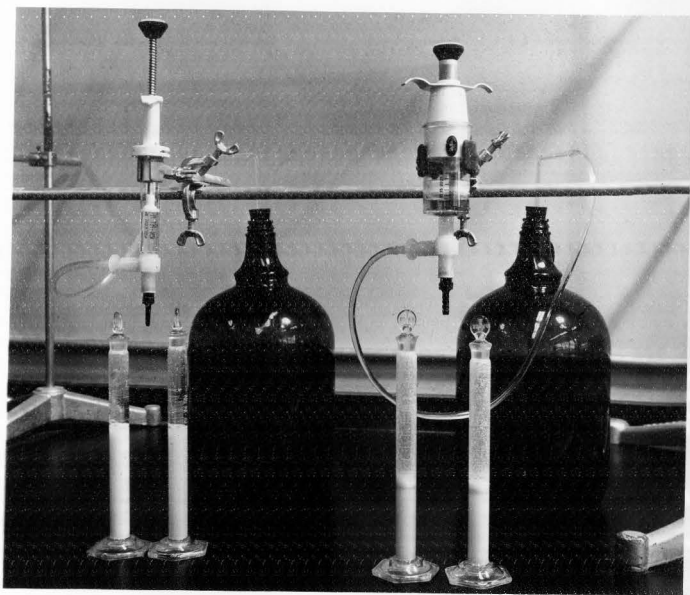


Figure 3. Special pipettes, cylinders and apparatus used for the semi-micro sedimentation tests.

wheat used per sample varied from 10 to 30 grams. The mechanical shaker was altered by an insert which changed the depth of the rack to accommodate the 25 ml cylinders. The rolls on the grinder were cleaned after each sample with a nylon bottle brush to prevent carry-over effects from sample to sample. Dewey (1963) showed that there may be a considerable carryover effect if the rolls are not cleaned after each sample.

Other related tests

Moisture and tempering tests. Before the sedimentation tests were started, several samples were brought into the lab and their moisture percentage determined with a Steinlite moisture meter. If the wheat is too dry, values are often erratic and meaningless. Moisture percentages falling much below 10 percent should be tempered. To determine if the samples would have to be tempered before running the sedimentation test, some of these samples were divided into two subsamples. One subsample was tempered overnight to a moisture percentage of about 14 percent and the other left untempered. Sedimentation tests then were run on all subsamples and the results examined.

One-half versus one-fourth amount of flour and reagents. Enough flour could be obtained from the F_2 samples to use one-half the amount called for in the standard test. If this were done, the large cylinders would have to be used. To find out if one-half the amount in the large cylinders would be more reliable than one-fourth the amount in the small cylinders, several F_3 samples were run using each method. The results were then compared with the result

obtained from the same F_3 sample using the standard test.

Semi-micro correlation tests. To be able to correlate the values of the semi-micro tests with the standard test values, 100 F_3 samples were run using both the standard and the semi-micro tests.

F_1 correlation tests. To see if the values obtained from the 10 gram F_1 samples were reliable and would correlate with the standard test, several F_3 's were re-run using 10 gram samples.

Statistical procedures

The correlation coefficient, r , was calculated for all correlation tests. The analysis of variance was calculated using the values obtained from the correlation tests. The analysis of variance was also run on the tempering experiment.

The variance, standard deviation, and coefficient of variation were run on the sedimentation values obtained from the parents and progeny of the three crosses.

The number of factor pairs affecting the inheritance and the type of gene action were also estimated using formulas suggested by Burton (1952).

EXPERIMENTAL RESULTS

Moisture and tempering tests

The moisture percentage of the samples tested ranged from 11.5 to 13.5 percent. The sedimentation values that were obtained from both tempered and non-tempered samples are listed in Table 1.

Table 1. Sedimentation values and means obtained from samples when one-half of each sample was tempered to approximately 14 percent moisture and the other half left untempered

Sample number	Sedimentation values	
	Not tempered	Tempered
1	25	27
2	55	57
3	39	38
4	52	52
5	54	48
6	52	50
7	64	61
8	51	44
9	42	37
10	56	53
11	32	30
12	<u>69</u>	<u>67</u>
	Mean 49.3	Mean 47.2

The analysis of variance of the tempering tests is given in Table 2. The differences in the means and the individual sample values were not considered to be large enough to warrant tempering.

Table 2. Analysis of variance of the sedimentation values of tempered versus non-tempered samples

Source of variation	Degrees of freedom	Mean square	F
Treatment	1	26.04	.166
Experimental error	22	157.27	

One-half versus one-fourth amount
of flour and reagents

The sedimentation values obtained from these tests are shown in

Table 3.

Table 3. Sedimentation values and mean differences obtained when a one-half scale test and the semi-micro test (a one-fourth scale test) were compared with the standard test

Sample number	Standard test	1/2 scale test	Semi-micro (1/4) test
1	51	44	54
2	66	52	64
3	57	42	50
4	45	40	45
5	44	36	42
6	43	36	39
7	40	34	40
8	40	32	38
9	44	34	43
10	67	56	64
11	34	26	32
	Mean 48.3	Mean 39.3	Mean 46.5
	Mean difference ^a 9.0		Mean difference ^b 1.8

^aStandard test mean minus 1/2 scale test mean.

^bStandard test mean minus semi-micro (1/4) test mean.

One of the values from the one-fourth test was three points higher and the rest ranged from zero to seven points lower, averaging 1.8 points lower, than values in the standard test.

The analyses of variance for these two methods compared with the standard test are listed in Tables 4 and 5. The F test in Table 4 shows significance at the 5 percent level, indicating that sedimentation values obtained by the one-half amount procedure differed significantly from those obtained by the standard method. The lack of significance in Table 5 indicates that results obtained by the semi-micro (1/4 amount) procedure did not differ significantly from those obtained with the standard test. The correlation coefficients for the one-half test and the one-fourth test, when compared with the

Table 4. Analysis of variance for one-half the amount of flour and reagents in the large cylinders compared with the standard test

Source of variation	Degrees of freedom	Mean square	F
Treatment	1	445.50	4.59*
Experimental error	20	97.12	

*Significant at 5 percent level.

Table 5. Analysis of variance for one-fourth amount of flour and reagents in the small cylinders compared with the standard test

Source of variation	Degrees of freedom	Mean square	F
Treatment	1	18.90	.167
Experimental error	20	113.01	

standard sedimentation test, are 0.966 and 0.981, respectively. Both of these tests, therefore, show a close correlation with the standard test. On the basis of the results of this comparative test, the author decided to use the small cylinders with one-fourth the amount of flour and reagents instead of one-half the amount in the large cylinders for the F_2 samples.

Semi-micro correlation tests

Once it was decided to use the semi-micro test on the F_2 samples, a more detailed correlation study was undertaken to arrive at a more precise relationship between the semi-micro and the standard tests. One hundred F_3 samples were analyzed by both methods. The data and their analysis are given in Tables 6 and 7. The semi-micro values averaged 0.8 points lower than the values from the standard test. The correlation coefficient in this study is .987 which shows a close correlation between the values for the two methods. The statistical analyses of the data indicate that the sedimentation values obtained by using the semi-micro sedimentation test on the individual F_2 plants are reasonably good estimates of the actual value and correlate closely with the F_3 data.

F_1 correlation tests

The sedimentation values obtained when 10 grams of wheat and one-fourth the amount of flour and reagents were used are tabulated in Table 8 along with the values obtained from the same samples using the standard test. The sedimentation values obtained when 10 grams of wheat were used were highly erratic, ranging from 2 to 17 points

Table 6. Sedimentation values and means obtained when the standard test and semi-micro test were run on 100 F₃ samples

Sample no.	Standard	Semi-micro	Sample no.	Standard	Semi-micro
1	31	29	46	36	34
2	64	55	47	46	48
3	56	55	48	37	38
4	42	41	49	45	43
5	20	21	50	36	35
6	63	61	51	58	59
7	64	57	52	63	56
8	65	65	53	41	38
9	60	57	54	56	53
10	56	55	55	56	60
11	50	54	56	70	69
12	65	62	57	45	50
13	56	57	58	45	43
14	63	60	59	57	58
15	63	63	60	69	69
16	63	61	61	69	64
17	46	45	62	63	62
18	61	59	63	68	68
19	59	60	64	28	27
20	44	43	65	27	25
21	28	28	66	67	66
22	44	45	67	43	45
23	56	61	68	53	54
24	60	60	69	70	68
25	40	36	70	38	37
26	65	63	71	55	54
27	61	60	72	53	54
28	44	46	73	60	57
29	39	38	74	64	63
30	58	58	75	51	52
31	52	52	76	48	48
32	40	38	77	40	38
33	60	58	78	35	34
34	47	47	79	65	65
35	45	46	80	40	41
36	44	40	81	35	36
37	56	58	82	44	39
38	51	51	83	61	52
39	56	57	84	62	62
40	52	48	85	49	50
41	44	40	86	52	54
42	43	43	87	68	64
43	62	60	88	40	40
44	25	25	89	61	60
45	48	44	90	28	28

Table 6. Continued

Sample no.	Standard	Semi-micro	Sample no.	Standard	Semi-micro
91	46	46	96	58	57
92	65	65	97	27	27
93	45	44	98	35	35
94	70	73	99	34	34
95	40	40	100	<u>65</u>	<u>62</u>
			Means	50.9	50.1

Table 7. Analysis of variance for the study comparing the standard sedimentation test and the semi-micro test

Source of variation	Degrees of freedom	Mean square	F
Treatment	1	38.72	.26
Experimental error	198	148.54	

Table 8. Sedimentation values and means obtained when the standard test was compared with the semi-micro test using just 10 grams of wheat

Sample number	Standard test	10 gram semi-micro	Sample number	Standard test	10 gram semi-micro
1	62	46	15	45	36
2	25	23	16	45	34
3	48	43	17	57	44
4	36	31	18	69	56
5	46	42	19	63	51
6	37	31	20	68	56
7	45	35	21	28	24
8	36	32	22	27	23
9	58	44	23	67	56
10	63	48	24	53	45
11	41	32	25	70	62
12	56	40	26	38	34
13	56	45	27	55	50
14	70	53	28	<u>53</u>	<u>39</u>
			Means	50.6	41.3

lower than the values from the standard tests, with an average of 9.36 points lower. In spite of this rather wide divergence in the actual values obtained by the two methods, the correlation between them was high (.962). This can be attributed to the fact that the values from the 10 gram samples were consistently lower than the corresponding values obtained by the standard method. The analysis of variance is presented in Table 9. The F test shows significance at the 5 percent level, indicating that sedimentation values resulting from the 10 gram semi-micro test are poor estimates of those obtained by the standard test.

Table 9. Analysis of variance for the correlation study between the semi-micro test using 10 grams of wheat and the standard test

Source of variation	Degrees of freedom	Mean square	F
Treatment	1	1,225.79	8.249**
Experimental error	54	148.59	

**Significant at the 1 percent level.

The sedimentation test

The raw data obtained from the sedimentation tests as they were run on the parents and progeny of each cross are presented in Table 10. The means, variances, standard deviations, and coefficients of variation for each group are given in Table 11. Tables 10 and 11 will be considered in detail in the Discussion section.

Table 10. Sedimentation values and their frequencies for the parents, F_1 's, F_2 's and F_3 's of each cross

Sedimentation values ^a	Frequency												
	Delmar	217-61-7-14	217-19-5	847			848			849			
				F_1	F_2	F_3	F_1	F_2	F_3	F_1	F_2	F_3	
10			1		2								
11					4								
12					3								
13					1								
14			1		8								
15			1		6						2		
16			2		9	2					1	1	
17					6	2					1		
18					12						2		
19					9	3							1
20					12	6					1	2	
21					6	3					3		
22					17	5					4		
23					7	6					3	2	
24					20	9					3	2	
25					12	5					6	2	
26					16	7					8		
27					9	5					6	6	
28					9	6		1			11	4	
29					4	6					8		
30					8	16					1	10	5
31					4	8					2	7	3
32		1			3	17		1			3	9	7
33					2	19					3	5	6
34					3	15		1			12	9	
35		1			1	14		1			9	7	
36					5	14		2		1	8	7	
37					1	7		3		2	7	4	
38					1	18		3			11	2	
39		1				8					7	5	
40						16		2			10	11	
41						6		1			5	7	
42						9	1	5	1		7	3	
43		2				13	1	3			3	8	
44						6		4			3	13	
45						6	2	4			2	11	
46						7	2	10			2	3	
47						8	1	5			1	4	
48						3		9			4	6	
49						6	1	5			2	5	
50						1		8	1			4	
51						3		3			1	7	
52						3		12	2		7	10	
53						2		3	4			11	

Table 10. Continued

Sedimen- tation values ^a	Delmar	217-61- 7-14	217-19-5	Frequency								
				847			848			849		
				F ₁	F ₂	F ₃	F ₁	F ₂	F ₃	F ₁	F ₂	F ₃
54							2	6	4		3	7
55								4			2	6
56					1	1	12	1				18
57					1	1	2	4				4
58					1		7	3				6
59					1		8	4				3
60							14	8			3	7
61						4	1	4	4		1	10
62								5	12			4
63								6	9			9
64								6	11			8
65						2		5	20			11
66								6	15			4
67								8	28			8
68								10	28			5
69								6	32			3
70								4	42			6
71	2							1	35			1
72	3								27			2
73									5			

^aAll F₁ and F₂ values recorded in this table have been multiplied by four.

Table 11. Means, variances, standard deviations, and coefficients of variation of the parents, F₁'s, F₂'s and F₃'s of each cross

Parents and generation	Mean	Variance	Standard deviation	Coefficient of variation
Delmar	71.6	.25	.5	.7
217-61-7-14	38.4	23.75	4.87	12.68
217-19-5	14.2	6.2	2.49	17.53
847 F ₁	24.7	.5	.71	2.88
847 F ₂	22.9	36.23	6.02	26.32
847 F ₃	35.9	82.03	9.06	25.27
848 F ₁	49.6	36.75	6.06	12.22
848 F ₂	55.1	73.49	8.57	15.56
848 F ₃	66.9	23.29	4.83	7.2
849 F ₁	39.7	5.55	2.36	5.94
849 F ₂	35.0	85.94	9.27	26.49
849 F ₃	49.0	165.71	12.87	26.29

A peculiar phenomenon was observed in a few of the samples in cross 847. During the time of settling, some of the sediment floated to the top of the liquid while the rest settled to the bottom. When this happened, the sample was run again so a correct reading might be obtained. Possibly the poor gluten quality that is exhibited in this cross contributed to this situation.

DISCUSSION

The frequency distributions of the three crosses are so different that no one type of gene action nor ratio has yet been discovered by the author which adequately explains all the results and distributions obtained.

As the frequency distributions from the crosses are examined, there are many noticeable peculiarities. These will be discussed individually and possible explanations will be presented.

Sedimentation values of the parents

The sedimentation values obtained from each of the parents indicate that Delmar and 217-19-5 are probably true breeding for the genes involved in the determination of sedimentation qualities. The coefficient of variation of the three parents are 0.7, 12.68, and 17.53 for Delmar, 217-61-7-14 and 217-19-5, respectively (Table 11). The range of variation within Delmar and 217-19-5 is relatively narrow (Delmar, 2 ml; 217-19-5, 7 ml), indicating that their observed variation is probably due mainly to environmental effects.

The author is fully aware that environmental effects during the growing season are not the only causes of non-genetic variation. The precision with which the sedimentation tests can be run is good but variation, usually not more than three units, occurs which does cause a little variation.

The variation which occurred in 217-61-7-14 (a range of 12 ml) seems too wide to be due just to environmental effects and

experimental error because the three parental rows were planted side by side in the five replications. If it were due just to these two factors, it seems reasonable to suspect more variation in the other two parents than occurred. One possible explanation for this is that the 217-61-7-14 parent might still be segregating for the factors which govern sedimentation properties.

Sosulski and Kaul (1966) also observed a wide parental range in two of their crosses (up to 14 ml). They suggested that the wide range indicates a marked response to variations in plant environment or a lack of genetic uniformity in each variety. Their values, however, were obtained from single plants only while the individual parental values in this study are from a composite of many plants in a 5-foot row. The environment would tend to cause greater extremes in variation on a single plant basis than it would in a 5-foot row, which is a composite of 50-100 plants.

If most of the variation was due to environment, the question may be asked as to why this particular parent varied the most. A possible explanation is that Delmar and 217-19-5 are at the extreme ends of the sedimentation scale and variation would likely be limited mostly to one side, the upper side of 217-19-5 and the lower side of Delmar. 217-61-7-14, being right in the middle, has an equal chance of variation on either side. Possibly the genotype of this parent is also more susceptible to environmental influences than the other two.

Sedimentation values of the F_1 's

In order to interpret the F_1 data and to correlate it with the

rest of the data, a correction factor will have to be introduced. The values obtained from the F_1 correlation test (Table 8) were too erratic to enable the values to be used as they are. Even though the mean difference was 9.3 points lower with the 10 gram samples than with the samples analyzed by the standard method, there was a general tendency for the variation to increase as the sedimentation values increased. Thus this mean difference cannot be used as an over-all correction factor.

If the genes were acting in an additive manner with no dominance, the theoretical mean of cross 847 F_1 should lie midway between the parental means and would be about 26.3. The correlated values around this region were from two to four units lower for the 10 gram samples, so if we add three units to the observed mean (25), we obtain a corrected mean of 28 which is slightly above but reasonably close to the theoretical mean.

The theoretical mean of the 848 F_1 , with the same assumptions, is 55. The deviations in this region of the correlation test were about nine points lower for the 10 gram samples. This would make the 848 F_1 corrected mean 59, which is a little above the theoretical mean but still close to it. The differences between the theoretical and corrected means in crosses 847 and 848 probably are not significant.

The F_1 mean of cross 849 approaches the theoretical mean less closely (again assuming simple additive gene action). The average deviation observed in the 10 gram versus 40 gram sample correlation test for values in the range of the 849 F_1 mean is about five units.

When this is added to the observed mean it becomes 38. The theoretical mean is 43. In contrast to crosses 847 and 848, the 849 corrected mean is several points lower than the theoretical mean.

There may be some significance in the differences between the theoretical and corrected means but this is doubtful because of the relatively small numbers, especially in 847, and because of the erratic values obtained when using only 10 grams of flour.

Sedimentation values of the F₂'s
and F₃'s

Cross 847. The frequency distributions of the parents and progeny of cross 847 have been tabulated in Table 12. The distributions of the F₂ and F₃ populations are also shown in Figure 4 in graphic form. The class intervals span five sedimentation units (ml). A class interval of five units was chosen so that it would be large enough to avoid the overlapping of experimental errors but small enough to point out genetic trends.

Table 12. Frequency distributions of sedimentation values of parents and progeny of cross 847

Parents and progeny	Class centers (in ml)											
	11	16	21	26	31	36	41	46	51	56	61	66
217-61-7-14					1	1	3					
217-19-5	1	4										
F ₁				3								
F ₂	10	41	51	66	21	11						
F ₃		4	23	32	66	68	52	30	15	3	5	2

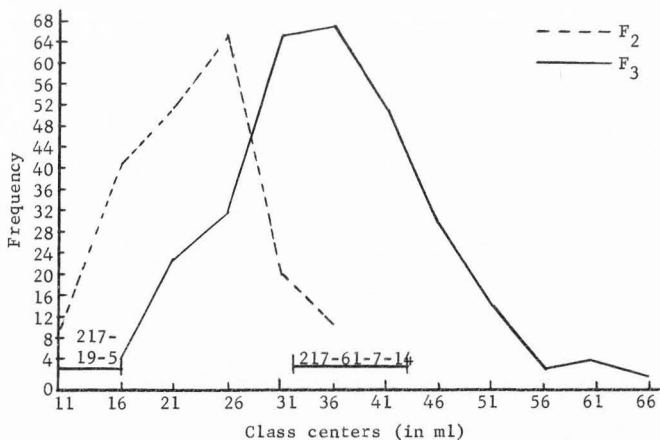


Figure 4. Frequency distributions of sedimentation values in F_2 and F_3 populations of cross 847.

The parental ranges are 32-43 for 217-61-7-14, and 10-16 for 217-19-5. In the F_2 progeny of this cross, 16 plants had sedimentation values that reached the range of the high parent, while 33 reached the low parental range. This is a total of 49 out of 200 plants in which we apparently recovered the parental combinations. Recovering this many parental types tends to indicate that there are possibly only one or two gene differences in this cross which are affecting the sedimentation values. This would appear reasonable since this cross involved the closely related parents 217-61-7-14 and 217-19-5.

The parental recovery in the F_3 's, however, is much more frequent and this time the high parental combination predominated. The

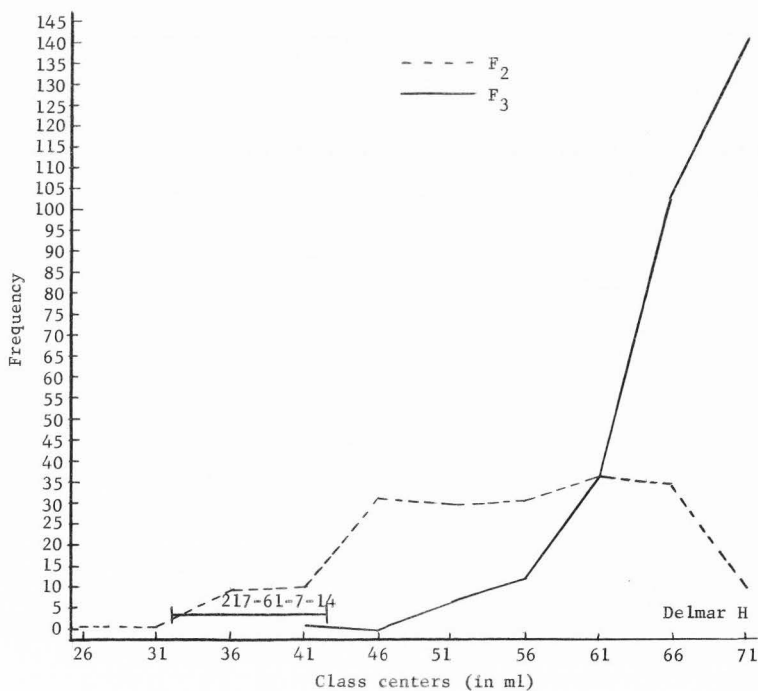
frequency of picking up the high parental range was 156 times out of 300. Only two values reached as low as the low parent. Fifty-six values were obtained which were higher than the high parental range making a total of 214 samples reaching or surpassing the parental ranges. This is the only cross which showed such a great amount of transgressive segregation. Both Table 12 and Figure 4 show this transgressive segregation very plainly.

The F_2 mean is 22.9. The correlation tests between the semi-micro (F_2) and the standard (F_3) tests showed that the values from the semi-micro tests averaged about .8 points lower than those from the standard test. Using .8 as a correction factor and adding it to the F_2 mean, the corrected mean becomes 23.7. This is slightly lower but close to the mean which might be expected (26.3) if the genes were acting in an additive manner with no dominance present. This is in contrast to the F_1 corrected mean which is 28 and the F_3 mean which increased to 35.9. Figure 4 shows this increase of 11 units in the F_3 mean over the F_2 mean quite clearly. This increase of the F_3 mean over the F_2 mean is obvious in all three crosses. This shift of the mean toward the high parent might indicate some partial dominance.

Cross 848. The parents of this cross, Delmar and 217-61-7-14, have sedimentation values which range from 71-72 and from 32-43, respectively. The frequency distributions of the parents and progeny of this cross are shown in Table 13. The F_2 and F_3 distributions are shown in graphic form in Figure 5.

Table 13. Frequency distributions of sedimentation values of parents and progeny of cross 848

Parents and progeny	Class centers (in ml)									
	26	31	36	41	46	51	56	61	66	71
Delmar										5
217-61-7-14		1	1	3						
F ₁				2	5	1	4	1		
F ₂	1	1	10	11	32	31	31	37	35	11
F ₃				1		7	12	37	102	141

Figure 5. Frequency distributions of cross 848 F₂ and F₃ populations.

This cross had relatively fewer parental types appear in the segregating populations than did 847. In the 200 plants selected from the F_2 population, only one had a value that reached the high parent, which is Delmar. There were 22 plants which were in the lower parental range, with one plant being just below this. This makes a total of 24 plants out of 200 which reached or exceeded the parental ranges.

There was a shift in the frequency of samples reaching the parental values in going from the F_2 to the F_3 . In the F_3 there were 62 values in the upper parental range, while only one was within the low parental range (in the F_2 only one segregate reached the upper parental range and 22 fell within the low parental range). There were also five samples that had a sedimentation value of 73, which is one unit higher than the Delmar range, making a total of 67 out of 300 samples that reached or surpassed the values of the parents. The high proportion of samples near the Delmar region makes a skewed distribution which is clearly shown in Figure 5. This, again, is suggestive of partial dominance for high sedimentation. The number of parental types recovered in the F_2 and F_3 in this cross suggests at least two genes are involved.

The mean of the F_2 is 55.1, and adding the correction factor of .8 obtained from the semi-micro correlation tests for the F_2 's, it becomes 55.9. This becomes .7 units above the theoretical mean and is probably not significant. The polygon representing the F_2 population in Figure 5 approaches a normal distribution but is skewed slightly to the right.

Cross 849. Very few samples in the F_2 and F_3 distributions in this cross reached the ranges of the parents, Delmar and 217-19-5 (Table 14 and Figure 6). In the F_2 generation, only three plants had sedimentation values in the range 217-19-5. There were none in the Delmar range. This situation reversed itself in the F_3 , where three samples had the same values as Delmar and only one was as low as 217-19-5.

Table 14. Frequency distributions of sedimentation values of parent and progeny of cross 849

Parents and progeny	Class centers (in ml)												
	11	16	21	26	31	36	41	46	51	56	61	66	71
Delmar													5
217-19-5	1	4											
F_1					9	3							
F_2		6	11	34	39	47	32	12	10	5	4		
F_3		1	5	14	21	29	34	37	37	41	33	36	12

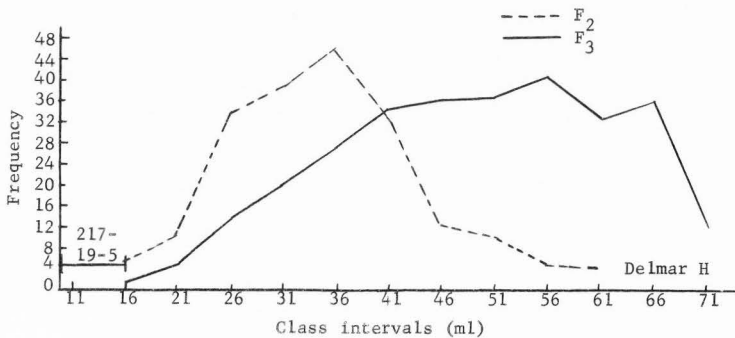


Figure 6. Frequency distributions of cross 849 F_2 and F_3 populations.

This reversal pattern of switching from more low parental types in the F_2 's to more, especially in crosses 847 and 848, in the high parental range in the F_3 's in all three crosses is a perplexing problem and a satisfactory answer which fits all three crosses is not immediately apparent.

The adjusted F_2 mean is 35.8, which is 7.7 points lower than the theoretical mean (43.5). This would tend to give the impression that the low parent is partially dominant, but as we examine the F_3 values we again see the F_3 mean several points higher than the F_2 mean. The F_3 mean in this cross is 49.0, indicating a partial dominance for the high parent. Table 14 and Figure 6 show this shift from the F_2 to the F_3 .

Estimate of the type of action and number of genes involved

The author has spent a considerable amount of time going over many of the countless possible different genetic actions and ratios which might be involved in these crosses and in reviewing other quantitative inheritance work in order to come up with a reasonable hypothesis and ratio which would fit the data of all three crosses and which would explain the action involved.

Two of the ways which are used to estimate the number of genes involved in inheritance studies are: (1) special formulas, and (2) observing the number of parental types recovered in F_2 populations. Both of these methods were used by the author to estimate the possible number of genes involved in the three crosses in this study. The formula suggested by Burton (1952) was used. The formula and

its components are listed below:

$$n = \frac{.25 (.75 - h + h^2) D^2}{\sigma^2_{F_2} - \sigma^2_{F_1}}$$

$$h = \frac{\bar{F}_1 - \bar{P}_1}{\bar{P}_2 - \bar{P}_1} \quad \text{and} \quad D^2 = (\bar{P}_2 - \bar{P}_1)^2$$

\bar{P}_1 = the mean of the smallest parent

\bar{P}_2 = the mean of the largest parent

\bar{F}_1 = the mean of the F_1 population

\bar{F}_2 = the mean of the F_2 population

When values were substituted into this formula, cross 849 was estimated to have at least three genes involved, and 848 and 847 both a minimum of one gene involved in the determination of the sedimentation properties.

According to the number of parental types recovered in the F_2 generation of the three crosses, it is estimated that cross 847 had at least one and possibly two genes involved. Cross 848 is estimated to have at least two genes involved, while 849 is estimated to have a minimum of three genes segregating for sedimentation properties. These estimates agree quite closely with the estimates obtained from using the formulas above.

Kaul and Sosulski (1964) estimated that two genes were responsible for the determination of sedimentation properties in the crosses they studied.

The author spent many hours trying different gene combinations and putting different weights on the genes such as simple additivity, geometric, major and minor genes, and guessing different values

which the different genes might possess, but none of these manipulations would fit all three crosses.

Burton (1952) suggested a method whereby the type of action of the genes, whether arithmetic or geometric, could be calculated.

The formulas used are listed below:

$$\text{Theoretical Arithmetic } \bar{F}_1 = \frac{\bar{P}_1 + \bar{P}_2}{2}$$

$$\text{Theoretical Arithmetic } \bar{F}_2 = \frac{\bar{P}_1 + 2\bar{F}_1 + \bar{P}_2}{4}$$

$$\text{Theoretical Geometric } \bar{F}_2 = \text{Antilogarithm of } \frac{\log \bar{P}_1 + 2 \log \bar{F}_1 + \log \bar{P}_2}{4}$$

The symbols used are the same as in the equation used to estimate the number of genes above.

If the theoretical arithmetic means were closer to the actual means than the theoretical geometric means, then the type of action was supposed to be additive. If the theoretical geometric means were closer to the actual means, the action was estimated to be geometric. This was calculated for each of the three crosses involved in this study but no real conclusion could be drawn on the basis of the answers obtained from the formulas. In cross 847 the answers both were just above the actual mean, in cross 848 they were just below, and in cross 849 they split the difference, one being above and the other below. This likely indicates that both are acting.

The F_1 and F_2 means suggest that the type of action by the genes is mainly additive; however, the F_3 means show a considerable trend toward the high parent, which might indicate partial dominance for high sedimentation. Kaul and Sosulski (1964) also found the

high sedimentation values to be partially dominant.

Some authors have used backcross data to aid in the interpretation of genetic data. There were no backcrosses made in this study. Had backcross data been available, they may have been helpful in clarifying the observed segregating patterns.

The author concludes from the data that there are probably one or two genes involved in cross 847, two genes involved in cross 848, and three in cross 849. The type of gene action appears to be primarily additive, but with possibly partial dominance for the high parent in each cross.

SUMMARY AND CONCLUSIONS

Three parents were crossed in all possible combinations and the inheritance of the sedimentation properties studied in the F_1 , F_2 and F_3 generations. The parents were the variety Delmar (high) and the breeding lines 217-61-7-14 (medium) and 217-19-5 (low). 217-61-7-14 x 217-19-5 was designated as cross 847, Delmar x 217-61-7-14 as cross number 848 and Delmar x 217-19-5 as 849. Sedimentation tests were run on five replications of the parents and 300 samples of the F_3 populations in each cross. A semi-micro sedimentation test (a one-four scale test) was run on 200 F_2 plants in each cross and on a few F_1 's. The distributions in each of the crosses were analyzed and the type of gene action and possible number of genes involved were estimated.

The sedimentation values ranged from 71-72, 32-43 and 10-16 for Delmar, 217-61-7-14 and 217-19-5, respectively. The F_1 means approximated the midway point between the parents in each cross.

The number of samples in the F_2 population in cross 847 which reached the parental ranges indicated that there are possibly only one or two genes segregating for sedimentation in this cross. Considerable transgressive segregation above the high parent was observed in this cross.

The frequency distributions in the F_2 and F_3 populations in cross 848 are skewed toward the high parent which suggests partial dominance for high sedimentation. The number of parental types

recovered in the F_2 and F_3 generations suggest at least two genes are involved.

In cross 849, the F_2 mean gives the impression that the low parent is partially dominant, but the F_3 mean is several points above the mid point between the parents which indicates partial dominance for the high parent. Three genes are estimated to be involved in this cross.

Two general trends are present in the progeny of all three crosses. (1) In the F_2 , there are more low parental types than high parental types recovered, then in the F_3 this situation is reversed and more high parental types are recovered than low parental types. (2) All three F_3 means are about 10 units higher than their respective F_2 means.

It is concluded that the gene action tends to be additive but shows some partial dominance for the high parent in each cross. It is also concluded that the probable number of genes involved in each cross are one or two in cross 847, two genes in 848, and three in cross 849.

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APPENDIX

Sedimentation Test for Wheat

Apparatus

1. Mill, motor-driven, with corrugated steel rolls equiv. to Tag-Heppenstall moisture meter rolls for small grains. (The distance between the rolls of the three mills approved for making this test by the U. S. Department of Agriculture are 0.023 \pm 0.002 in. for the Tag Mill, 0.030 \pm 0.002 in. for the Strand Roll Mill, Model SRM, and 0.045 \pm 0.002 in. for the Straub Wheat Mill, Model W-1.) If the Tag-Heppenstall moisture meter rolls are employed, the flaxseed shims may be used to help attain the desired clearance.

2. Sieve, 100-mesh (U.S. Std. No. 100 woven wire cloth), diam. 8 inc., equipped with bottom pan. Openings, 149 μ .

3. Sieve shaker. The mechanical sieve shaker should have a horizontal circular motion such that any point on sieve will describe circles about 2 in. in diam. at rate of about 200 rev. per min. (see Note 3).

4. Dual-chambered automatic pipets, 25- and 50-ml. capacity, which should empty and fill in less than 10 and 15 sec. respectively.

5. Glass or Teflon-stoppered 100-ml. graduated cylinder, preferably made from precision-bore tubing having a distance of 180-185 ml. between zero mark at bottom and 100 ml.

6. Stop-watch or interval timer.

7. Mixer. Rack approx. 23 by 12 by 2 in. is pivoted at center of each end and oscillates thru 60 degrees, 30 degrees each side of horizontal position, at rate of ca. 40 times per min. Rack is so designed that eight graduated cylinders can be quickly and securely placed while mixer is in motion. Power is supplied by small electric motor.

Reagents

1. Isopropyl alc., 99-100% N.F. or equiv.

2. Distd. or deionized water. All water used to make reagents and hydration water should contain no more than 2 p.p.m. of mineral matter.

3. Hydration water (bromophenol blue soln.): add bromophenol blue to distd. water so that it will contain 4 mg. per liter.

4. Lactic acid stock soln. Dilute 250 ml. U.S.P. 85% lactic acid to 1 liter with distd. water. Reflux dild. acid 6 hr. without loss of vol. (see Note 2).

5. Reagent: Mix thoroly 180 ml. lactic acid stock soln. (reagent 4), 200 ml. isopropyl alc. (reagent 1), and distd. water to make 1 liter. Let stand 48 hr. Stdze. to 0.50 \pm 0.01 normal against 0.10 sodium or potassium hydroxide. Specific gravity should be 0.985 \pm 0.001 at 60/60^D F. Protect against evaporation.

Procedure

1. Grind ca. 200 g. clean wheat by passing it thru mill five times. If moisture has been detd. on Tag-Heppenstall moisture meter, the crushed wheat should still be passed thru mill five times. If the ground wheat flakes, it should be crumbled with the fingers between passes. Rolls should be brushed between millings.
2. Place ground wheat on 100-mesh sieve equipped with bottom pan, and shake mechanically for 90 sec.
3. Weigh 3.2 g. flour and place in 100-ml. stoppered, graduated cylinder.
4. Simultaneously start timing and addition of 50 ml. brom-phenol blue water. Mix flour and water thoroly by moving stoppered cylinder horizontally lengthwise, alternately right and left, thru space of 7 in., twelve times in each direction in 5 sec. Flour should be completely swept into suspension during mixing.
5. Place cylinder in mixer (about 15 sec. required to this point from addition of water). Mix until period of 5 min. has elapsed.
6. Remove from mixer, add 25 ml. lactic acid reagent (4) and return to mixer until period of 10 min. has elapsed from start of timing.
7. Remove from mixer. Immediately place cylinder in upright position and let stand exactly 5 min.
8. At end of exactly 5 min. read vol. in ml. (estimating tenths of ml.). This is uncorr. sedimentation value.
9. To obtain corr. sed. val. (14 m.b.) multiply uncorr. sed. val. by appropriate factor in table below (see Note 7).

Wheat Moisture %	Factor	Wheat Moisture %	Factor	Wheat Moisture %	Factor
8.0	1.14	11.0	1.00	14.0	1.00
8.5	1.10	11.5	0.99	14.5	1.02
9.0	1.07	12.0	0.98	15.0	1.04
9.5	1.05	12.5	0.98	15.5	1.07
10.0	1.03	13.0	0.98	16.0	1.10
10.5	1.01	13.5	0.99		

Notes

1. The sedimentation test reflects differences in quantity and quality (from bread-baking standpoint) of gluten in wheat (or flour) and hence is a rough measure of baking strength.
2. Concd. lactic acid normally contains associated molecules which on diln. gradually dissociate in part until state of equilibrium is reached. Attainment of equilibrium after diln., which is necessary for consistent sedimentation test results, is greatly hastened by refluxing. Refluxed stock soln. should be ca. 2.78N. The mineral content of lactic acid may vary. It is important that

total minerals should not exceed 10 p.p.m. in the stock or 2 p.p.m. in the reagent. The isopropyl alcohol should be mineral-free also.

3. Be certain sieve is clean before using. Material passing thru sieve is essentially a white flour and is used for sedimentation test. Flour must be thoroly mixed before testing. Flour yield should be about 30 g.

4. If suitable automatic pipets are used for dispensing solns. tests may conveniently be run in groups of eight. Lacking automatic pipets, it is best to measure correct amount of reagents into small beakers or graduates and to make delivery from these containers at the appropriate time interval.

5. Deviations of 10-15 sec. during stops 4 thru 7 are not serious. It should be emphasized, however, that reading of uncorr. sed. val. (step 8) must be made exactly 5 min. after final mixing. The 5-min. period of settling must be very accurately timed, since at this stage sedimentation may still be progressing rapidly. Readings taken at longer time intervals show smaller differences between wheats of good and poor baking quality. Readings at shorter intervals are sometimes not clear. Line of demarcation between sediment and supernatant liquid in cylinder is ordinarily sharp and distinct, so that readings may be made directly to nearest ml. and estimated to nearest 0.1 ml. Duplicate detns. of sed. val. usually agree within less than 1 ml. Temp. of reagents within range of 65°-95°F. have no significant effect on results. Sedimentation readings range from less than 20 for low-protein wheat of inferior bread-baking strength to maximum of 78 for very high-protein wheat of superior bread-baking strength.

6. Moisture content of wheat when ground as directed partly detns. content of ash and of protein in resultant flour. Ash, protein, and granularity of flour influence sed. results. Factors in table are designed to compensate for effect of variations in the three variables and also to correct sed. values to 14% m.b.

7. See reference for description of hand-shaking and hand-sieving procedure.



