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9. ABSTRACT
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Investigations of the Genetics of Bread Wheat Baking Quality

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PROTEIN QUALITY and protein quantity are key factors in bread baking quality. However, these two factors are not independent of the carbohydrates and lipids, especially glycolipids, in their effect on bread baking quality. When the other factors are equivalent, bread loaf volume is highly correlated with protein content (Fig. 1). When the protein content of two flours is similar, the difference between loaves of bread baked from these flours is usually a matter of protein quality. Differences in bread wheat protein quality may be due to genetic factors (Fig. 2) or to environmental factors (Fig. 1). Therefore, the cooperative wheat research project of the University of Nebraska and the Crops Research Division, ARS, U. S. Department of Agriculture has included both objectives of increasing protein content and of improving protein quality for bread production.

Increasing Protein Content in Bread Wheat

Flours for satisfactory bread production should contain about 12 percent protein. Wheat produced in the Great Plains area had ample flour protein until native soil fertility declined. This decline was hastened by the increased productiveness of new varieties. Also, there tends to be a reduction in grain-protein content as yield is increased. Therefore, one of the objectives of the Nebraska wheat research project was the increase of grain-protein content through genetic means. Earlier studies as reported in the literature were not very encouraging regarding the prospects. However, the basis for our optimism was the release of the 'Atlas' wheats by the North

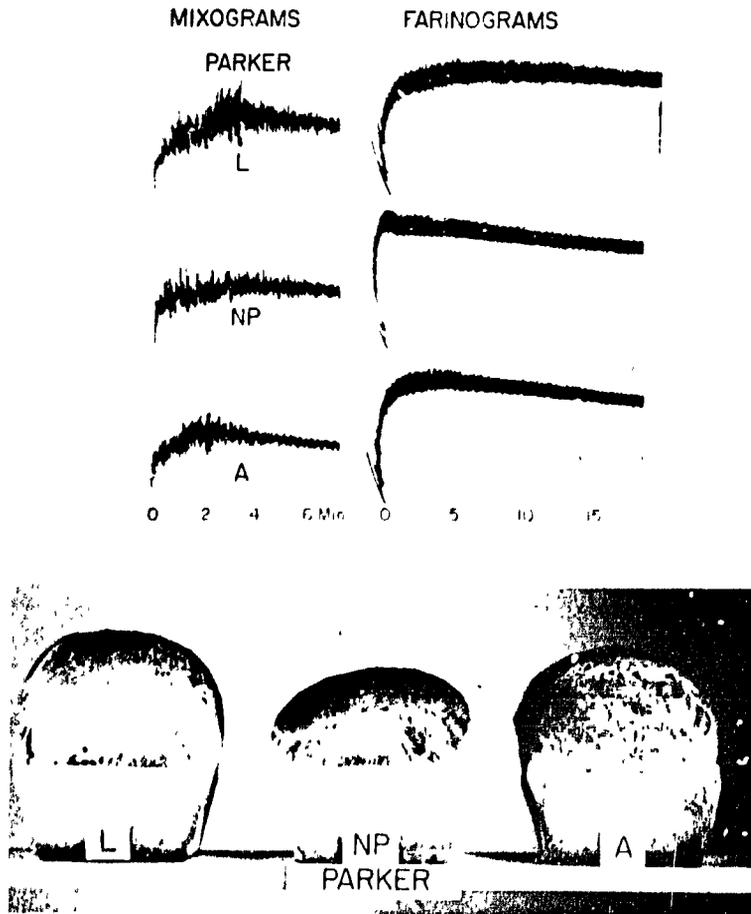


Figure 1. Effect of environment on the grain-protein quality and quantity of the Parker hard red winter wheat variety at three Nebraska locations in 1966. L — Lincoln, protein content 11.0 percent, NP — North Platte, protein content 10.9 percent, A — Alliance, protein content 14.8 percent. Conditions at Lincoln, normal, at North Platte, high yield environment, at Alliance, low yield with drought environment.
Top: Mixograms and farinograms typical for these environments.
Bottom: Loaves of bread showing the reduced loaf volume at North Platte due to low protein content and the harsh crust at Alliance due to high protein content in a drought environment.



Figure 2. Differences in flour mixing curves due to genetic or varietal differences; both varieties were grown the same year at the same location and had identical grain-protein content.

Carolina Agricultural Experiment Station. Both Atlas 50 and Atlas 66 were shown to be substantially higher in protein content than the soft red winter wheats of that region.

The Atlas wheats along with two hard red winter wheats, Comanche and Wichita, were grown at a number of Great Plains stations to see whether the protein content superiority of the Atlas wheats would prevail in this region. The data shown in Table 1 are typical of the results. With these and similar data at hand, a study of the feasibility of improving protein content in hard red winter wheats through breeding was initiated. The Atlas wheats, especially

Table 1. YIELD OF GRAIN AND GRAIN-PROTEIN CONTENT OF ATLAS 66, COMANCHE, AND WICHITA WHEATS GROWN IN FOUR TESTS IN THE SOUTHERN GREAT PLAINS IN 1958

Variety	Four-test Mean	
	Yield	Protein
	<i>Bu/A</i>	%
Atlas 66 ...	24.9	19.4
Comanche ...	21.7	17.5
Wichita ...	18.6	15.4
LSD ₀₅	ns	0.7

Table 2. GRAIN PROTEIN HERITABILITY ESTIMATES FOR ATLAS 66 x WICHITA POPULATIONS

Method	Estimate
Heritability in the broad sense, using P_1 , and P_2 , and F_2 variances as estimates of nonheritable variance (greenhouse soilbed data)	0.68
Heritability in the narrow sense, using F_2 and backcross variances (greenhouse soilbed data)	0.82
Regression of F_2 on F_1 (data coded in standard units, field data)	0.58

Atlas 66, were used as high-protein parents in crosses with Wichita and Comanche, low and intermediate protein-content parents, respectively. Typical distributions of the protein content of individual F_2 plants and plant samplings of the parental varieties are shown in Figure 3. The F_2 population was intermediate to the parents, but plants with protein content as high as the high parent mean could be recovered easily. Additive gene action for high protein content proved to be important.

Previous studies had reported that large environmental effects made for slow if any progress in improving grain protein content. However, the Atlas 66 Wichita and Atlas 66-Comanche populations gave heritability estimates (Table 2) sufficiently high to warrant the belief that good progress in increasing grain protein content could be made.

The Atlas varieties were released by the North Carolina Station for their leaf rust resistance. The high grain-protein content was obtained as an adjunct to their program for leaf rust resistance. Their studies, as well as ours, soon showed that a major portion of

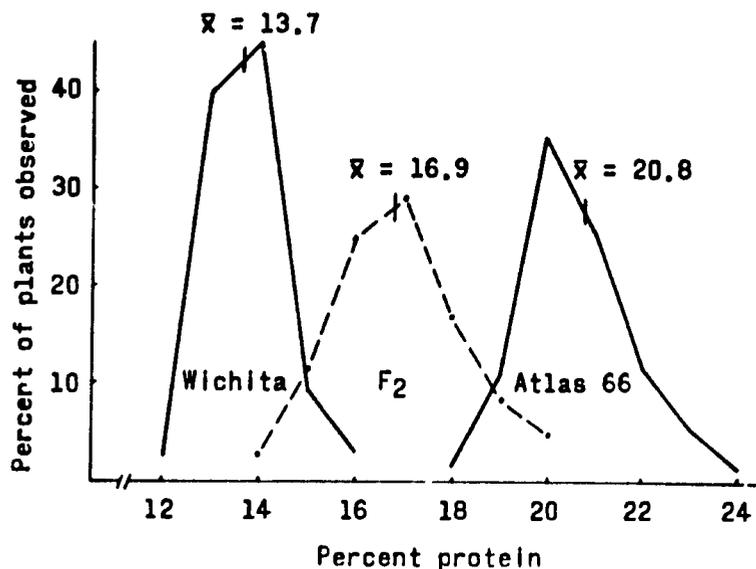


Figure 3. Grain-protein frequency distribution of Wichita, Atlas 66, and Atlas 66 x Wichita F₂ plants grown in a greenhouse soilbed.

this grain-protein increase accompanied the transfer of a simply inherited dominant gene for leaf rust resistance. Our selection for high protein content in this material today depends heavily on the association between leaf rust resistance and high protein content. So far we have not established whether this is close linkage, pleiotropism, or an artifact. The latter is a possibility since the leaves of the high grain-protein plants stay green longer and allow for better transport of nitrogenous compounds from the leaves to the grain.

The question of nitrogen transport or translocation assumed importance when it was discovered that low grain protein varieties and high grain protein lines absorbed nitrogen from a nutrient solution in approximately the same amount. Field studies (Fig. 4) confirmed this since the low grain protein variety Warrior had foliage nitrogen levels as high as or higher than a high grain protein line of comparable maturity, but the latter variety had significantly higher grain-protein content. This experiment has been repeated a number of times with similar results. These data suggest to us that the Atlas wheats were more efficient in transport or translocation of nitrogen or nitrogenous compounds from foliage to the grain. This

was substantiated, at least in part, when the low grain-protein Wichita and a high grain-protein experimental line were defoliated after blooming. Defoliation of the low grain-protein variety Wichita had little effect on grain protein content, while defoliation of the normally high grain protein line reduced its protein content to the Wichita level (Fig. 5). However, this could be an artifact since the leaves on the undefoliated Wichita plot were attacked by leaf rust and deteriorated rapidly, while the high grain-protein line remained green much longer.

We have accumulated much data to show that these high grain-protein lines will maintain this superiority of 2 to 3 percent (that is, 17 percent versus 14 percent) actual grain protein content increase at yield levels up to 40 to 45 bushels and from year to year. Bread-baking data also show that high grain protein content, in this case, is independent of protein quality. For example, the lines shown in Figure 6 have similar high grain-protein levels, yet they represent a range in dough-mixing types. Similarly, they may have a range in bread loaf volumes.

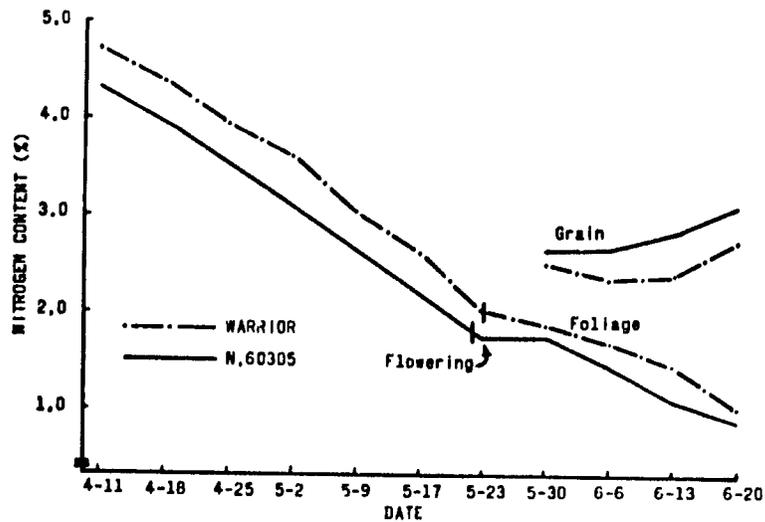


Figure 4. Nitrogen content of grain and foliage of Warrior and an experimental high grain-protein selection during the 1963 spring growing season at Lincoln, Nebraska.

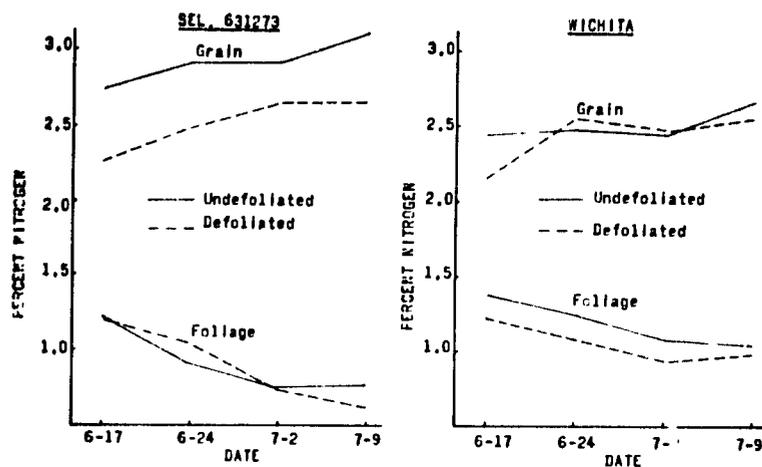


Figure 5. Effect of defoliation on grain-protein content of a high grain-protein experimental line and Wichita winter wheat at Lincoln, Nebraska

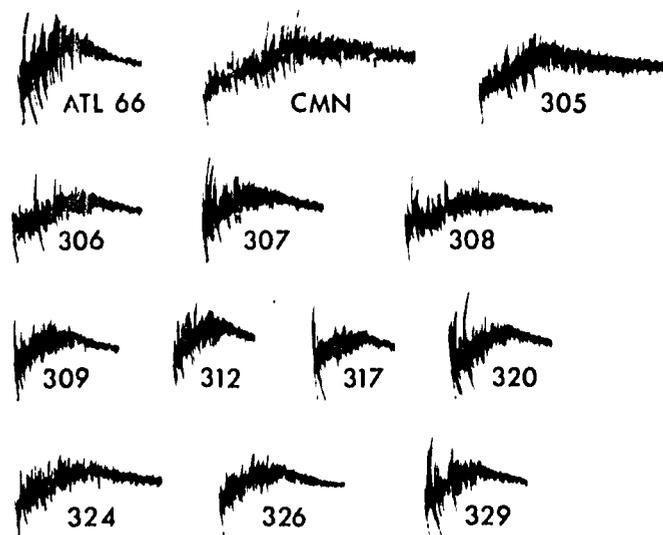


Figure 6. Range in dough-mixing curves of flours of Atlas 66 x Comanche derivatives and the parental varieties at nearly constant protein levels.

Table 3. GRAIN YIELDS, GRAIN-PROTEIN CONTENT, AND POUNDS OF PROTEIN PER ACRE PRODUCED BY WHEAT VARIETIES AND THEIR HYBRIDS AT LINCOLN, NEBRASKA, 1966

Variety or hybrid	Yield	Protein	Protein per acre
	<i>Bu/A</i>	<i>%</i>	<i>Lbs.</i>
Scout	58.6	12.30	432
Scout hybrid	45.8	14.55	400
Gage	47.4	13.40	381
Gage hybrid	40.4	15.75	382
Restorer line	31.2	14.95	280

An interesting by-product of our hybrid wheat research has been the identification of high grain protein content in male-fertility restorer lines (Table 3). The ability of these lines to transmit this high protein content to their hybrids was shown consistently in 1966-68 with a number of different restorers and hybrid combinations. Therefore, these lines are being used as high grain-protein parents in our conventional wheat breeding program.

Finally, recent soil fertility experiments show (Fig. 7) that these lines maintain this grain protein superiority as increasing amounts of nitrogen fertilizer are applied. This suggests, again, that high grain-protein content is concerned with what happens within the plant and is not due to differential nitrogen uptake. Therefore, the release of high grain-protein varieties will not solve the basic problem of low protein wheat in Nebraska. This is still a matter of soil fertility. However, substantial genetic progress for increased grain-protein content is possible with the germplasm currently available. At present, the World Wheat Collection is being searched for additional sources of high grain-protein content. Nebraska researchers are interested in improved nutritional value as well as bread-baking quality.

Protein Quality in Bread Wheat

Physical dough-handling properties of bread wheat flours are largely a matter of protein quality. However, these properties, as well as protein content, have an influence on loaf volume and texture. Since the Cheyenne variety has long been a quality standard in Nebraska, it was chosen for studies of the genetics of bread-baking quality. Heyne and Finney (1965, and in earlier unpublished

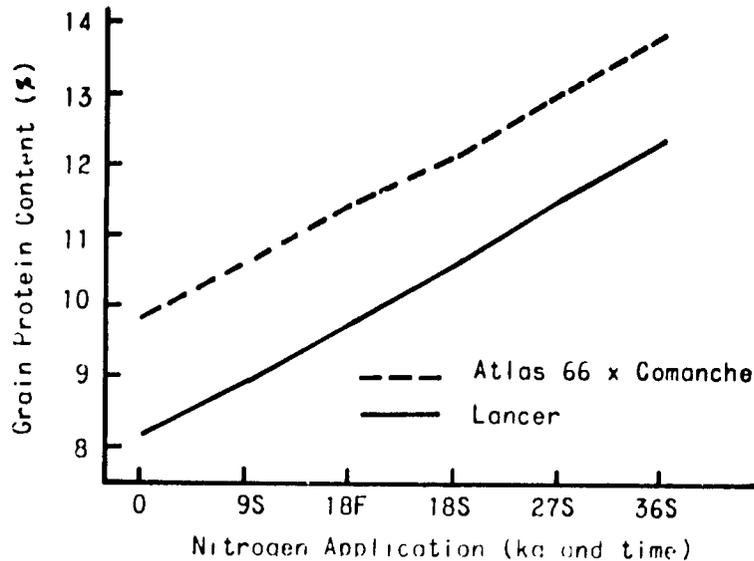


Figure 7. Maintenance of grain-protein content superiority of an Atlas 66 x Comanche selection to Lancer over a range of nitrogen fertility levels, 1968.

reports) of the Kansas Agricultural Experiment Station showed that, in crosses with weaker wheats, Cheyenne quality characteristics were partially dominant and due to a small number of genes. On this basis, it appeared that either the monosomic analysis or the chromosome substitution method could be used in a detailed study of the protein quality of Cheyenne wheat.

For the monosomic analysis method, the monosomic set (21 $2n-1$ lines) of the Wichita variety was used in crosses with Cheyenne. Bulk F_2 progenies from monosomic F_1 plants failed to identify individual Cheyenne chromosomes with factors for strong dough-mixing characteristics (Fig. 8). The drastic effect on dough mixing due to the monosomic condition of chromosome 1D reported earlier by Welsh and Hehn (1964) was the only demonstrable effect. Obviously, this method did not supply the information we were seeking.

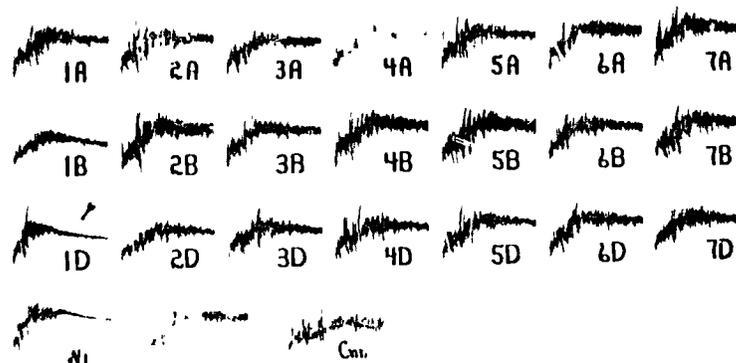


Figure 8. Dough-mixing curves for flours milled from the grain of the 21 F. monosomic populations of Wichita monosomic x Cheyenne disomic crosses, the parental varieties, Wichita (Wi) and Cheyenne (Cm), and a typical disomic population. The populations are identified by chromosome number and genome (2A = XIII, 2B = II).

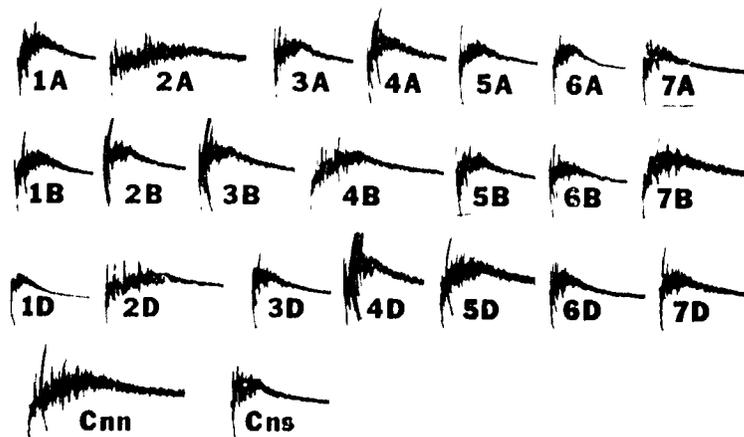


Figure 9. Dough-mixing curves for 21 Cheyenne substitution lines and parental varieties, Cheyenne (Cnn) and Chinese Spring (Cns). The substitution lines are designated by chromosome number and genome (in this paper 2A = XIII and 2B = II). In this figure, the 2A and 2D lines had insufficient backcrosses and do not represent the mixing types observed in later backcross lines.

Dr. E. R. Sears, ARS, USDA, University of Missouri, had available appropriate cytogenetic stocks of the variety Chinese Spring for a chromosome substitution approach. This variety has poor bread-baking quality. Each of the 21 Cheyenne chromosomes was substituted singly for the corresponding Chinese Spring chromosome giving us 21 stocks. Each stock had 20 pairs of Chinese Spring chromosomes and 1 pair of the Cheyenne variety chromosomes. Lines were at the fourth backcross stage except for 2A, 2B, 2D, and 7A. Seed was increased at Fort Collins, Colorado, and Aberdeen, Idaho, and then composited for physical dough tests and bread baking. The effect of environment (location) according to test mixing and baking did not influence the relative position of the lines. That is, the lines maintained relative differences regardless of the location.

In the process of milling these substitution lines, it was observed that line 5D (having 20 pairs of chromosomes from Chinese Spring and the 5D pair from Cheyenne) milled more nearly like Cheyenne hard wheat than any other line. The visual identification (from bran cleanup) of the 5D line as having the Cheyenne chromosome that promotes kernel hardness was substantiated by physical flour characteristics as shown in Table 4.

The physical dough-handling characteristics of the flours of each of the 21 lines and the parents were determined from patterns produced when 30 grams of flour were mixed in a Swanson-Working Mixograph operated at 25°C. Water absorptions were adjusted to optimum for bread dough. Results are shown in Figure 9. Lines 2A (XIII) and 2D had insufficient backcrosses at this point. After additional backcrosses they were shown to have mixing characteristics similar to Chinese Spring. Of the remaining lines, 4B, 7B, and 5D had dough-handling characteristics clearly superior to those of Chinese Spring. The strong gluten qualities of the Cheyenne variety, then, are due to factors located on these three chromosomes. Mixing curves for lines 4A, 3B, and 4D are somewhat better than those for Chinese Spring.

Loaf volumes and loaf characteristics of these same lines are shown in Figure 10. The A genome of Cheyenne, with the possible exception of 1A, does not appear to contain any bread quality factors that would improve on bread baked from Chinese Spring flour. In contrast, at least three lines of the B genome, 1B, 4B, and 7B are improved over Chinese Spring in loaf volume and grain

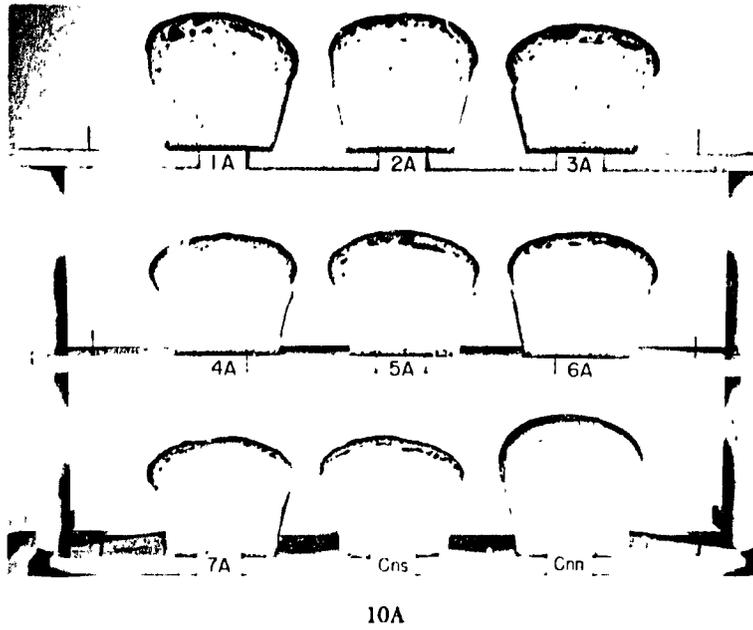
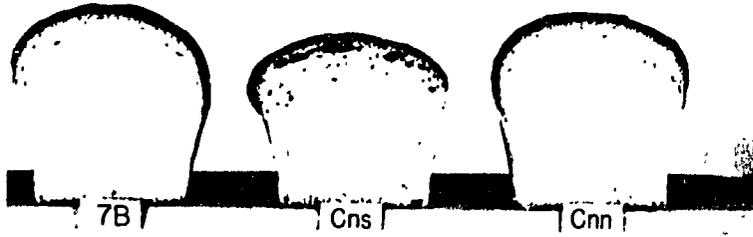
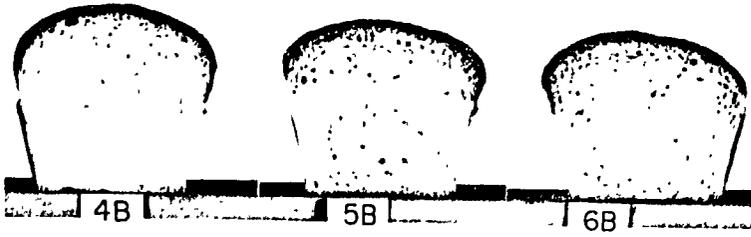
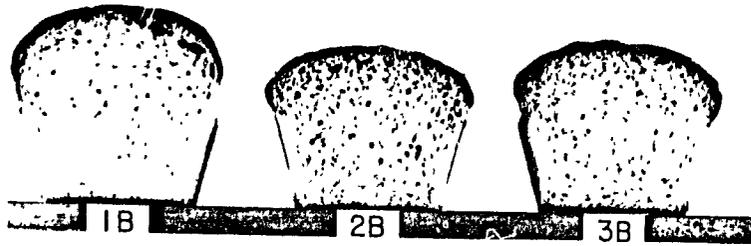
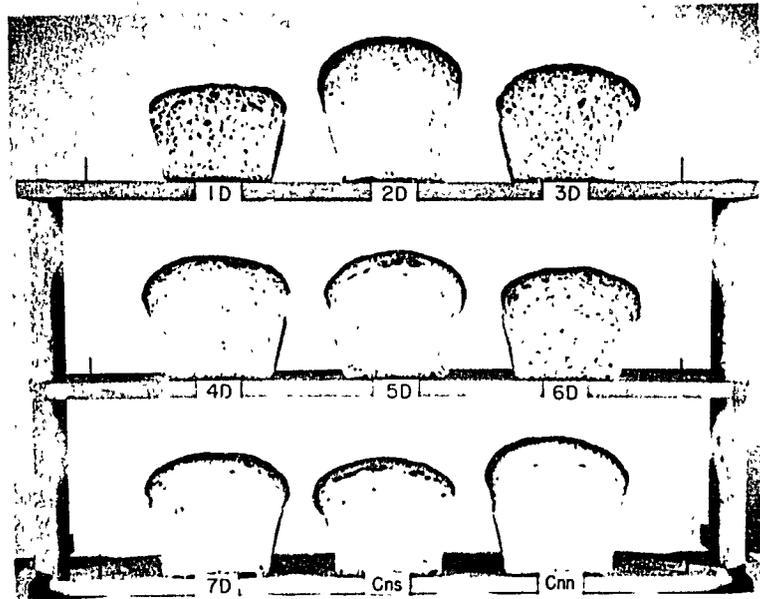


Figure 10. A, B, and C. Interior surfaces of loaves of the Cheyenne substitution lines. Loaf volumes of lines 2A and 2D shown in this figure do not represent those observed in later backcross lines.



10B



10C

Table 4. MILLING DATA FOR CHEYENNE SUBSTITUTION LINES AND THE PARENTAL VARIETIES, CHEYENNE (Cnn) AND CHINESE SPRING (Cns) GROWN AT ABERDEEN, IDAHO, IN 1963; SUBSTITUTION LINES ARE DESIGNATED BY CHROMOSOME NUMBER AND GENOME (2A = XIII, 2B = II)

Sample	Kernel count (50 g)	Flour yield %	Micron size '75	Maltose	Flour ash %
1A Cns ⁵ x Cnn	1945	63.5	90	68	.752
2A Cns ¹ x Cnn	1686	61.0	86	83	.520
3A Cns ⁵ x Cnn	1813	61.0	92	76	.702
4A Cns ⁵ x Cnn	1660	63.0	85	85	.774
5A Cns ⁵ x Cnn	1810	64.8	90	78	.764
6A Cns ⁵ x Cnn	1690	65.3	84	76	.532
7A Cns ³ x Cnn	2007	64.5	89	74	.505
1B Cns ⁵ x Cnn	1909	64.3	78	74	.490
2B Cns ³ x Cnn	1934	67.5	92	109	.612
3B Cns ⁵ x Cnn	1824	63.2	86	76	.780
4B Cns ⁵ x Cnn	2418	65.0	86	85	.532
5B Cns ⁵ x Cnn	1756	62.4	88	71	.556
6B Cns ⁵ x Cnn	1897	64.3	86	56	.488
7B Cns ⁵ x Cnn	2212	65.4	96	90	.596
1D Cns ⁵ x Cnn	2278	61.7	84	78	.734
2D Cns ² x Cnn	1600	67.4	94	96	.545
3D Cns ⁵ x Cnn	2069	64.1	93	68	.940
4D Cns ⁵ x Cnn	1985	64.0	90	88	.494
5D Cns ⁵ x Cnn	2418	68.0	100	145	.632
6D Cns ⁵ x Cnn	1596	56.7	88	78	.814
7D Cns ⁵ x Cnn	2525	60.4	84	85	.740
Cheyenne	1349	71.0	103	161	.495
Chinese Spring	2071	61.3	61	75	.635

and texture. In the D genome only 5D shows any appreciable improvement over Chinese Spring. Line 2 D in later backcrosses had no advantage over Chinese Spring. Line 1D is even poorer than Chinese Spring and shows the effect first reported by Welsh and Hehn. However, there is some doubt about the exact chromosomal composition of this line. In summary, three lines, 4B, 7B, and 5D appear to carry major factors that give the Cheyenne variety strong gluten properties. Line 1B appears to carry factors that improve loaf characteristics.

Simultaneous with the development of these substitution lines, a flour fractionation method developed by Maes (1962) was experimented with and modified. In this fractionation, 1-gram flour samples were mixed with 2g of pumice and 25g of sand and placed in

a glass column of 1.9 cm diameter and 19 cm long. When a solvent sequence of 40 percent isopropyl alcohol (V/V), 0.2 percent, sodium chloride (W/V), 3.85 percent lactic acid (W/V), and 0.1 percent potassium hydroxide (W/V) was introduced into this column, from 95 to 100 percent of the protein present was recovered. Volumes of solvents collected in the above sequence were 60, 75, 60, and 100ml, respectively.

The gliadins and the glutenins are the principal components of wheat gluten. On the basis of known solubilities, the alcohol solubles would be expected to be the gliadin proteins and the alkali solubles high molecular-weight glutenins. Protein compositions, according to this fractionation method, of the flours of three strong-gluten varieties are shown in Table 5. Mattern and Sandstedt (1957) have shown that increasing percentages of gliadin in wheat flours shorten dough-mixing requirements. Therefore, lines with high percentages of alcohol solubles would be expected to have poorer mixing patterns. However, direct comparisons between varieties and lines are subject to errors introduced by total protein recovery and by the flour protein content. All are subject, also, to aliquot sampling error. A more valid comparison appears to be the ratio of alcohol solubles to alkali solubles—the lower this ratio the stronger the physical dough properties. Of the varieties shown in Table 5, Red River 68 is considered to be the strongest gluten variety, Guide, the next in strength, and C.I. 13881, the weakest of the three, although still a strong-gluten variety. The alcohol solubles/alkali solubles ratio arranges these in this same order in Table 5.

Flours of the 21 substitution lines and the parent varieties, Cheyenne and Chinese Spring, also were subjected to the modified fractionation procedure to see whether the physical dough-handling and baking properties could be associated with the alcohol solubles/alkali solubles ratio. These data are shown in Table 6. The ratio data for the parental varieties for the two years are quite comparable: for Cheyenne, 1.48 in 1963 and 1.54 in 1965; for Chinese Spring, 2.11 in 1963 and 2.06 in 1965. In the substitution set the ratios agreed with visual scoring of mix curves and baked loaves. Flours of Chinese Spring lines carrying the singly substituted Cheyenne chromosomes 5A, 6A, 2B, 5B, 6B, 1D, 3D, 6D, and 7D have mixing and baking properties as poor as or poorer than Chinese Spring itself. The ratios also agree that lines carrying substituted Cheyenne chromosomes 1A, 1B, 3B, 4B, 7B, and 5D have improved either

Table 5. PROTEIN COMPOSITION EXPRESSED AS PERCENT OF TOTAL PROTEIN RECOVERY OF TWO WINTER WHEAT VARIETIES GROWN AT THREE LOCATIONS IN NEBRASKA IN 1966 AND ONE SPRING WHEAT VARIETY GROWN AT LINCOLN IN 1968

Variety	Flour protein content*	Alcohol solubles	Salt solubles	Acid solubles	Alkali solubles	Ratio	Total
						Alch. sol.	
			Lincoln				
Guide	13.50	52.2	4.1	6.2	36.4	1.43	98.9
C.I. 13881	16.20	52.7	2.2	5.5	33.7	1.56	94.1
Red River 68	12.50	48.6	2.9	9.1	34.9	1.39	95.5
			North Platte				
Guide	12.20	50.6	4.6	7.1	37.4	1.35	99.7
C.I. 13881	12.00	49.3	5.0	7.9	36.4	1.35	98.6
			Alliance				
Guide	15.3	54.3	3.1	3.6	37.3	1.46	98.3
C.I. 13881	15.2	50.7	5.2	5.6	33.6	1.51	95.1

* 14% MB.

Table 6. PROTEIN COMPOSITION OF TWENTY-ONE CHEYENNE X CHINESE SPRING^a CHROMOSOME SUBSTITUTION LINES AND PARENTAL VARIETIES EXPRESSED AS PERCENT OF TOTAL PROTEIN RECOVERY

Substitution line	Flour protein content*	Alcohol solubles	Salt solubles	Acid solubles	Alkali solubles	Ratio	TOTAL
						Alch. sol.	
							Alk. sol.
a. Seventeen lines and parents grown in 1963							
1A	12.20	56.4	3.3	7.7	29.5	1.91	96.9
3A	11.80	59.1	2.9	7.8	30.0	1.97	99.9
4A	11.40	58.8	3.3	8.0	30.0	1.96	100.1
5A	11.70	58.3	3.3	7.6	28.8	2.02	98.0
6A	11.75	60.8	2.9	8.0	27.5	2.21	99.2
1B	11.30	57.7	3.0	7.3	31.0	1.86	99.0
3B	11.30	56.6	3.2	7.6	31.0	1.83	98.4
4B	12.35	58.7	2.8	6.2	30.3	1.94	98.0
5B	12.05	59.1	2.8	6.8	28.3	2.09	97.0
6B	10.55	58.4	3.0	7.1	28.8	2.03	97.3
7B	12.90	56.7	2.7	6.8	31.7	1.79	97.9
1D	10.15	63.0	3.2	7.4	25.2	2.50	98.8
3D	12.45	59.0	1.8	6.4	27.4	2.15	94.6
4D	12.30	57.8	1.8	6.4	28.5	2.03	94.5
5D	14.45	57.2	2.2	6.6	30.2	1.89	96.2
6D	12.60	61.1	2.0	6.5	27.3	2.24	96.9
7D	10.55	60.5	2.5	6.8	27.5	2.20	97.3
Cheyenne	12.85	53.4	5.5	7.8	36.2	1.48	102.9
Chinese Spring	13.10	54.0	2.8	7.0	25.6	2.11	89.4
b. Four lines and parents grown in 1965							
2A (XIII)	11.25	56.0	3.1	9.6	29.2	1.92	97.9
2B (II)	11.55	58.0	3.5	8.9	28.7	2.02	99.1
2D	10.95	55.8	2.2	8.0	29.8	1.87	95.8
7A	11.95	55.5	3.4	8.9	30.5	1.82	98.3
Cheyenne	13.85	53.0	3.6	7.3	34.4	1.54	98.3
Chinese Spring	11.50	58.8	3.6	7.8	28.6	2.06	98.8

* 14% MB.

mixing or baking properties or both. Line 7B which was visually scored as having the best mixing and baking properties also had the lowest (best) ratio, 1.79, of all of the lines as compared to the two-year average ratio of 1.51 for Cheyenne.

Conversely, line 1D which had extremely poor mixing and baking properties, also had the highest ratio, 2.50, compared with the two-year mean value of 2.09 for Chinese Spring. Lines 2A, 3A, 4A, 7A, 2B, 2D, and 4D had lower alcohol solubles/alkali solubles ratios than expected from the visual scoring of loaves and mixing properties. Flours of lines 4A and 4D had somewhat better mix curves than the remaining lines of this group.

On the basis of these initial results, it is believed possible to associate protein quality with protein composition. None of the lines had values very close to the strong (quality) parent, but this is expected if the strong quality of Cheyenne is due to the action and/or interaction of a number of genes on different chromosomes.

Summary

Work in the area of improving protein quality and quantity for bread production has been reported and discussed. Results show that grain-protein content can be increased and that, in part, protein quality can be described in terms of the effects of contributions of certain chromosomes on grain-protein composition.

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