Variation of Seed Storage Proteins Within Hard Red Spring Wheat Cultivars and Effect on End-Use Properties[1]

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ABSTRACT

The baking properties of hard red wheats (*Triticum aestivum* L.) are influenced by the gluten endosperm proteins in the kernel. In this study, we found that five of 22 spring wheat cultivars contained intracultivar variation of endosperm proteins as revealed by sodium dodecyl sulfate-polyacrylamide gel electrophoresis. We defined each gluten variant as a biotype and derived pure lines from each biotype for four of the cultivars. The purified biotypes were grown for two years in replicate trials. They were compared to each other and to the original cultivar for agronomic and quality differences. Agronomic differences were associated with a gliadin variant in the cultivar Sheridan, while biotypes of Wampum showed dough quality differences primarily associated with variation at the glutenin locus *Glu-D1*. Our results suggested that, in most instances, purification of cultivars based on gluten composition may be possible without altering agronomic and end-use properties. In the event of biotype differences, the superior type could be selected.

Gliadin and glutenin proteins, collectively referred to as glutens, are the predominant protein in the endosperm of wheat kernels. Gluten gives wheat dough its unique cohesive and elastic properties that allow it to be used for baking bread. Gliadins are relatively small proteins that consist of a complex mixture of polypeptides primarily encoded by genes on the group 1 and 6 chromosomes (Payne et al 1984). A single-hexaploid wheat genotype may produce approximately 25 major gliadin polypeptides and several minor components (Wrigley and Sheperd 1979). Glutenins are larger molecules made from different subunits that are linked by disulfide bonds (Wall 1979). Treatment of glutenins with reducing agents causes breakage of the disulfide bonds, and the glutenins dissociate into subunits. These subunits may be classified as high molecular weight (HMW) and low molecular weight (LMW) subunits (Payne et al 1979). They are encoded by genes on the group 1 chromosomes (Payne et al 1984). Storage proteins of wheat flour typically consist of 50% gliadin, 10% HMW glutenin subunits, and 40% LMW glutenin subunits (Payne et al 1984).

Considerable allelic variation exists for the wheat storage proteins (Payne 1987); this allelic variation has been the basis for studying the relationship between particular gluten proteins and wheat bread-baking properties. Payne et al (1979, 1981) reported an association between HMW glutenin subunits and flour quality. In particular, subunits 5 + 10 (Payne and Lawrence 1983) encoded by the *Glu-D1* locus were associated with desirable dough strength, while the alternative allele-encoding subunits 2 + 12 were associated with poor dough strength. Similar results have been reported in other studies (Payne et al 1984, 1987; Branlard and Dardevet 1985; Lawrence et al 1987, 1988; Mansur et al 1990). Other HMW subunits encoded by different loci have been shown to be correlated either positively or negatively with dough strength or extensibility (Branlard and Dardevet 1985; Lawrence et al 1987, 1988). Certain gliadin and LMW glutenin subunits were also associated with certain flour quality traits in both bread wheat and durum wheat (Kosmolak et al 1980; du Cros et al 1982, 1983; Autran et al 1987; Pogna et al 1988; Singh and Sheperd 1988; Gupta et al 1989).

In addition to quality differences associated with gluten variation, Carrillo et al (1990) showed an association between several HMW glutenin subunit alleles and grain yield. In particular, analysis of recombinant inbred lines derived from a cross between Anza spring wheat (poor quality, high yield) and Cajeme 71 (good quality, low yield) showed that yield variation was significantly associated with HMW glutenin differences. In other words, higher yielding lines tended to have particular HMW glutenin alleles. The strongest association involved alleles at the *Glu-D1* locus.

Lawrence et al (1987) showed that 10 Australian wheat cultivars contained two or three storage protein biotypes, where biotypes were defined as naturally occurring variants found within a cultivar. Biotypes are most likely segregants from the original cross. For cultivars with biotypes at the *Glu-D1* locus, the 5 + 10 subunit conferred superior dough strength compared to that of the 2 + 12 subunit. Gupta and Sheperd (1990) found that at least five Australian hexaploid wheat cultivars contained biotypes for LMW glutenins. Mecham et al (1985) found that approximately one third of 52 western U.S. wheat cultivars contained biotypes. In this report, 22 hard red spring wheat cultivars were examined for gluten biotypes. The gluten variants were compared in replicated trials for agronomic and end-use properties.

MATERIALS AND METHODS

Derivation of Biotypes

Twenty-two spring wheat cultivars were selected on the basis of current or historical importance. Certified seed was obtained for cultivars currently in commercial production. Stocks maintained by the Montana Spring Wheat Breeding Program served as the source for cultivars no longer in the certified seed program. At least 20 random seeds were taken from each cultivar, surface-sterilized in 5% bleach for 5 min, and cut in half. The embryo portion was stored at 4°C. Seed storage proteins were extracted from the brush end of the seed (Laemmli 1970) and fractionated by sodium dodecyl sulfate-polyacrylamide gel electrophoresis (SDS-PAGE) (Payne et al 1981). Gels were examined for within-cultivar variation. When variants were noted, the embryo portion of the seed was matched to the gel profiles. Three to four half-seeds per biotype were germinated, and two generations of seed increase were conducted in the greenhouse. Seed from like biotypes was bulked. For this report, biotypes were given a letter designation following the cultivar name (e.g., Fortuna-A and Fortuna-B), while the original cultivar was designated by the letter "C" (e.g., Fortuna-C). Biotypes were purified from cultivars Borah, Fortuna, Sheridan, and Wampum. (See Fig. 1.)

Experimental Design

Replicate trials were planted at the Post Research Farm near Bozeman, MT, in 1990 and 1991. Both trials were designed as randomized split-plot experiments (with cultivars as main plots and variants as subplots). In 1990, subplots consisted of one 3-m row; in 1991, subplots consisted of four 3-m rows. Three replicates were grown in 1990 and four replicates were grown 1991. Agronomic data was collected throughout the season. Grain was harvested in August of both years for quality analysis.

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End-use properties were evaluated using approved methods (AACC 1983). Grain protein content was determined by near-infrared reflectance according to AACC method 39-10. Buhler-milled flour was evaluated for dough properties (AACC methods 26-10, 54-40A [1990 samples], and 54-21 [1991 samples]). Bake tests for 1991 samples were analyzed using AACC method 10-10B, and bake tests for 1990 samples were analyzed using a modification of that method. Test weight of 1991 samples was determined by AACC method 55-10. Kernel weight for 1990 and 1991 samples was determined by counting 30 g of seed and calculating 1,000-kernel weight. For all traits, we analyzed three replicates of 1990 samples and four replicates of 1991 samples. Analysis of variance was conducted using MSUSTAT (Lund 1987). Variants were compared to each other and to the initial variety using least significant difference (LSD). Because plot technique and baking methodology differed slightly between years, the analyses were not combined for the two years.

RESULTS

Occurrence of Biotypes in Spring Wheat Cultivars

Gluten variants were not observed for Alex, Amidon, Coteau, Era, Glenman, Hi-Line, Newana, Olaf, Oslo, Protor, Rambo, Tioga, or Waldron. Variants, represented by 1–2 seeds in a sample of 20, were observed in Butte, Fortuna, Lew, and Pondera. This rare occurrence suggested possible contamination rather than a true biotype within the variety. Pure lines derived from these rare types showed obvious morphological and agronomic differences relative to the original variety (data not shown). Thus, these were likely to be contaminants and were not further investigated. Borah, Fortuna, Sheridan, Thatcher, and Wampum all contained variant types in relatively high frequencies (Table I), and thus appeared to be biotypes that were part of the original cultivar. Pure lines were derived from biotypes of Borah, Fortuna, Sheridan, and Wampum.

Description of Biotypes

Biotypes within Sheridan and Wampum varied for HMW glutenins. The SDS-PAGE profiles of these biotypes were compared to reference cultivars as described by Payne and Lawrence (1983). The HMW glutenin subunits for biotypes within Sheridan and Wampum are shown in Table I. Biotypes within Fortuna, Thatcher, and Borah varied for LMW proteins on SDS-PAGE gels, indicating variation for either LMW glutenins or gliadins. The two-step SDS-PAGE procedure of Singh and Sheperd (1988) was conducted for these biotypes to determine whether variant proteins were LMW glutenins or gliadins. In this procedure, proteins were electrophoresed before being reduced, whereby the gliadins migrate rapidly and the unreduced LMW glutenins remain near the electrophoretic origin. The portion of the gel near the origin (now free from gliadins) is excised from the gel, reduced with 2-mercaptoethanol, applied to the top of a second polyacrylamide gel, and electrophoresed again. This allowed visualization of the LMW glutenins free of gliadins. This procedure indicated that the biotypes within Fortuna and Thatcher were due to gliadin variation. The results for the Borah biotypes were difficult to interpret due to poor separation of gliadins and glutenins. The Borah biotypes were either gliadin or LMW glutenin variants.

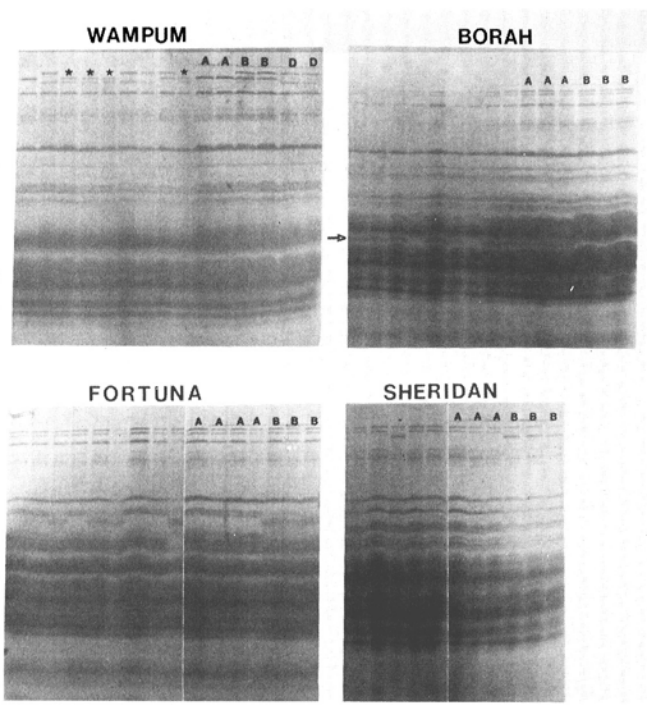

Fig. 1. Sodium dodecyl sulfate-polyacrylamide gel electrophoresis comparisons of biotypes and original cultivars for four spring wheat cultivars. Purified biotypes are designated with letters A, B, and D. Lanes containing samples from the original cultivar are not lettered. * = apparent biotype not purified or tested.

Agronomic Evaluation of Biotypes

Results in 1990 samples indicated that biotypes of Sheridan varied significantly for grain yield; Sheridan-A produced approximately 30% more grain than did the original cultivar (Table II). Differences among biotypes were not significant in the 1991 samples, although Sheridan-A did have approximately 10% higher yields than those of either Sheridan-B or Sheridan-C (Table III). Other agronomic differences among biotypes in the 1991 samples were test weight and 1,000-kernel weight variations among the Wampum biotypes and test weight variation among the Fortuna biotypes. No other agronomic differences were detected in either the 1990 or 1991 samples.

Quality Evaluation of Biotypes

Grain harvested from field trials in 1990 and 1991 was analyzed for end-use properties important in breadmaking (Tables II and III). No variation was observed among biotypes of Sheridan or Borah in samples from either year. Grain protein varied between the Fortuna biotypes; both biotypes were greater than the Fortuna-C in 1990 samples (Table II), but no significant differences were detected in 1991 samples (Table III).

Several quality differences were detected among biotypes of Wampum. In particular, wheat protein, mixograph peak time, and dough mix time varied significantly in 1990 samples. Farinograph absorption, dough mix time, and grain protein showed significant variation among Wampum biotypes in 1991 samples. Wampum-D tended to be the most extreme biotype for these analyses. This biotype contains the *Glu-D1* 5 + 10 alleles, whereas Wampum-A and Wampum-B contained the *Glu-D1* 2 + 12 alleles (Table I).

TABLE I
Differences Among Biotypes for Five Hard Red Spring Wheat Cultivars

Cultivar	Biotype	Seeds Observed per Biotype	Seeds Bulked per Biotype	High Molecular Weight Subunits[a]		
				Glu-A	*Glu-B*	*Glu-D*
Wampum	A	8/34	3	Null	7+9	2+12
	B	12/34	3	1	7+9	2+12
	D	8/34	3	1	7+9	5+10
Fortuna[b]	A	19/34	4	2	7+8	5+10
	B	15/34	3	2	7+8	5+10
Sheridan	A	22/32	4	Null	6+8	5+10
	B	10/32	3	Null	7+8	5+10
Borah[b]	A	18/30	3	2	7+9	5+10
	B	12/30	3	2	7+9	5+10
Thatcher[b]	A	22/33	3	2	7+9	5+10
	B	11/33	3	2	7+9	5+10

[a]Based on the method of Payne and Lawrence (1983).
[b]Cultivar varied for gliadins or low molecular weight glutenins.

DISCUSSION

Five of 22 hard red spring wheat cultivars were heterogeneous for gluten proteins. These results were compatible with that of Mecham et al (1985), who found that 17 of 52 western U.S. wheat varieties had gluten biotypes. Although this fact may complicate varietal identification by SDS-PAGE, heterogeneity of gluten proteins per se would unlikely be detrimental in regard to varietal performance. However, such variation might provide the opportunity for selection based on gluten profiles, which may lead to improvements in traits of interest if particular variant alleles are associated with agronomic or end-use traits. We tested this possibility by purifying four cultivars on the basis of gluten composition and comparing biotypes with the original cultivar for agronomic and quality factors.

Of the four cultivars that were purified based on gluten types, Wampum and Sheridan varied in regard to HMW glutenins, Fortuna varied in regard to gliadins, and Borah varied in regard to either gliadins or LMW glutenins. Agronomic differences detected included a yield advantage for Sheridan-A in 1990 samples, increased test weight for biotypes of Fortuna in 1991 samples, and reduced kernel weight and test weight for Wampum biotypes in 1991 samples. The variation in Sheridan was associated with the *Glu-B1* locus, where subunits 6 + 8 were associated with higher yields than were subunits 7 + 8. A compatible result was reported by Carrillo et al (1990), who found that certain HMW glutenin alleles were associated with yield differences among recombinant inbred lines derived from a cross between Anza and Cajeme 71 spring wheats. However, in their experiments, the higher yielding Anza-types contained subunits 7 + 8, while the lower yielding Cajeme 71-types contained the subunits 17 + 18. Our results, and those of Carrillo et al (1990), likely indicate linkage between the gluten alleles and alleles influencing grain yield.

The only biotypes to show flour quality differences were those derived from Wampum. In particular, mixograph peak time and baking mix time were both highest for Wampum-D, which contains the 5 + 10 allele at the *Glu-D1* locus. This indicated greater dough strength and was compatible with previous studies showing a similar association (Payne et al 1979, 1981, 1987; Branlard and Dardevet 1985; Lawrence et al 1987, 1988; Mansur et al 1990; Manley et al 1992). Lawrence et al (1987) found that biotypes of Australian wheat varieties that differed at *Glu-D1* for subunits 5 + 10 and 2 + 12 also showed the greatest differences in dough strength. Interestingly, the Wampum-D biotype had higher grain protein percent than did Wampum-B biotype in samples of both years. Other significant differences among Wampum biotypes included a higher farinograph absorption for

TABLE II
Agronomic and Quality Evaluation of Biotypes Derived from Four Hard Red Spring Wheat Cultivars (1990 Samples)[a]

Cultivar	Biotype[b]	Grain Yield (kg)	Kernel Wt. (g)	Grain Protein (%)	Mixo. Abs. (%)	Mixo. Pk. Time (min)	Mixo. Pk. Ht. (cm)	Bake Abs. (%)	Mix Time (min)	Loaf Vol. (cm)
Wampum	A	42.6	33.5	13.2 AB[c]	69.6	3.3 A	7.1	70.3	5.7 A	275.0
	B	39.6	31.9	13.0 A	69.5	3.4 A	7.0	69.2	5.6 A	271.7
	C	47.4	32.7	12.6 A	70.5	3.6 AB	7.5	70.9	5.7 A	265.0
	D	38.6	31.6	13.8 B	69.2	4.5 B	6.9	69.8	6.7 B	255.0
Fortuna	A	20.9	41.0	17.1 B	75.4	2.9	8.9	78.3	5.1	270.0
	B	23.1	38.4	17.2 B	75.4	2.8	8.9	78.4	5.0	263.3
	C	26.0	39.7	16.2 A	73.6	3.1	8.3	78.1	4.4	261.7
Sheridan	A	44.8 B	32.2	16.0	69.3	2.9	6.9	75.8	5.4	246.7
	B	32.8 A	31.3	15.9	70.3	2.9	7.3	76.3	5.2	263.3
	C	27.6 A	30.9	16.0	70.7	3.3	7.4	76.1	5.2	253.3
Borah	A	34.6	30.0	14.0	70.2	3.2	7.2	73.5	5.0	260.0
	B	34.1	30.7	14.1	69.9	3.4	7.2	74.0	4.8	265.0
	C	31.9	29.9	14.4	69.4	3.3	7.0	73.3	4.9	253.3

[a]Kernel Wt. = 1,000-kernel weight; Mixo. Abs. = mixograph water absorption; Mixo. Pk. Time = time from first addition of water to maximum dough consistency; Mixo. Pk. Ht. = distance in mixograph units when curve reaches maximum height; Bake Abs. = the amount of water added to prepare flour for baking; Mix time = the time needed to bring dough to optimum consistency for baking; Loaf Vol. = final loaf volume based on rape seed displacement.
[b]C represents the original cultivar.
[c]Only means followed by letters are significantly different ($P \leq 0.05$).

TABLE III
Agronomic and Quality Evaluation of Biotypes Derived from Four Hard Red Spring Wheat Cultivars (1991 Samples)[a]

Cultivar	Biotype[b]	Grain Yield (kg)	Test Wt. (lb/bu)	Kernel Wt. (g)	Kernel Protein (%)	Flour Yield (g)	Far. Abs. (%)	Far. Peak (cm)	Far. Stab. (min)	Mix Time (min)	Loaf Vol. (cm)
Wampum	A	35.8	56.3 B[c]	24.0 AB	15.8 AB	65.0	62.8 B	25.1	17.6	3.4 B	1,147
	B	37.7	55.7 A	25.3 B	15.4 A	64.1	60.7 A	22.2	21.3	2.9 A	1,157
	C	35.4	57.6 C	22.6 A	15.8 AB	65.3	60.6 B	22.5	16.0	4.0 C	1,140
	D	35.7	57.7 C	22.5 A	16.0 B	65.8	60.9 A	25.2	15.6	3.7 BC	1,150
Fortuna	A	33.4	60.6 B	31.2	16.0	67.2	67.0	21.5	12.5	2.7	1,125
	B	32.4	60.3 AB	30.1	16.1	67.4	65.6	18.2	13.7	2.4	1,140
	C	33.0	60.1 A	28.8	15.9	66.8	65.6	18.7	16.0	2.7	1,100
Sheridan	A	30.1	56.7	23.2	16.7	62.9	66.8	17.0	12.1	2.8	1,124
	B	27.1	56.7	23.0	16.7	63.3	67.0	23.3	11.7	3.0	1,145
	C	27.8	57.2	25.0	16.3	64.4	66.9	18.9	16.2	2.9	1,123
Borah	A	38.5	55.4	21.4	15.6	66.4	64.0	22.8	13.0	3.2	1,193
	B	37.3	55.7	21.8	15.4	66.7	64.4	21.9	10.3	3.2	1,168
	C	36.7	55.4	22.0	15.5	67.1	64.4	21.8	15.4	3.3	1,154

[a]Kernel Wt. = 1,000-kernel weight; Far. Abs. = amount of water estimated from the farinograph curve; Far. Pk. = time from first addition of water to maximum dough consistency; Far. Stab. = departure time minus arrival time at the 500 Farinograph unit reference line; Mix Time = time needed to bring dough to optimum consistency for baking; Loaf Vol. = final loaf volume based on rape seed displacement.
[b]C represents the original cultivar.
[c]Only means followed by letters are significantly different ($P \leq 0.05$).

Wampum-A, which was null for the *Glu-A1* allele, in the 1991 sample. The observed variation at *Glu-A1* did not appear to effect dough strength, as it had in previous studies (Grama et al 1987; Lawrence et al 1987). However, in these previous studies, variation at *Glu-A1* was found to be less important than *Glu-D1* variation.

Our results show that gluten biotypes occured in hard red spring wheat varieties. Also, some differences, both in end-use quality and agronomic properties, may be associated with gluten variation. The most dramatic difference in our experiments may be the yield differences associated with variation at the *Glu-B1* locus in Sheridan. The grain protein advantage observed for Wampum-D over that of Wampum-C may have some economic importance. Although quality differences in Wampum were associated with variation at *Glu-D1*, our experiments showed that current hard red spring wheat varieties possessed the favorable allele at this locus. Carrillo et al (1990) noted that HMW variation accounted for no more than 25% of the dough quality variation observed in the recombinant inbred lines. Hamer et al (1992) found that prediction of quality based on analysis of glutenin-A alleles was of limited value in a Dutch breeding program. Thus, although some differences may be associated with certain gluten biotypes, it is not clear that extraction and evaluation of biotypes with specific gluten genotypes would result in improved quality of hard red spring wheat varieties.

However, a second aspect may be important in regard to the heterogeneity observed in wheat cultivars. SDS-PAGE of gluten proteins is commonly used for cultivar identification and evaluation of cultivar purity. Heterogeneity certainly complicates these uses. Mecham et al (1985) suggested that it would be desirable to reselect heterogeneous cultivars to a uniform type to avoid these complications, especially if the purification process did not alter cultivar performance. Our results suggested that, although cultivar performance may be influenced in some cases, it should be relatively straightforward to select the superior biotype in these cases.

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