Indirect selection for grain protein in winter wheat

by Maher Noaman Mohamed Noaman

A thesis submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Crop and Soil Science
Montana State University

Abstract:
Increasing grain protein content is an important wheat breeding goal. A previous study by Noaman and Taylor (1988b) showed the combination of protein content in the head, peduncle, and flag leaf of winter wheat at heading provided a good estimate for grain protein. The objectives of this research were to study the heritability of protein content in these plant parts and to apply these results in indirect selection scheme for grain protein improvement.

Two random populations of winter wheat from four parents in double crosses were used in this study. Sixty random F2-derived F5 and F6 lines were grown in randomized complete block experiment with 3 replicates in two years.

Significant differences for grain yield, grain protein, and vegetative protein content were detected among F5 and F6 lines in both populations. The genotypic and phenotypic correlations between grain protein and protein content in different plant parts were in agreement. Estimates of narrow sense heritability of protein content using variance components method ranged from 0.46 to 0.94 for leaf 2 at anthesis and head at heading, respectively, in population 1, and, from 0.63 to 0.89 for peduncle and head at heading, respectively, in population 2. The parent offspring regression method for calculating the heritabilities gave similar results. Correlation coefficient (r) between predicted and observed grain protein ranged from 0.50 to 0.88 and from 0.37 to 0.84 in populations 1 and 2, respectively. The highest r was obtained from the combination of head, peduncle, and flag leaf protein at heading. Correlation between protein in plant parts and grain yield was very small and not significant.

The high heritability of vegetative protein at heading allows the identification of genotypes before pollination which are likely to produce high grain protein. These can be intercrossed in a recurrent selection scheme to increase grain protein content. Indirect selection for head, peduncle, and flag leaf protein should result in increased grain protein without yield reduction noted in other breeding schemes.

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APPROVAL

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Maher Noaman Mohamed Noaman

This thesis has been read by each member of the thesis committee and has been found to be satisfactory regarding content, English usage, format, citation, bibliographic style, and consistency, and is ready for submission to the College of Graduate Studies.

August 11, 1988
Date

G. Allan Taylor
Chairperson, Graduate Committee

Approved for the Major Department

August 12, 1988
Date

James W. Bauder
Head, Major Department

Approved for the College of Graduate Studies

8-12-88
Date

M. Malone
Graduate Dean

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ABSTRACT

Increasing grain protein content is an important wheat breeding goal. A previous study by Noaman and Taylor (1988b) showed the combination of protein content in the head, peduncle, and flag leaf of winter wheat at heading provided a good estimate for grain protein. The objectives of this research were to study the heritability of protein content in these plant parts and to apply these results in indirect selection scheme for grain protein improvement.

Two random populations of winter wheat from four parents in double crosses were used in this study. Sixty random F2-derived F5 and F6 lines were grown in randomized complete block experiment with 3 replicates in two years.

Significant differences for grain yield, grain protein, and vegetative protein content were detected among F5 and F6 lines in both populations. The genotypic and phenotypic correlations between grain protein and protein content in different plant parts were in agreement. Estimates of narrow sense heritability of protein content using variance components method ranged from 0.46 to 0.94 for leaf 2 at anthesis and head at heading, respectively, in population 1, and, from 0.63 to 0.89 for peduncle and head at heading, respectively, in population 2. The parent offspring regression method for calculating the heritabilities gave similar results. Correlation coefficient (r) between predicted and observed grain protein ranged from 0.50 to 0.88 and from 0.37 to 0.84 in populations 1 and 2, respectively. The highest r was obtained from the combination of head, peduncle, and flag leaf protein at heading. Correlation between protein in plant parts and grain yield was very small and not significant.

The high heritability of vegetative protein at heading allows the identification of genotypes before pollination which are likely to produce high grain protein. These can be intercrossed in a recurrent selection scheme to increase grain protein content. Indirect selection for head, peduncle, and flag leaf protein should result in increased grain protein without yield reduction noted in other breeding schemes.

INTRODUCTION

It is necessary to increase protein productivity of grain crops to meet present and future world protein requirements. Grain protein content of wheat is a major contributor to nutritional quality and plays a decisive role in the baking performance of wheat flour (Sampson et al., 1983). Grain protein content is the end result of complex physiological processes and is controlled by many genes. Recent emphasis on improving the nutritive value of wheat has resulted in greater efforts to increase grain protein content. Plant scientists are searching for germplasm and for techniques that help maintain or enhance grain protein content as grain yields are increased. Unfortunately, the negative relationship between grain yield and grain protein presents a challenging problem. At least two approaches may be used to overcome or reduce this inverse relationship. First, increasing both N uptake and carbohydrate synthesis simultaneously which requires understanding N movement before grain formation. Second, by indirect selection for characters which are positively correlated to both grain yield and grain protein.

Noaman and Taylor (1988b) showed the combination of protein content in the head, peduncle, and flag leaf at heading provided good prediction for grain protein. The objectives of this study were; 1) to apply these results to test the validity of using these relationships as an indirect selection technique to predict grain protein, and, 2) to estimate the heritability of protein content in these plant parts.

LITERATURE REVIEW

Relationship Between Grain Protein and Vegetative Protein

Carbohydrates and protein comprise more than 90% of grain dry weight, with carbohydrates comprising the larger fraction. Nitrogen is absorbed by plant roots, stored in stems and leaves, and then translocated to the developing grain where it is incorporated into protein. Carbohydrates, on the other hand, are photosynthesized by the plant and then translocated to the grain. Haunold et al. (1962b) reported that protein in the grain of wheat results from the translocation of nitrogenous compounds from other parts of wheat plant. Presumably, the level of nitrogen in the plant influences the amount ultimately translocated to the wheat grain. The level of nitrogen in the wheat plant, in turn, is affected by the availability of nitrogen in the soil in which the wheat grows.

The relationship between plant N and grain protein has been the subject of much research. Grain protein content appears to act as a highly heritable trait when studied independently of other plant characteristics (Haunold et al., 1962a; Chapman and McNeal, 1970). However, when studied in conjunction with related characteristics, grain protein content seems to be largely determined by plant growth processes (Army and McNeal, 1958; McNeal et al., 1968, 1971). McNeal et al. (1968) reported a close relationship between grain N content and the amount of top growth. McNeal et al. (1972) found that grain N yield is closely related to the amount of N in the plant ($r = 0.96$). They postulated that grain protein content would then be dependent on the amount of carbohydrates photosynthesized and distributed to grain, which in turn would be influenced by kernel size and kernel number per plant. Woodruff (1972) concluded that breeding cultivars with more prolonged leaf area development and similar, or lower harvest index would increase grain nitrogen concentrations for a given yield level. Cox et al. (1985) showed that total N assimilation was correlated ($r = 0.68$ to 0.86; $P < 0.01$) with grain and grain protein yields. Nair and Abrol (1978) suggested that for genotypic improvement of grain N, the capacity of the upper leaf blades for NO3-assimilation and mobilization of reduced N is important. Rao et al. (1977) suggested that no single identifiable factor can be used as a physiological criterion in selecting wheat genotypes for efficient N utilization. Selection must consider several factors simultaneously, including long-term capacity for N absorption, in vivo reduction of nitrate, and efficient translocation of vegetative N to the developing grains. The synthesis of more protein or more carbohydrate in the grain requires the availability of additional photosynthesis to developing grains. Furthermore, an increment in nitrogen input is needed to produce additional protein. Alternatively, more efficient utilization of assimilates towards grain production would achieve the same results. In a study of 13 soft red winter wheat cultivars, no association was found between protein content and grain yield, especially among cultivars with 'Frondosa' and 'Fronteira' in their parentage (Middleton et al., 1954). Close relationship between grain protein and vegetative protein at heading was found by Noaman and Taylor (1988b). They established five prediction equations for grain protein using vegetative protein as independent variables. They concluded that the combination of head protein, peduncle protein, and flag leaf protein at heading provided a good prediction for grain protein content in winter wheat.

Inheritance of Grain and Vegetative Protein Content

The first published report in the United States of genetic investigation of the quantity of protein in the grain of wheat date to the work of Clark (1926). Since then, grain protein content in wheat has been studied by various investigators, who have postulated the genetic control of protein by gene numbers ranging from one to eight factor pairs (Aamondt and Torrie, 1935; and Warner, 1952). Most of wheat studies have concluded that grain protein is genetically controlled and heavily influenced by environmental factors. Multigenic control of the high grain protein characteristic was indicated (Haunold et al, 1962b).

Kuspira and Unrau (1957) studying chromosome substitution lines of Thatcher spring wheat in a Chinese Spring background, indicated that genes on at least five different chromosomes were associated with the expression of grain protein content of Thatcher.

Most of the characteristics with which the plant breeder works exhibit the continuous variation generally explained by the multiple factor hypothesis. An understanding of the nature of the hereditary mechanism controlling these characters should enhance the development of superior cultivars. Heritability has been defined by Lush (1940) as that fraction of total variance within a segregating population attributable to additive genetic effects. Heritability estimates of grain protein as high as 0.86 have been calculated (Stuber et al., 1962). Johnson et al. (1963) obtained F2 derived families from an 'Atlas 66' x 'Comanche' cross that were more productive and had higher grain protein than Comanche, the lower protein parent. This suggests significant potential for progress in selecting for high grain protein content. Using the regression of F3 lines on F2 plants, Sunderman et al. (1965) obtained estimates of heritability of grain protein of from 0.15 to 0.26. Davis et al. (1961) obtained broad sense heritability estimates of 0.54 to 0.69. Haunold et al. (1962a) obtained heritability estimates as high as 0.65 for grain protein content by using parent offspring regression techniques for several selfed generations. Baker et al. (1971) obtained heritability for grain protein of 0.89 using variance components.

MATERIALS AND METHODS

Genetic Materials

Two winter wheat populations used in this study involved parents differing in grain protein content, grain yield, and other agronomic characters (Table 1). Population 1 was formed from the cross (ID 103/MT 7811//PLV/Manning). All are hard red winter wheats except MT 7811 which is a hard white winter wheat. Population 2 was formed from the cross (MT 8001/MAR-5//ID 103/MT 7840). All are hard red winter wheats. The four parents and 60 random F2-derived F5 and F6 lines from each population plus a hard red winter wheat with high grain protein 'Redwin' and one with low grain protein 'Brule' as check cultivars were used. In 1986 the F5 and in 1987 the F6 lines were planted at one location and two locations, respectively. No selection was practiced for grain protein during the testing period.

Experimental Design

The 66 entries were grown in randomized complete block experiments each with 3 replicates in each environment. Plots were 3.5 m long and consisted of 3 rows 30.5 cm apart (each plot consisted of a single entry). The middle row was used for yield evaluation and the outer two rows for plant sampling. The planting rate was 8 g of seed per 3.5 m row. Each population was planted and treated as a separate experiment.

The two experiments (populations) were conducted in 1986 and 1987 at the Montana State University, Post Field Research Laboratory, Bozeman, Montana. In 1987, in addition to the Post Farm location, they were planted at Fort Ellis 5 miles east of Bozeman. Experimental design, plot dimensions, and planting rates were the same for both years and locations. In the years, 1985-86 and 1986-87, about 110 kg/ha and 150 kg/ha of available N(NO3-N), respectively, were present in the upper one meter of the soil profile at the Post Farm location. Consequently, we added 100 kg and 140 kg N/ha of ammomium nitrate (34%) as a source of N in both years, respectively. About 90 kg/ha of available N(NO3-N) were present in the soil profile at Fort Ellis location. We added 100 kg N/ha of ammonium nitrate in this location for 1986-1987. Adequate P, K, and S were present in the profile in both locations in both years. Crop year precipitation (September 1985 to August 1986) was 47.07 cm. The second year precipitation (September 1986 to August 1987) was 44.68 cm. The average growing season temperature was 6.7°C in the first season and 6.9° C in the second season. Soil type in both locations was similar (Bozeman series, Fine-silt, mixed, Argic Pachic Cryoborall). Random plant samples were taken from the outer rows, separated into head, peduncle, flag leaf, and second leaf (from plant top) at heading and anthesis. These samples were collected, oven-dried to a constant weight at 60°C, then ground in a Udy Cyclone Mill (0.5 mm screen). The Technicon Infralyzer TM 400 instrument was used to estimate protein content in the ground plant samples (Noaman et al., 1988a). Data were analyzed by standard analysis of variance. Least significant difference (LSD) was used to test means for significant differences among genotypes (Steel and Torrie, 1980). Heritability of each character (as the additive portion of total genetic variance) was estimated as the ratio of genotypic (G) to the phenotypic (G + E) variance, where G was the component of variance due to average differences among cultivars and E was the component due to deviations from average performance (measurement errors and genotype x year and location interactions). Genotypic variance was computed from the expected mean squares from the analysis of variance. Confidence intervals for heritability estimates were computed using methods described by Knapp et al. (1985).

Table 1. Means of plant height, days to heading, grain yield, and grain protein of parents involved in the two double crosses.†

Parents	Origin	Plant height cm	Days to heading‡	Grain yield kg/ha	Grain protein g/kg
Population 1					
ID 103	Idaho	81.2	160	2227	138
MT 7811	Montana	99.6	157	2479	144
Plainsman V	Private	85.5	159	1472	178
Manning	Utah	100.8	167	2215	130
Population 2					
MT 8001	Montana	85.8	160	2049	152
Martonvasar	Hungary	97.5	161	1196	142
ID 103	Idaho	81.2	160	2233	138
MT 7840	Montana	91.9	159	2117	147
Checks					
Redwin	Montana	105.6	165	2061	139
Brule	Nebraska	95.3	153	2472	119

† Average of three locations and two years.
‡ The number of days from January 1 until approximately 50% of the heads had emerged from the flag leaf sheath.

The other common method of estimating the heritability percentages is by the progeny-parent regression procedure proposed by Lush (1940). This procedure involves regressing of the mean value of a character in the progeny of F6 upon the value of the same character in the parent (F5).

Simple correlations among traits were calculated at both genotypic and phenotypic levels. Phenotypic correlations were computed using entry means. The genotypic correlations were estimated using genetic variance and covariance components isolated from the appropriate mean square or mean product.

RESULTS AND DISCUSSION

Variation Among Lines for Grain Yield and Protein Content

Protein content varied greatly in both populations at the three environments. Significant differences (P < 0.01) for grain yield, grain protein content, and protein content in plant parts were detected among F5s and F6s in all three test environments (Tables 2, 3 & 4). This variability, if genetic, should permit genetic advance through selection.

Table 2. Mean squares for protein content in different plant parts at various growth stages, grain protein (GP), and grain yield (GY) for the F5 in populations 1 and 2 at Post Farm.

		Heading				Anthesis	Ripe	
Source	df	Head	Peduncle	Leaf1	Leaf2	Leaf2	GP	GY
				Population 1				
Reps.	2	0.32	0.02	3.83	0.59	0.23	0.30	9739
Genotype	65	6.07 **	0.73 **	3.62 **	4.64 **	0.56 **	2.43 **	5030 **
Error	130	0.21	0.17	0.39	0.51	0.25	0.09	2566
				Population 2				
Reps.	2	0.04	0.05	1.50	0.04	0.08	0.03	4515
Genotype	65	4.19 **	0.51 **	5.69 **	2.98 **	0.97 **	3.41 **	6236 **
Error	130	0.25	0.18	0.33	0.51	0.40	0.11	1097

** Significant at 1% level of probability.

Table 3. Mean squares for protein content in different plant parts at various growth stages, grain protein (GP), and grain yield (GY) for the F6 in populations 1 and 2 at Post Farm.

		Heading				Anthesis	Ripe	
Source	df	Head	Peduncle	Leaf1	Leaf2	Leaf2	GP	GY
				Population 1				
Reps.	2	0.66	0.43	0.97	1.20	0.19	0.90	1532
Genotype	65	4.45 **	0.61 **	3.70 **	3.17 **	0.40 **	3.87 **	5398 **
Error	130	0.26	0.21	0.51	0.60	0.36	0.17	540
				Population 2				
Reps.	2	1.60	0.05	0.27	0.21	0.54	0.01	552
Genotype	65	2.95 **	0.43 **	3.90 **	1.68 **	0.94 **	3.33 **	8303 **
Error	130	0.41	0.23	0.58	0.62	0.35	0.13	465

** Significant at 1% level of probability.

Table 4. Mean squares for protein content in different plant parts at various growth stages, grain protein (GP), and grain yield (GY) for the F6 in populations 1 and 2 at Fort Ellis.

		Heading				Anthesis	Ripe	
Source	df	Head	Peduncle	Leaf1	Leaf2	Leaf2	GP	GY
				Population 1				
Reps.	2	0.34	0.23	1.19	0.89	0.08	0.26	45500
Genotype	65	4.64 **	0.53 **	2.93 **	2.09 **	0.46 **	2.14 **	15450 **
Error	130	0.30	0.22	0.36	0.51	0.21	0.14	1494
				Population 2				
Reps.	2	0.96	0.08	0.37	0.76	0.25	0.17	11610
Genotype	65	2.83 **	0.42 **	2.63 **	1.69 **	0.97 **	1.54 **	15810 **
Error	130	0.32	0.15	0.36	0.54	0.27	0.14	1196

** Significant at 1% level of probability.

Pooled analyses of variance (Table 5) show genotype (G) x environment (E) interactions. The G x E interactions were highly significant for most measurements across the three test environments for both populations. Peduncle protein at heading in both populations and leaf 2 protein at anthesis in population 1 showed no G x E interaction. This indicates that genotypes react differently when evaluated in different environments. Although the G x E interaction effect was significant for most of the measured variables, the magnitude of the mean square for interaction compared to those for genotypes was fairly low. In no instances were these interaction mean squares as large as the genotype mean squares. It seems that the need for sampling of several environments (years and locations) in a testing program is important. For protein content and grain yield, G x E were similar in the two populations.

The means of parents, midparents, and progenies, and the range of means and standard deviations of the F5 and F6 progenies for grain yield and grain protein are shown in Table 6. All the means of the progenies of F5 and F6 in both populations at the three environments exceeded the means of the midparents for grain yield. Transgressive segregation for grain yield was apparent where some of the F5 and F6 progeny means exceeded the highest parents in both populations and some of the progeny means were lower than the low yielding parent.

Without exception, all the means of the mid-parent in population 1 exceeded the mean of the progeny of F5 and F6 for grain protein. This was due to the high protein parent 'Plainsman V' which elevated the mean of the parents. Thus, none of the progeny means exceeded the protein content of this cultivar. In population 2, the situation was reversed where all the means of the progenies exceeded the mean of the parents. Some of the progeny means exceeded the highest protein parents in all environments.

Table 5. Mean squares for protein content in different plant parts at various growth stages, grain protein (GP), and grain yield (GY) for populations 1 and 2 over three environments.

		Heading				Anthesis	Ripe	
Source	df	Head	Peduncle	Leaf1	Leaf2	Leaf2	GP	GY
				Population 1				
Environ.(E)	2	9.16	10.11	4.43	12.18	2.28	261.48	64842
Reps./ E	6	0.44	0.23	1.99	0.89	0.17	0.78	6294
Genotype(G)	65	13.71 **	1.48 **	9.11 **	8.25 **	0.94 **	6.64 **	15835 **
G x E	130	0.72 **	0.19 ns	0.57 *	0.83 **	0.24 ns	0.74 **	7191 **
Error	390	0.26	0.20	0.42	0.54	0.27	0.12	1518
				Population 2				
Environ.(E)	2	6.58	4.90	9.09	7.72	0.69	256.09	362838
Reps./ E	6	0.87	0.06	0.71	0.34	0.29	0.73	5696
Genotype(G)	65	8.78 **	1.08**	10.55 **	4.74 **	3.00 **	5.89 **	16853 **
G x E	130	0.59 **	0.13ns	0.84 **	0.80 **	0.44 **	0.93 **	6598 **
Error	390	0.33	0.19	0.42	0.56	0.27	0.12	894

*, ** Significant at 5% and 1% levels of probability, respectively.
ns Not significant.

No one line in population 1 combined a maximum expression for both grain yield and grain protein. In other words, none of the progeny means exceeded both high grain yield and high grain protein parents simultaneously. In population 2, however, five progeny means had both higher grain yield and grain protein than the highest parents in the Post Farm F5 experiment. These five lines and the other three lines from population 2 at Fort Ellis experiment (F6) exceeded the highest parent in grain yield and grain protein significantly.

Averaged over two locations, only 3 F6 lines combined high GY with reasonably high GP but not higher than the high protein parent in population 1. None of the progeny means exceeded the combination of the highest GY and GP parents. In population 2, two progeny means combined both higher GY and higher GP than the highest parents, simultaneously. These results indicate that selection for high grain yield and grain protein simultaneously can be achieved as was suggested by Stuber et al. (1962) and Johnson et al. (1971).

In population 1 none of the lines combined both GY and GP higher than the highest check cultivar. In population 2, only one line exceeded both the check cultivars in GY and GP simultaneously.

It might be possible to select for any desired combination of GY and GP, but some compromise or trade off would have to be made in the lines selected. The combined experiments indicate potential for selecting lines with high GY and high GP in these populations.

In both populations at the three environments the 60 progenies showed continuous distribution in protein content and grain yield with no breaks in the distribution (Tables 7 & 8). Differences in protein and grain yield may result from minor genes whose individual effects are influenced by the environment. In general, the most frequent class of each progeny contained, or was close to, the progeny mean. These results

Table 6. Means, range of means, and standard deviation for grain yield (kg/ha) and grain protein (g/kg) for parents, F5s, and F6s in three environments.

	Parent means				Mid-parent mean	Progeny		
	P1	P2	P3	P4		Mean	Range	SD
				Post Farm (F5)				
Population 1								
Grain yield	4533	5046	3003	4521	4276	4502	3225-5578	365.6
Grain protein	138	144	178	130	148	145	129-161	18.0
Population 2								
Grain yield	4171	2438	4228	4312	3787	4241	3000-5441	239.0
Grain protein	152	142	133	147	143	147	124-168	19.0
				Post Farm (F6)				
Population 1								
Grain yield	5846	5387	3066	5016	4828	4893	3858-5975	167.8
Grain protein	115	124	181	119	135	129	109-150	24.0
Population 2								
Grain yield	3987	2537	5608	4475	4152	4521	2703-6221	155.6
Grain protein	135	140	116	126	129	131	111-155	20.0
				Fort Ellis (F6)				
Population 1								
Grain yield	6041	3900	5233	3946	4780	4916	2616-6558	279.0
Grain protein	118	119	161	110	127	122	108-137	22.0
Population 2								
Grain yield	2425	2703	4158	3966	3313	3482	2158-5728	249.6
Grain protein	118	132	118	121	122	125	111-142	22.0
				Average (F6) Post Farm+Fort Ellis				
Population 1								
Grain yield	5943	4643	4150	4481	4805	4901	3425-5850	538.0
Grain protein	117	122	171	114	131	126	111-140	87.0
Population 2								
Grain yield	3206	2621	4896	4220	3736	4000	2737-5965	639.7
Grain protein	126	126	117	123	123	128	113-145	73.0

are similar to those of Sampson et al. (1983), Haunold et al. (1962a), and Stuber et al. (1962). Table 7 shows that in the two populations, none of the progeny means had lower grain yields than the low parent in either of the two environments. More than half of the progenies of F5 and F6 have higher yield than midparent values in all environments but few exceeded the high parent.

Table 7. Frequency distribution of grain yield in progenies of the two populations, and number of progeny lines with lower and higher grain yield than the low- and high-parent means in three environments.

	Grain yield (kg/ha) class points					Yield below		Yield above	
	1250-2500	2501-3750	3751-5000	5001-6250	6251-7500	LP†	MP‡	HP#	MP
			Post Farm (F5)						
Population 1	---	2	48	10	---	0	19	9	41
Population 2	---	11	42	7	---	0	11	29	49
			Post Farm (F6)						
Population 1	---	34	26	---		0	24	1	36
Population 2	---	6	40	14	---	0	13	1	47
			Fort Ellis (F6)						
Population 1	---	5	25	28	2	8	24	5	36
Population 2	12	27	18	3	---	6	29	12	31

† LP Low parent
‡ MP Mid parent
# HP High parent

Table 8 shows none of the population 1 lines exceeded the high protein parent but many exceeded the midparent values. Very few of the progeny means for both populations were lower than the low protein parents, but many of them were lower than the midparent values, especially in population 1. In population 2, 21, 12, and 8 lines in F5, F6, and F6, respectively, exceeded the high protein parent.

In general, the progeny means for grain protein content and grain yield were in the most frequent class. Frequency distributions of F5 and F6 lines resembled a normal distribution and provided evidence that these two traits were under polygenic control.

No evidence or indication was apparent of dominant genes for either trait. Variation of GY and GP lines, in general, was slightly greater in F6 than in F5 in both populations.

Table 8. Frequency distribution of grain protein in progenies of the two populations, and number of progeny lines with lower and higher grain protein than the low- and high-parent means in three environments.

	Grain protein (g/kg) class midpoints							GP below		GP above	
	105	115	125	135	145	155	165	LP†	MP‡	HP#	MP
					Post Farm (F5)						
Population 1	---	---	1	15	27	15	2	1	39	0	21
Population 2	---	---	2	13	12	26	7	7	21	21	39
					Post Farm (F6)						
Population 1	3	7	25	18	6	1	---	3	43	0	17
Population 2	---	13	9	25	12	1	---	6	19	12	41
					Fort Ellis (F6)						
Population 1	2	17	29	12	---	---	---	2	44	0	16
Population 2	---	12	29	18	1	---	---	8	15	8	45

† LP Low parent
‡ MP Mid parent
# HP High parent

Genotypic and Phenotypic Correlations of Grain Yield, Grain Protein, and Vegetative Protein

Progress in breeding is conditioned by the magnitude, nature, and interrelations of genetic and nongenetic variations in the various significant plant characters.

Many publications contain sections dealing with character relationships described by correlation coefficients. Although correlation coefficients measure the degree of relationship between two characters in a population, they do not indicate how much of the measured relationship is heritable. So, we must eliminate some of the environmental variance by calculating genetic correlation.

The simple genotypic (rg) and phenotypic (rp) correlations between grain protein content, and protein content of plant parts were calculated for both populations at all locations (Table 9). Due to the large populations, correlation coefficient as low as 0.25 was statistically significant. In general, the genotypic correlations agreed closely with phenotypic correlations. The values of rg were higher than rp because they did not have any environmental effect, but only represent the heritable part of the total correlation. In general, the highest correlations were found between GP and head protein at heading in both populations at the three environments. Leaf 1 protein at heading for both populations and leaf 2 protein at anthesis for population 2 were not correlated with grain protein at any environment (Table 9). When used in a single correlation with grain protein, Leaf 1 (flag leaf) did not

Table 9. Genotypic (rg) and phenotypic (rp) correlations between grain protein and protein content in different plant parts at various growth stages in populations 1 and 2 in three environments.

	Heading								Anthesis	
	H1†	H2	P1	P2	L11	L12	L21	L22	L21	L22
					Post Farm F5					
rg	.96**	.80**	-.95**	-.92**	.09ns	-.05ns	.70**	.89**	-.62**	-.08ns
rp	.93**	.77**	-.82**	-.74**	.08ns	-.04ns	.65**	.80**	-.44**	-.06ns
					Post Farm F6					
rg	.82**	.79**	-.62**	-.37**	-.05ns	.02ns	.39**	.51**	-.34**	-.03ns
rp	.79**	.72**	-.49**	-.35**	-.04ns	.02ns	.35**	.43**	-.27*	-.02ns
					Fort Ellis F6					
rg	.71**	.71**	-.51**	-.20ns	-.06ns	.07ns	.34**	.25*	-.25*	-.11ns
rp	.64**	.64**	-.36**	-.17ns	-.06ns	.08ns	.28*	.21ns	-.16ns	-.07ns

*,** Significant at 5% and 1% levels of probability, respectively.
ns Not significant.
† 1 and 2 at the end indicate populations 1 and 2.

correlate with grain protein, but when it was used in combination with head and peduncle protein in a multiple regression, as discussed later, gave the highest R . Peduncle protein was consistently negatively correlated ($P < 0.01$) with grain protein in both populations at all environments, except for population 2 at Fort Ellis where it was also negative but not significant.

The high positive correlation between head protein at heading and grain protein indicates that this character might be used as a predictor for grain protein to differentiate among genotypes at heading.

Genotypic correlation coefficients provide a measure of the genotypic associations between characters and give an indication of a character that may be useful as an indicator of the more important ones under consideration. They also may help to identify characters that have little or no importance in the selection program. In any event, they provide basic information extremely useful to the breeder in understanding the species with which he works.

The practical utility of selection for a given indicator character as a means of improving another major character depends on the extent to which improvement in the major character is facilitated by selection for the indicator. Such improvement depends not only on the genotypic correlation but also on the phenotypic correlation and the variances, both genotypic and phenotypic, of all characters included in the selection scheme or index. Characters which have no value in themselves and are not normally measured in the selection program are worthy of inclusion in the selection scheme if their inclusion results in cost and/or time efficient improvement of the important character.

In addition, correlations between indicator characters and those of major importance must be in the same direction in different populations if selection for the indicators is to be useful. Negative genotypic correlation between characters selected for in a breeding program may result in slower improvement for some of the characters than could be attained if the correlation were positive or non-existent.

The genotypic correlations were appreciable in magnitude in both populations and may be of practical value in selection for increased grain protein content.

Heritabilities of Plant and Grain Protein

The wheat breeder needs a test which does not require a defined climate to differentiate among cultivars. Response to selection for a quantitative trait is directly proportional to its heritability and its genetic variance. Heritability is a measure of the ability of the plant breeder to recognize genetic differences among cultivars, and genetic variation indicates the potential for improvement in a population. In a given population successful selection is dependent upon a high heritability. Plant breeders, therefore, strive to improve their ability to estimate heritability by wise choice of testing procedures. The evaluation of a cultivar over several years will give a more accurate estimate of its potential. In other words, heritability is increased by testing over multiple years and/or locations. However, if genotype x year interaction is negligible, the same increase in heritability can be realized by more extensive testing in a single year. The latter approach would be more desirable in a breeding program. One must have both an estimate of the genotype x environment interaction and of the error of each analytic measurement to plan effective selection progress for a particular character or groups of characters. Special experiments must be designed to provide this type of information.

Heritability can be thought of as a measure of the degree to which the phenotype reflects the genotype. This is a nonrestrictive definition (Rasmusson, 1967). In this case, heritability ratio could be estimated in 1) the broad sense where the numerator of the ratio contains the total of the genetic variance, 2) the narrow sense where the numerator contains only additive genetic variance, or 3) as a ratio whose numerator contains less than total genetic variance, yet more than the additive genetic variance. The estimates obtained in this study are of the latter type, as are most estimates obtained by geneticists and breeders concerned with self pollinated crops. Generally, these estimates are not directly comparable because they are not estimates of the same thing. Neverthless, they have become an integral part of the literature and are widely used. The most cogent objections to a nonrestrictive definition are overcome if the experimental procedures and method of heritability estimation are carefully described. The use of the various kinds of heritability estimates, in conjunction with the selection differential, to predict advance from selection for hypothetical testing programs appears advantageous.

Narrow sense heritabilities of all measurements determined from both populations over the three environments using components of variance method are presented in Table 10.

The heritabilities for all measurements, including grain yield and grain protein content and protein content in plant parts, were high. The highest heritability was obtained from head protein of population 1 at heading and the lowest, but still significant one ($P < 0.05$) was obtained from leaf 2 of population 1 at anthesis. This low heritability was probably due to large genotype x environment interaction at this stage. Grain protein and grain yield were highly heritable characters in both populations.

Table 10. Heritability estimates (h) and confidence intervals (CI) for protein content in different plant parts at various growth stages, grain yield, and grain protein using variance components method for populations 1 and 2 over three environments.

	Heading								Anthesis		Ripe			
	H1†	H2	P1	P2	L11	L12	L21	L22	L21	L22	GY1	GY2	GP1	GP2
Vg	1.44	.91	.14	.11	.95	1.08	.82	.44	.08	.28	960	1139	.66	.55
Vp	1.53	1.02	.21	.17	1.09	1.22	1.00	.62	.17	.37	1466	1437	.94	.69
h	.94	.89	.67	.63	.87	.87	.82	.70	.46	.75	.65	.79	.69	.79
	**	**	**	**	**	**	**	**	*	**	**	**	**	**
CI	.03	.04	.06	.06	.04	.04	.03	.05	.07	.05	.06	.03	.05	.03

*,** Significant at 5% and 1% levels of probability, respectively.
† 1 and 2 at the end indicate populations 1 and 2.
Vg & Vp Genotypic variance and phenotypic variance, respectively.

In general, the heritabilities indicate the presence of considerable genetic variability for protein content in both populations. The standard deviations and heritabilities indicate the differences can be detected.

Another method of determining the heritability percentages of attributes in plants is by the parent-offspring regression procedure proposed by Lush (1940). This procedure was used to regress the mean value of characters in the progeny of F6 upon the value of the same characters in the parent (F5). Narrow sense heritability for protein content and grain yield for different locations using parent-offspring method are given in Table 11. All measured parameters had high heritability at all environments in both populations except for grain yield of both populations when the F6 at Fort Ellis was regressed on F5 at Post Farm. In general, the two methods of estimating heritability closely agreed in the trend of the values but not in the magnitude. This assumed that both estimate narrow sense heritability and that no dominance variance is involved in the total genetic variance. Only additive variance in those advanced generations (F5 and F6) is involved. Estimates of heritability calculated by the variance components method for all characters in both populations were higher than those calculated by the regression method.

Table 11. Heritability estimates (h^2) for protein content in different plant parts at various growth stages, grain yield, and grain protein using the parent offspring regression method for populations 1 and 2 in three environments.

	Heading								Anthesis		Ripe			
	H1†	H2	P1	P2	L11	L12	L21	L22	L21	L22	GY1	GY2	GP1	GP2
	Post Farm (F6) on Post Farm (F5)													
h^2	0.72	0.73	0.66	0.71	0.90	0.74	0.71	0.61	0.46	0.53	0.54	0.82	0.74	0.67
	**	**	**	**	**	**	**	**	*	**	**	**	**	**
SE	0.06	0.06	0.08	0.07	0.06	0.05	0.05	0.06	0.09	0.06	0.11	0.10	0.08	0.07
	Fort Ellis (F6) on Post Farm (F5)													
h^2	0.70	0.63	0.47	0.52	0.69	0.51	0.44	0.36	0.32	0.41	0.22	0.26	0.67	0.36
	**	**	**	**	**	**	**	**	*	**	ns	ns	**	**
SE	0.06	0.067	0.09	0.09	0.08	0.06	0.06	0.08	0.11	0.07	0.22	0.20	0.08	0.07
	Average of Post Farm+Fort Ellis (F6) on Post Farm (F5)													
h^2	0.71	0.68	0.57	0.61	0.79	0.63	0.57	0.49	0.40	0.47	0.38	0.54	0.59	0.51
	**	**	**	**	**	**	**	**	**	**	**	**	**	**
SE	0.06	0.06	0.08	0.07	0.07	0.05	0.05	0.06	0.09	0.06	0.12	0.12	0.06	0.06

*,** Significant at 5% and 1% levels of probability, respectively.
ns Not significant at 5% level of probability.
† 1 and 2 indicates population 1 and 2.
SE Standard error.

In a selection program, a plant breeder can use only the genetic differences among the lines. In general, heritabilities reported in this study suggest that the inheritance of these protein measurements may be more simple than was supposed. When several traits are involved in evaluation of quality, it is desirable to determine genotypic and phenotypic correlations among these traits. When two characters are highly correlated and a choice is to be made, the one with the highest heritability should be the preferred measurement.

Prediction for Grain Protein Using Vegetative Protein

Table 13 summarizes the correlations between observed and predicted protein content using different combinations of plant part protein content for both populations in the three environments. The predicted values were calculated from the prediction equations (Noaman and Taylor, 1988b) in Table 12. The highest correlation coefficient (r) was obtained when the combination of head, peduncle, and leaf 1 protein content at heading for both populations was used in a multiple regression with grain protein. This was true for all three environments in both years except for population 1 at Fort Ellis when the highest r was obtained from head protein at heading (Table 13).

The same variables included in the prediction equations for grain protein were used in a multiple regression for grain yield (Table 14). It is significant that correlations of protein content in plant parts and grain yield are very small and not significant. This indicates that within the populations studied no strong genetic association was found

Table 12. Multiple regression equations expressing grain protein content as a function of protein content in different plant parts and growth stages (Noaman and Taylor, 1988b).

Heading		Anthesis
$\hat{Y}$ = 11.60 + HPC (0.51) + L1PC (-0.14) + L2PC (0.48)	+	L2PC (-0.50)
$\hat{Y}$ = 11.43 + HPC (0.35) + L1PC (0.18) + PPC (-0.43)		
$\hat{Y}$ = 5.86 + HPC (0.44) + L2PC (0.23)		
$\hat{Y}$ = 9.45 + HPC (0.56)		

$\hat{Y}$ Predicted grain protein.
HPC Head protein content.
PPC Peduncle protein content.
L1PC First leaf protein content.
L2PC Second leaf protein content.

Table 13. Correlation coefficient (r) between predicted and observed grain protein using multiple regression equations for F5 and F6 of the two populations in three environments.

	Post Farm (F5)		Post Farm (F6)		Fort Ellis (F6)	
	Popn.1	Popn.2	Popn.1	Popn.2	Popn.1	Popn.2
HH+L1H+L2H+L2A	0.81 **	0.79 **	0.74 **	0.72 **	0.50 **	0.37 **
HH+L1H+PH	0.88 **	0.84 **	0.86 **	0.84 **	0.66 **	0.75 **
HH+L2H	0.86 **	0.81 **	0.79 **	0.76 **	0.50 **	0.42 **
HH	0.86 **	0.59 **	0.81 **	0.76 **	0.70 **	0.71 **

** Significant at 1% level of probability.
HH Head protein at heading.
PH Peduncle protein at heading.
L1H Leaf 1 protein at heading.
L2H Leaf 2 protein at heading.
L2A Leaf 2 protein at anthesis.

which would prevent selection for high grain protein. There would be little or no effect on grain yield. This is in contrast to the negative relationship between grain protein and grain yield found by other researchers. It appears that no serious barriers exist in breeding high protein cultivars of winter wheat with relatively high grain yield.

Table 14. Coefficient of multiple determination (R^2) between grain yield and protein content in plant parts at heading and anthesis for F5 and F6 of the two populations in three environments.

	HH	HH+L2H	HH+L1H+PH	HH+L1H+L2H+L2A
Post Farm F5				
Popn. 1	0.11 ns	0.14 ns	0.11 ns	0.20 ns
Popn. 2	0.11 ns	0.12 ns	0.16 ns	0.14 ns
Post Farm F6				
Popn. 1	0.12 ns	0.13 ns	0.19 ns	0.18 ns
Popn. 2	0.08 ns	0.12 ns	0.12 ns	0.14 ns
Fort Ellis F6				
Popn. 1	0.01 ns	0.01 ns	0.08 ns	0.04 ns
Popn. 2	0.01 ns	0.03 ns	0.03 ns	0.04 ns

ns Regression is not significant at 5% level of probability.
HH Head protein at heading.
PH Peduncle protein at heading.
L1H Leaf 1 protein at heading.
L2H Leaf 2 protein at heading.
L2A Leaf 2 protein at anthesis.

The correlation coefficients of grain yield and grain protein for the original population progeny lines and top 10 progeny lines resulting from indirect selection for grain protein at heading are in Table 15. The top 10 lines were selected on the basis of their vegetative protein at heading which predicted the grain protein at ripe. Indirect selection for grain protein using vegetative protein reduced the negative relationship between grain protein and grain yield to non-significance in both populations at all three environments ($P < 0.05$). Five of the six correlations between grain yield and actual grain protein were both negative and highly significant (Table 15). None of the six correlations

Table 15. Correlation coefficients (r) between GY and GPC, mean grain yield (GY), kg/ha, and mean grain protein content (GPC), g/kg, in the original 60 progeny lines and the top 10 lines resulting from indirect selection for grain protein at heading

	F5 Post Farm		F6 Post Farm		F6 Fort Ellis	
	Popn.1	Popn.2	Popn.1	Popn.2	Popn.1	Popn.2
	Correlation (r) between GY and GPC					
Progeny lines (60)	- 0.36 **	- 0.43 **	- 0.55 **	- 0.57 **	- 0.15 ns	- 0.33 **
Indirect selected top 10 lines	- 0.19 ns	- 0.27 ns	0.02 ns	- 0.16 ns	- 0.23 ns	- 0.18 ns
	Mean GPC					
(60 lines)	145.0	147.0	130.0	131.0	123.0	125.0
(10 lines)	154.0	161.0	155.0	159.0	157.0	160.0
% GPC increase in 10 selected lines	6.2%	9.5%	19.2%	21.4%	27.6%	28.0%
	Mean GY					
(60 lines)	4500.0	4238.0	4888.0	4550.0	4913.0	3550.0
(10 lines)	4363.0	3925.0	4663.0	4200.0	4887.0	3213.0
% GY reduction in 10 selected lines	3.1%	7.4%	4.6%	7.7%	0.5%	9.5%

between grain yield and grain protein were significant for the top 10 progeny group in which indirect selection for grain protein at heading was applied. This indicates that indirect selection for grain protein using vegetative protein at heading can result in increased grain protein without significant reduction in grain yield.

Mean grain protein content for the selected lines exceeded that of the original progeny lines in all three environments for both populations (Table 15). However, the mean grain yield of these selected lines were less than the original 60 lines. The percent increased grain protein in the selected lines ranged from 6.2% to 28.0%. The percent reduction in grain yield ranged from 0.5% to 9.5%. Although the inverse relationship between grain protein and grain yield was not negated, indirect selection for grain protein at heading time greatly reduced the usual negative correlation to a point of non-significance.

SUMMARY

A large amount of variation exists among genotypes in the populations studied with high heritability of grain protein and protein content in plant parts. This indicates selection among lines for these variables would permit genetic advance. Evaluating breeding lines over several environments should give more accurate estimate of their potential for increased grain protein. Although G x E interaction effect was significant for most of the measured variables the magnitude of variance compared to that of genotypes was fairly low. Transgressive segregation for both grain yield and grain protein content was observed. Three lines of population 2 combined high grain yield and high grain protein simultaneously while exceeding the highest parents for these two traits. These results are very encouraging and indicate that simultaneous selection for grain yield and grain protein in a breeding program is possible.

In both populations at the three environments the 60 progenies showed continuous distribution in protein content and grain yield. High correlation was observed between protein content of the combination of the head, flag leaf, and peduncle at heading and grain protein as was reported by Noaman and Taylor (1988b). Heritability estimates of these plant part-protein contents were high and significant ($P < 0.01$) in both populations which indicates that these variables can be used as indicators for grain protein prediction. The correlation between the

observed and the predicted values for grain protein was very high using these three plant part-protein contents at heading. The very low correlations between these variables and grain yield indicates there is no strong genetic association that would prevent indirect selection for high grain protein with no effect on grain yield. It appears from this study that no serious barriers exist in breeding high protein cultivars of winter wheat with high grain yield.

Improving both grain yield and grain protein content in wheat could include:

(1) A survey of wheat cultivars for plant part protein content at heading and mature grain protein in order to determine which parents to be used in making crosses for recurrent selection population.

(2) Identify and intercross potentially high grain protein segregants at heading.

(3) Repeat steps (1) and (2) in a recurrent selection scheme including indirect selection for grain protein content and grain yield by selecting progenies with the appropriate plant part protein content.

(4) Recombination and concentration of desired grain protein and yield genes by use of genetic male sterility or male gametocides.

(5) Evaluation of wheat lines for agronomic and quality traits at any point. Superior lines could be recycled into the continuing recurrent selection program.

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