HERITABILITIES AND INTERRELATIONSHIPS OF GRAIN PROTEIN AND OTHER TRAITS IN THREE POPULATIONS OF WINTER WHEAT

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CHAPTER I

INTRODUCTION

With the continually increasing world population, quantity and quality of nutrition has become a great concern. Wheat (Triticum aestivium L.) has long been recognized as one of the major dietary mainstays to two thirds of the earth's four billion people. Although commonly classified as a calorie source, wheat and other cereals are also the worlds most important protein source (13). Deficiency of protein is a very serious problem, especially among children in under-developed countries where no other source of protein is readily available. The development and use of high yielding, high protein content wheat could help alleviate world hunger.

Wheat has the highest protein content, per unit dry weight of grain, of all the cereals. Approximately 12,600 common wheats, from the USDA world collection have been examined for protein. The range of protein content was from 6 to 22 percent, with an average of 12 percent. This variation was thought to be due primarily to environmental rather than genetic factors (13).

Some environmental influences which affect grain protein content are available soil moisture, residual and applied soil fertility, and soil temperature. Protein levels can be increased by the application of nitrogen fertilizers, but the inherent differences of grain protein content rest upon the genetic factors that control the trait. Several high protein wheat genotypes are now available to the plant breeder. However, most of them are characterized by low yield potential and poor agronomic type.

An increase in grain protein content of 0.5 to 1.0 percentage points would make Oklahoma's winter wheat crop more competitive with the northern spring wheats in terms of both local markets and world export.

The objectives of this study were: 1) to estimate the heritability of grain protein content in crosses involving 'Plainsman V', a high protein cultivar, and 2) to study the relationship of grain protein to yield and other characters.

CHAPTER II

LITERATURE REVIEW

The importance of cereal grains to world nutrition is well recognized. Although wheat has the highest grain protein content per unit weight of the cereal grains, protein levels in wheat are not high enough to supply the amount needed for sufficient nutrition. Apart from nutrition, the bread-making industry and growers in the Hard Red Winter wheat region of the United States would tend to benefit by the use of higher protein bread wheats. Therefore, there is a great need to develop new cultivars of wheat which have higher grain protein content while maintaining acceptable levels of quality and yield. Olson and Sander (22) reported that quality of protein is primarily limited to the amount and balance of four essential amino acids: lysine, threonine, isoleucine, and methionine. Researchers (13, 14, 19) have observed that as grain protein percent increases, there is a marked imbalance of these amino acids i.e. lysine quantity decreases. Mattern et al. (19) reported that progenies of crosses made between 'Atlas 66' and two hard red winter wheats produced one to three percentage points higher protein than the hard red winter wheat parents, but maintained good amino acid balance, resulting in higher protein quality.

Bhatia (3) stressed the importance of the source-sink interaction in the plant. Nitrogenous materials stored in the leaves during the vegetative phase of growth are translocated to the developing grains (sink). When the sink size is small (low grain yield and harvest index) compared to the source, the grain protein tends to be high. In the reverse situation i.e. high grain yield and harvest index, the sink is large while the source is small, and consequently the grain protein percent tends to be low. Other investigators (12, 26) showed that wheat cultivars differed in their ability to translocate nitrogen. There is some evidence to suggest that high protein genotypes have a greater ability to translocate nitrogenous compounds (26).

The identification of wheat genotypes possessing inherently high levels of grain protein was reported by Middleton et al. in 1954 (20). They studied a group of cultivars from crosses involving either 'Frondoso' or 'Frontirea' in their parentage. These two cultivars are sister lines of South American origin. Five cultivars with either Frondoso or Frontirea in their background had higher protein and higher yield than other cultivars grown in a regional nursery. One of the cultivars was 'Atlas 66'. Cowley and Wells (5) reported that the genotype 'Hand' also had high grain protein. Programs to transfer the high protein trait, by crossing standard protein wheats with known high protein genotypes, has resulted in progeny with elevated protein levels (2, 14, 19).

Maximum benefits in breeding high protein cultivars can best be achieved with a knowledge of heritability of grain protein. Chapman and McNeal (4) reported that significant additive genetic effects were found for percent protein. No evidence of a preponderance of dominant genes was found by Haunold et al. (10). They reported that a relatively low number of genes conditioned protein content in the grain of F_2 plants from crosses involving Atlas 66. The F_2 means were intermediate to parental values. A heritability estimate of 0.65 led to the conclusion that rapid progress would be made by selecting for high protein. Davis et al. (6) obtained broad-sence heritability estimates of 0.54, 0.65 and 0.69 and concluded that there was notable genetic variability for grain protein content in the populations they observed. Narrow-sense heritability estimates of 0.68 and 0.83 for grain protein were reported by Stuber et al. (26). They concluded that protein content was under polygene control, but only a few genes were involved, because of the ease of selecting high protein lines. High heritability indicates effective selection on an individual plant basis would be possible.

Breeding for high grain protein content generally has an inverse effect on yield. Stuber et al. (27) reported a negative correlation, although low, between grain yield and protein content. However, they recovered F_2 plants in which high yield and high protein content were combined, indicating that selection for high protein could also be accompanied by higher yield. Several other investigators (6, 10, 15) also reported negative correlations between yield and protein. However, Johnson et al. (12) reported no relationship between grain yield and grain protein content existed under the conditions of their study.

Mattern et al. (19) studied progenies of Atlas 66 and 'Comanche', a hard red winter wheat of normal protein level. F_2 families were recovered that were higher in yield and protein content than Comanche. They concluded that is was possible to select for high protein and maintain acceptable yield levels.

Balla (2) found no correlation between protein and plant height, while selecting for short straw and high protein. Others (3, 8, 15, 24) found negative correlations between protein content, kernels per spike, plant height, and yield.

Environmental influences as well as genetic factors have a marked effect on grain protein content. Smika and Greb (24), studying protein content of winter wheat in the Great Plains, found that protein decreased as more soil water was available at seeding time, but reported an increase in yield. Air temperatures above 32^{o}C the last 15 days of growth have been reported to decrease protein content (24). An increase in soil temperature at plant crown level increased nitrogen uptake which increased grain protein content. Residual N in the soil has an impact on protein response. Larger amounts of N (50 - 60 kg/ha) are required for maximum protein expression (21). Johnson et al. (12) and Karathanasis et al. (16) reported differences among genotypes in respect to N requirements. With certain nitrogen application levels, both yield and protein content increased. However, above those levels, yield decreased while protein content continued to rise. This reaction was highly correlated with genotype (12).

Studies have been conducted in which selections from crosses between Atlas 66 and two hard red winter wheat cultivars were evaluated at different levels of nitrogen fertilizer. The authors (17, 19) reported difficulty in breeding for a fixed protein level because of environmental influences. However, the selections maintained significantly higher protein levels than either of the hard red winter wheat parents. Also they reported that Atlas 66 consistantly produced high protein levels in different environments.

Cowley and Wells (5) reported that two South Dakota sister lines of wheat, Hand and 'Flex' had high protein levels. When Hand was crossed with 'NE68513', an Atlas 66 derivative, transgressive segregates resulted, which suggests that Hand and Atlas 66 contain different high protein genes. Johnson et al. (14) also observed transgressive segregation for elevated protein in a cross of 'Nap hal'/Atlas 66. Guthrie (9) conducted an analyses of diallel crosses involving high protein wheats. She found no hybrid as high as Atlas 66 for percent protein, suggesting that the genes for high protein content in Atlas 66 were incompletely dominant. 'Plainsman V', developed by Seed Research Inc., Scott City, Kansas, is a high protein wheat but no information as yet has been published on the genetic control of protein in this cultivar (25).

Hard red winter wheats with higher grain protein levels are needed. Genetic variation for protein content exists in common wheat; types are known which are two to three percentage points higher in protein content than standard types. Environmental influences produce some effect on protein content but, generally, the heritability of protein is intermediate to high and selection for high protein would be expected to be effective in early generations. Though there are exceptions, protein content has been found to be negatively correlated with yield. Improvement in yield and grain protein content is now a challenge for wheat breeders.

CHAPTER III

MATERIALS AND METHODS

Parental Lines and Generations

This experiment was conducted during the 1979-80 growing season at the Agronomy Research Station, Stillwater, Oklahoma, on a Norge Loam soil type (Udic Paleustoll) with 1 - 3 percent slope. Three populations of winter wheat (*Triticum aestivum* L. em Thell), each involving Plainsman V as one parent, comprised the basic set of materials for this study. Population 1 was derived from Plainsman V/'Vona', Population 2 from Plainsman V/'Newton', and Population 3 from Plainsman V/'Payne'. Plainsman V, a high protein cultivar, was developed by Seed Research, Inc., Scott City, Kansas and released in 1974. Plainsman V is a semidrawf wheat with early maturity and good straw strength. It is resistant to the soil borne mosaic virus (1). Plainsman V is currently being grown under contract in southern Kansas and northern Oklahoma, with protein stipulations in the contract (25).

Vona was released by Colorado State University in 1976. It is an early maturing, semidwarf cultivar, and produces good grain yields (29). Newton was released by Kansas State University in 1977. It is a semidwarf wheat, with medium maturity and resistance to soil borne mosaic virus. It is moderately resistant to leaf rust and stem rust and produces above average grain yields (11). Payne was released in 1978 by

Oklahoma State University. It is a semidwarf wheat with medium maturity and resistance to leaf rust. It produces good grain yields (25). Vona, Newton, and Payne are currently grown in the Southern Great Plains area.

For each population, the following generations were studied: P_1, P_2, F_1, F_2, B_1, and B_2. The various crosses, to produce these generations, were made in the greenhouse during the 1977, 1978, and 1979 crossing seasons. Seeds were planted in flats October 11, 1979. The seedlings were partially vernalized at outside temperatures and then transplanted to the field on November 27, 1979.

Field Layout and Management

The experiment was arranged in a randomized complete block design with three blocks (replications) for each of the three crosses. Ten plants of each entry were spaced 30 cm apart in single-row plots 3 m long. Rows were spaced 30 cm apart. Each block contained one row each of P_1, P_2, and F_1, three rows each of B_1 and B_2, and six rows of F_2. These 15 single-row plots were randomized within each block. Plants of an awnless cultivar, 'NR 31-74', bordered each population. No preplant application of fertilizer was made, however on March 3, 1980, a top dressing of ammonium nitrate was applied at the rate of 56 kg/ha actual N. Supplemental water was applied by sprinkler system on December 19, 1979. An insecticide, Rebelate, was applied at a rate of 1.3 l/ha on April 29, 1980, to control greenbugs. Weeds were controlled manually.

The study was harvested June 23 and 24, 1980, by pulling and bagging individual plants. Eight bordered plants were taken from each single row plot. However, there were one or two atypical plants in many of the plots, so all plots were eventually reduced to seven plants. In those plots with all typical plants, one plant was removed at random.

Characters Evaluated

Plant height, number of tillers/plant, kernels/spike, kernel weight, grain yield, and percent grain protein were evaluated in this experiment. The measurements were made on each plant as follows:

Plant Height

The measurement of this character was taken as the distance in centimeters from the soil line to the top of the tallest spike, excluding awns.

Tiller Number

Tiller number was the number of fertile (seed-bearing) spikes at maturity.

Kernels/Spike

The number of kernels per spike was determined by selecting one of the largest heads from each plant. The head was threshed and seeds counted and recorded.

Kernel Weight

One hundred seeds were counted and weighed to the nearest 0.01 gram. This weight was multiplied by 10 and recorded as grams per 1,000 kernels.

Grain Yield

Grain yield was the weight in grams of the threshed grain from each individual plant, including that of the head selected for kernels per spike count.

Percent Protein

Percent grain protein of each plant was estimated by the Udy dye-binding procedure. In the Udy analysis, a two gram grain sample is ground in a cyclone mill. A 600 milligram sample of the flour is mixed with an orange dye solution. This mixture is shaken for 40 minutes to allow the dye to form a complex with the amino acids of the protein. The dye-protein complex is filtered out and the amount of dye left in solution is measured by a colorimeter. There is an inverse relationship between the amount of dye left in solution and the protein content of the sample. The percent protein is then determined by a Udy conversion chart. Plainsman V and Vona check samples were placed at the beginning and end of each replication. The percent protein of these check samples was also determined by the Kjeldahl method. Udy protein levels of the check samples were consistent with, but slightly less than the Kjeldahl protein levels. However, these differences would not affect the validity of the test. Udy analysis was conducted in the OSU Agronomy Department Crop Physiology laboratory. High standards were maintained in the laboratory to minimize error from poor laboratory technique (18).

Statistical Analysis

Variances, means, and standard errors of means were calculated for the six characters. Phenotypic correlation coefficients were calculated for percent protein and the other five traits. Narrow-sense heritability estimates were obtained according to the procedure outlined by Warner (28). Heritability (narrow-sense) is defined as $\frac{\frac{1}{2}D}{\frac{1}{2}D + \frac{1}{4}H + E}$ where:

$\frac{1}{2}D$ = Additive genetic component of variance and

$\frac{1}{4}H$ = Dominance genetic component of variance and

E = Environmental component of variance.

Heritability is estimated by $\frac{2VF_2 - (VB_1 + VB_2)}{VF_2}$ where:

VF_2 estimates $\frac{1}{2}D + \frac{1}{4}H + E$ and

$2VF_2$ estimates $D + \frac{1}{2}H + 2E$ and

$VB_1 + VB_2$ estimates $\frac{1}{2}D + \frac{1}{2}H + 2E$.

CHAPTER IV

RESULTS AND DISCUSSION

This study was designed to estimate the heritability of grain protein in three populations based on Plainsman V (abbreviated as PMV in tables), a high protein cultivar. The study was also designed to estimate correlations between grain protein and five other traits, including grain yield.

During the course of this study there were no serious problems with insects or diseases. However, the plants experienced low temperatures shortly after transplanting which set them back from which they never completely recovered. At maturity, plants were shorter than normal and lacked expected vigor. This, no doubt, had some effect on the results of the study. There was a weed problem in late spring and moisture stress was experienced just before grain maturity.

Means and Standard Errors

Means and their associated standard errors for the six characters studied are presented in Tables I, II, and III, which represent Populations 1, 2, and 3, respectively.

Population 1 (PMV/Vona)

Plainsman V, the high protein parent, was slightly less than two percentage points higher than Vona in protein content (Table I). Means for protein of the F_1, F_2, B_1, and B_2 fell within the range of the two parents for this trait. B_1 (backcross to Plainsman V) was nearly one percentage point higher in protein than B_2, as would be expected from the difference in the parents. Vona had a higher number of kernels per spike than Plainsman V. This trend was carried over to the backcrosses with approximately the same magnitude of difference. The B_2 exceeded the other generations for number of kernels per spike. Grain yield of Plainsman V was higher than that of Vona, which is not normally observed. B_2 had the highest grain yield of any generation, although there was also a marked increase in F_1, F_2, and B_1 yields above that of the parents.

Population 2 (PMV/Newton)

There was essentially no difference in percent protein content between Newton, Plainsman V, the F_2, B_1, and B_2 in Population 2 (Table II). The best explanation for this is that of environmental effect on protein content of Newton and Newton crosses. Normally Newton does not show elevated protein levels as it did in this study. The F_1 was approximately one percentage point lower than the other generations. No reasonable explanation can be offered for this. Plainsman V was considerably shorter than Newton which was reflected in the same magnitude in the B_1 and B_2 generations. The F_2 was intermediate in height to the two parents. Newton had more kernels per spike than Plainsman V. Although not as large, the difference was repeated in the backcrosses. The F_2 was intermediate to the parents for this trait. This difference is attributed to the increased spike size of Newton.

Population 3 (PMV/Payne)

Plainsman V was 1.28 percentage points higher in protein content than Payne (Table III). The F_2 protein value was about the same as that of the low protein parent. The backcrosses were about 0.5 percentage points lower than their respective parents, but B_1 (backcross to Plainsman V) still maintained 1.11 percentage points higher protein than B_2. Payne had more tillers than Plainsman V and the difference is approximately of the same magnitude in the backcrosses, although B_1 and B_2 had more tillers than their respective backcross parents. The F_2 mean for tillers was larger than that of either parent. Plainsman V had fewer kernels per spike than Payne and this difference was reflected in the backcrosses. The F_1 and F_2 were intermediate to the parents for this trait. The highest grain yield was produced by B_2, but the protein content of this generation was below that of either parent. The high protein parent, Plainsman V, had a lower mean yield than Payne. The relationship of B_1 to B_2 was of the same magnitude as P_1 to P_2, as would be expected.

Heritability Estimates for Six Characters

Variance components for F_2, B_1, and B_2, as well as estimates of heritability conducted according to Warner (28) are shown in Table IV, for the six characters. The heritability estimates shown in Table IV were calculated using all plants and ignorning blocks.

The heritability estimates for percent grain protein (Table IV) were .967 for Population 1 (Vona cross), .115 for Population 2 (Newton cross) and .559 for Population 3 (Payne cross). Grain protein content was the primary trait of interest in this study and since these three heritability estimates varied so widely, heritability for each of the three blocks was calculated to examine consistency from block to block. Their estimates will be discussed later.

Heritability of plant height was intermediate in Populations 2 and 3 (.441 and .598) but low in Population 1 (-.407 set at 0.0), this was because the variances of the backcrosses were high in relation to that of the F_2. The estimate for tiller number was .590 and .664 respectively in Populations 2 and 3. Both of these estimates are much higher than expected based on previous work (7). Population 1 had a negative estimate for tiller number which was set at 0.0. Heritability estimates for kernels per spike were low, although higher than those reported in other studies (17, 23). Estimates for kernel weight were high in Populations 1 and 2 (respectively, .789 and .942) while the observed estimate in Population 3 of .222 was lower than that reported by Ketata et al. (17). The heritability estimate for grain yield in Population 2 (.876) was much higher than the estimate reported by Sidwell et al. (23). Population 1 had a negative estimate for yield which was set at 0.0. Population 3 had a low (.321) heritability estimate for grain yield which was more in line with expected estimates for this trait.

Heritability Estimates of Grain Protein by Block

Table V contains five estimates of heritability of percent protein for each population. The first set is the overall heritability estimates ignoring blocks as per Table IV. The next three are estimates for each of the blocks, while the last set is an adjusted estimate with an 'offending' block removed.

An examination of block estimates for Population 1 revealed that Block 2 was excessively large (1.361). When Block 2 was removed, the adjusted heritability estimate was .882, a value which can be considered a more reliable estimate than .967, the overall estimate. For Population 2, Block 2 had a negative estimate (-.866). When this block was removed, the adjusted heritability estimate was .600. In Population 3, Block 1 had a negative estimate (-.403). When this block was removed, the adjusted estimate was .700. The three adjusted estimates ranged from .600 to .882. These values are consistant with reports by other workers (6, 26). The relative order of rank from high to low remains the same as in the overall estimate.

Chapman and McNeal (4) reported a marked trend i.e. the greater the difference between parents, the greater the value of additive genetic effect. The results from this study seem to substantiate this. The parents of Population 1 were the most diverse for protein content (15.30 for Vona and 17.14 for Plainsman V) and this population had the highest heritability estimate (.882 adjusted). In Population 2, the parents were nearly identical in protein content (17.20 for Newton and 17.17 for Plainsman V). The estimate for this population (.600 adjusted) was the lowest of the three populations. In Population 3, there was a difference of 1.28 percentage points protein between the two parents (16.52 for Payne and 17.80 for Plainsman V). This population had an adjusted heritability estimate of .700.

Means for Grain Protein by Block

In an attempt to understand why some of the block estimates of heritability were so far out of line, the means of individual blocks were examined for grain protein content (Table VI). The means in each set of three blocks per generation, per population, showed very little variation among blocks, so no explaination could be found here. The explanation must lie in extreme variation (high and low values) for protein among the individual plants in certain blocks.

Phenotypic Correlations Among Characters

Phenotypic correlation coefficients of percent protein and the other five characters are presented in Table VII. Only correlations between percent protein and the listed characters were calculated because the relationship of protein to other characters was of primary interest in this part of the study.

Population 1 (PMV/Vona)

In Population 1, plant height and kernel weight exhibited a highly significant negative correlation with percent protein, with correlation coefficients of -0.25** and -0.43** respectively. The correlation between grain protein and grain yield was -0.18**, which was significantly different from zero but of relatively low magnitude (Table VII).

Population 2 (PMV/Newton)

The correlation between percent protein and kernel weight was -0.29** in Population 2 (Table VII). Grain protein and grain yield had a highly significant negative correlation of 0.24**.

Population 3 (PMV/Payne)

In Population 3, all correlations were either low or nonsignificant statistically. The correlation between grain protein and kernel weight was -0.16**, while that between grain protein and yield was also -0.16**. Both of these correlation coefficients were significantly different from zero but of low magnitude (Table VII).

Correlation coefficients between grain protein and kernel weight and between grain protein and grain yield were statistically significant in all three populations. Correlations between grain protein and kernel weight were negative in all cases and ranged from -0.16** to -0.43**. Gill et al. (8) reported a negative correlation of -0.12 between grain protein and kernel weight. A similar relationship was found between protein and yield with a range of -0.16** to -0.24**. This is in agreement with reports of other workers (3, 9, 15).

High Protein, High Yield Selections

Individual plants of the F_2, B_1, and B_2 generations from each population which exceeded the mean for grain yield and the mean for percent grain protein are listed in Tables VIII - XIII. These potentially promising plants are identified for the project leader for subsequent use in the wheat breeding program at Oklahoma State University. No data was referenced to them in this thesis, other than to report there was a relatively large number of plants in each population which had high percent grain protein along with high grain yield. Selections made among these plants can be used in future studies involving the development of cultivars with high grain protein content.

CHAPTER V

SUMMARY AND CONCLUSIONS

The objectives of this study were to estimate the heritability of grain protein in crosses involving Plainsman V, a high protein cultivar, and to study the relationship of grain protein to yield and other characters. The study was conducted on the Agronomy Research Station, Stillwater, Oklahoma, during the 1979-80 crop season. Plainsman V was crossed with three adapted cultivars, Vona, Newton, and Payne to form three populations. Each population consisted of P_1, P_2, F_1, F_2, B_1, and B_2 generations. The three populations were space planted in a randomized complete block design. Each population consisted of three blocks, with 15 single-row plots per block. Each block consisted of one row each of P_1, P_2, and F_1, six rows of F_2 and three rows each of B_1 and B_2. There were 10 plants per row from which seven bordered plants were harvested by pulling and bagging individual plants. Measurements taken were plant height, number of tillers, kernels per spike, kernel weight, grain yield, and percent grain protein; all on an individual plant basis. Means and standard errors of means, as well as heritability estimates (Warner's method) were claculated for grain protein and the other five traits. Relationships between percent protein and the other traits were examined by computing phenotypic correlation coefficients.

The heritability estimates for percent protein were first calculated using all plants in the F_2 and backcross generations, ignoring blocks.

The estimate for Population 1 (PMV/Vona) was .967, Population 2 (PMV/Newton) .115, and Population 3 (PMV/Payne) .559. Due to the wide range in these estimates, heritabilities were calculated on a block by block basis. In Population 1, Block 2, the estimate was 1.361 which is higher than theoretically possible. Upon removing this block and averaging blocks 1 and 3 an adjusted estimate of .882 was obtained. In Population 2, Block 2 had an estimate of -.866. The removal of this block, resulted in an adjusted estimate of .600. In Population 3, Block 1 was -.403. The removal of this block resulted in an adjusted estimate of .700. These adjusted estimates were more in line with those reported by Stuber et al. (26) and others (6, 10).

Phenotypic correlation coefficients of grain protein with other traits tended to be negative, but of low magnitude. The correlation between grain protein and kernel weight was negative in all three populations with values of -.43**, -.29** and -.16** for Populations 1, 2, and 3 respectively. The negative correlations indicated that high protein plants tended to have smaller kernels. Of primary interest was the correlation between grain protein and grain yield. Protein was negatively correlated with yield (-.18**, -.24**, and -.16** respectively for all Populations 1, 2, and 3). These values are in agreement with those reported by Johnson et al. (15) and others (6, 10, 26). Although statistically significant, these correlations were not of such magnitude to preclude selection of high protein, high yielding types.

In this study approximately 25 percent of the F_2 and backcross generations in each cross exceeded the means for grain protein and grain yield. These individual plants were identified for the benefit of the wheat breeding project leaders. The information will be used in future studies and breeding efforts dealing with grain protein content.

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APPENDIX

TABLE I

MEANS AND STANDARD ERRORS FOR SIX CHARACTERS IN POPULATION 1 (PMV/VONA)

Generation1/ and No. of Plants		Grain Protein (%)	Plant Height (cm)	Tiller Number (per plant)	Kernels/ Spike	Kernel Weight (g/1000)	Grain Yield (g/plant)
P_1	21	17.14±0.25	60.81±0.81	15.10±0.74	43.76±1.25	20.35±0.35	7.81±0.52
P_2	21	15.30±0.21	58.62±0.91	14.95±1.19	50.57±1.51	17.85±0.44	6.47±0.58
F_1	21	15.56±0.17	64.38±1.02	15.95±0.91	52.62±1.42	20.51±0.44	9.04±0.67
F_2	126	16.47±0.13	63.13±0.43	17.09±0.35	60.42±0.86	20.12±0.29	9.87±0.29
B_1	63	16.56±0.13	62.37±0.57	15.75±0.55	51.83±0.92	20.85±0.30	9.08±0.40
B_2	63	15.80±0.12	65.52±0.74	18.14±0.61	61.83±1.25	20.42±0.34	11.01±0.54

1/ P_1 = PMV, P_2 = Vona, B_1 = F_1 x PMV, B_2 = F_1 x Vona

TABLE II

MEANS AND STANDARD ERRORS FOR SIX CHARACTERS IN POPULATION 2 (PMV/NEWTON)

Generation1/ and No. of Plants		Grain Protein (%)	Plant Height (cm)	Tiller Number (per plant)	Kernels/ Spike	Kernel Weight (g/1000)	Grain Yield (g/plant)
P_1	21	17.17±0.23	61.43±0.58	18.95±0.82	44.95±1.45	20.51±0.47	10.39±0.61
P_2	21	17.20±0.27	71.05±0.70	15.71±0.67	63.86±2.68	18.81±0.66	9.28±0.68
F_1	21	16.34±0.21	66.76±0.50	17.71±0.73	49.95±1.22	21.89±0.37	11.13±0.57
F_2	126	17.23±0.09	66.77±0.46	18.80±0.40	53.88±0.81	20.48±0.30	11.41±0.34
B_1	63	17.28±0.13	63.14±0.48	17.38±0.45	49.33±0.94	20.18±0.29	10.02±0.34
B_2	63	17.27±0.13	67.84±0.66	16.65±0.49	54.32±1.44	19.47±0.32	9.52±0.39

1/ P_1= PMV, P_2= Newton, B_1= F_1x PMV, B_2= F_1x Newton

TABLE III

MEANS AND STANDARD ERRORS FOR SIX CHARACTERS IN POPULATION 3 (PMV/PAYNE)

Generation1/ and No. of Plants		Grain Protein (%)	Plant Height (cm)	Tiller Number (per plant)	Kernels/ Spike	Kernel Weight (g/1000)	Grain Yield (g/plant)
P_1	21	17.80±0.17	57.81±0.58	14.43±1.05	44.33±1.72	20.84±0.47	8.19±0.72
P_2	21	16.52±0.20	62.81±0.74	16.86±1.27	52.71±1.63	20.99±0.77	11.04±0.96
F_1	21	16.32±0.19	64.05±0.63	17.90±0.99	47.71±1.68	23.47±0.69	12.79±0.75
F_2	126	16.50±0.10	65.08±0.45	18.67±0.51	51.06±0.70	21.53±0.28	12.12±0.41
B_1	63	17.12±0.10	62.14±0.48	16.57±0.58	49.06±0.88	21.16±0.35	10.07±0.47
B_2	63	16.01±0.13	66.41±0.57	20.33±0.59	55.25±0.92	23.92±0.38	16.18±0.60

1/ P_1= PMV, P_2= Payne, B_1= F_1x PMV, B_2= F_1x Payne

TABLE IV

VARIANCE COMPONENTS AND ESTIMATES OF HERITABILITY FOR SIX CHARACTERS IN THREE POPULATIONS OF WINTER WHEAT

Character	Popn	Variance F_2	Variance B_1	Variance B_2	h^2
Grain Protein	1 (PMV/Vona)	1.977	1.074	0.970	0.967
	2 (PMV/Newton)	1.130	1.107	1.023	0.115
	3 (PMV/Payne)	1.203	0.612	1.122	0.559
Plant Height	1 (PMV/Vona)	22.800	20.752	34.124	0.000[1/]
	2 (PMV/Newton)	26.979	14.254	27.813	0.441
	3 (PMV/Payne)	25.066	14.641	20.504	0.598
Tiller Number	1 (PMV/Vona)	15.552	18.999	23.641	0.000[1/]
	2 (PMV/Newton)	19.936	12.982	15.134	0.590
	3 (PMV/Payne)	32.544	21.378	22.097	0.664
Kernels/ Spike	1 (PMV/Vona)	93.222	53.501	98.985	0.364
	2 (PMV/Newton	82.890	55.516	130.833	0.000[1/]
	3 (PMV/Payne)	62.085	48.544	53.386	0.358
Kernel Weight	1 (PMV/Vona)	10.564	5.638	7.155	0.789
	2 (PMV/Newton)	10.993	5.260	6.375	0.942
	3 (PMV/Payne)	9.646	7.825	9.321	0.222
Grain Yield	1 (PMV/Vona)	10.465	10.279	18.430	0.000[1/]
	2 (PMV/Newton)	14.810	7.231	9.411	0.876
	3 (PMV/Payne)	21.586	13.891	22.354	0.321

[1/] In accordance with accepted procedure, negative value is set at 0.000.

TABLE V

ADJUSTED HERITABILITY ESTIMATES FOR GRAIN PROTEIN IN THREE POPULATIONS OF WINTER WHEAT

Type of Estimate and Number of $F_2/(B_1 + B_2)$ plants		Population 1 (PMV/Vona) h^2	Population 2 (PMV/Newton) h^2	Population 3 (PMV/Payne) h^2
Ignoring Blocks (From Table IV)	126/126	0.967	0.115	0.559
Block 1	42/42	0.840	0.836	-0.403
Block 2	42/42	1.361	-0.866	0.796
Block 3	42/42	0.923	0.363	0.603
Adjusted[1/] (Offending Block Removed)	84/84	0.882	0.600	0.700

[1/] Average of two blocks with offending block removed (offending blocks are 2, 2, 1 respectively for populations 1, 2, 3).

TABLE VI

MEANS FOR GRAIN PROTEIN BY BLOCK FOR THREE POPULATIONS OF WINTER WHEAT

Population	Block	P_1 (n=7)	P_2 (n=7)	F_1 (n=7)	F_2 (n=42)	B_1 (n=21)	B_2 (n=21)
Popn. 1	1	16.95	15.66	14.87	16.44	16.82	15.50
(PMV/Vona)	2	17.71	15.28	15.81	16.42	16.58	15.92
	3	16.76	14.95	15.99	16.56	16.28	15.98
Popn. 2	1	17.62	17.24	16.89	17.50	17.45	17.70
(PMV/Newton)	2	17.39	17.35	16.20	17.23	17.55	17.07
	3	16.50	17.01	15.93	16.96	16.83	17.03
Popn. 3	1	17.94	16.21	16.25	16.73	17.15	16.11
(PMV/Payne)	2	17.83	16.59	16.11	16.16	16.72	15.68
	3	17.62	16.76	16.61	16.60	17.50	16.24

TABLE VII

PHENOTYPIC CORRELATION COEFFICIENTS BETWEEN GRAIN PROTEIN AND FIVE OTHER CHARACTERS IN THREE POPULATIONS OF WINTER WHEAT

Grain Protein vs	Plant Height	Tiller Number	Kernels/ Spike	Kernel Weight	Grain Yield
Popn. 1 (PMV/Vona)	-0.25**	-0.09	0.14*	-0.43**	-0.18**
Popn. 2 (PMV/Newton)	-0.11	-0.12*	0.06	-0.29**	-0.24**
Popn. 3 (PMV/Payne)	0.03	-0.08	0.15*	-0.16**	-0.16**

Degrees of freedom = 270
*Significant at the .05 level.
**Significant at the .01 level.

TABLE VIII

INDIVIDUAL F_2 PLANTS EXCEEDING THE MEANS FOR GRAIN YIELD AND GRAIN PROTEIN IN POPULATION 1 (PMV/VONA)

Plant Number	Plant Height (cm)	Tiller Number (per plant)	Kernels/ Spike	Kernel Weight (g/1000)	Grain Yield (g/plant)	Grain Protein (%)
26003-2	67	16	77	18.1	14.3	16.67
26005-1	66	13	60	21.4	10.4	16.53
26005-2	67	14	59	24.7	14.3	16.80
26005-3	67	14	84	16.5	12.3	19.47
26005-4	66	18	54	17.3	10.6	18.67
26012-7	69	20	68	22.2	13.4	18.40
26013-1	70	24	72	20.2	13.3	16.80
26013-6	70	22	76	25.4	14.9	16.67
26015-7	64	19	65	22.1	10.6	16.93
26022-7	63	22	78	25.3	13.7	18.40
26028-1	65	18	59	20.0	10.4	16.93
26028-2	67	19	72	20.5	11.5	17.07
26028-3	68	15	66	20.4	12.4	18.00
26028-5	69	19	70	18.7	14.2	17.20
26032-2	67	18	74	22.2	10.1	17.20
26032-4	64	19	69	19.8	12.0	19.20
26033-4	59	22	56	17.1	11.7	17.33
26033-6	67	16	66	23.9	11.1	17.20
26035-1	64	16	88	19.4	11.0	18.27
26035-4	64	27	69	16.5	10.7	21.73
26042-3	65	22	70	21.8	14.8	17.47
26042-4	62	22	75	20.6	13.2	17.07
26050-7	60	22	65	22.3	10.2	16.67
Mean	--	--	--	--	9.9	16.47

TABLE IX

INDIVIDUAL BACKCROSS PLANTS EXCEEDING THE MEANS FOR GRAIN YIELD AND GRAIN PROTEIN IN POPULATION 1 (PMV/VONA)

Plant Number	Plant Height (cm)	Tiller Number (per plant)	Kernels/ Spike	Kernel Weight (g/1000)	Grain Yield (g/plant)	Grain Protein (%)
			B_1(PMV/Vona//PMV)			
26001-2	51	21	51	19.4	14.0	17.47
26001-7	71	31	68	19.6	23.6	17.60
26002-2	64	12	50	17.8	9.1	18.93
26014-5	63	22	55	21.8	13.1	17.47
26014-6	60	22	59	22.7	15.1	17.07
26024-2	66	14	53	23.9	10.2	16.67
26024-6	65	20	60	16.7	10.2	18.00
26041-3	64	22	64	21.1	11.9	17.07
26041-5	62	20	59	18.7	10.5	17.07
26041-6	61	18	54	22.4	9.6	16.80
26041-7	56	19	44	17.8	9.3	18.13
26043-6	60	22	62	20.1	11.1	16.80
26043-7	63	19	53	22.3	10.0	16.67
26054-7	61	19	54	21.3	10.6	17.20
Mean	--	--	--	--	9.1	16.56
			B_2(PMV/Vona//Vona)			
26004-3	66	23	83	21.9	13.7	16.27
26004-5	77	21	79	22.6	16.0	16.13
26006-1	76	13	64	23.3	12.1	16.40
26011-1	72	28	72	22.5	21.9	16.80
26027-4	70	22	64	18.4	13.1	16.40
26048-3	63	21	60	17.8	12.6	16.00
26048-6	63	17	71	18.2	12.5	17.33
26051-2	67	19	67	20.8	11.1	16.27
Mean	--	--	--	--	11.0	15.80

TABLE X

INDIVIDUAL F_2 PLANTS EXCEEDING THE MEANS FOR GRAIN YIELD AND GRAIN PROTEIN IN POPULATION 2 (PMV/NEWTON)

Plant Number	Plant Height (cm)	Tiller Number (per plant)	Kernels/ Spike	Kernel Weight (g/1000)	Grain Yield (g/plant)	Grain Protein (%)
26102-2	76	26	79	24.2	16.5	18.27
26104-1	76	21	65	25.3	14.4	18.00
26104-5	73	18	57	21.2	12.8	19.60
26104-6	71	16	62	23.5	11.9	17.33
26107-3	64	21	48	21.3	11.6	17.47
26107-5	69	23	65	18.3	14.1	18.13
26107-6	66	18	46	16.4	11.8	17.87
26108-1	64	18	70	24.4	12.0	18.00
26108-6	68	16	62	25.8	12.8	17.60
26124-1	82	19	60	19.4	12.0	17.60
26124-5	75	25	83	21.9	12.8	17.60
26129-2	77	17	54	21.3	11.5	18.17
26129-5	71	20	65	19.3	15.0	17.90
26133-1	75	27	55	15.2	16.2	19.10
26144-2	64	17	54	23.8	11.5	17.47
26151-3	78	28	66	19.3	18.6	19.07
26151-6	79	24	64	17.5	13.5	18.67
26155-7	62	22	47	26.2	15.0	17.87
Mean	--	--	--	--	11.4	17.23

TABLE XI

INDIVIDUAL BACKCROSS PLANTS EXCEEDING THE MEANS FOR GRAIN YIELD AND GRAIN PROTEIN IN POPULATION 2 (PMV/NEWTON)

Plant Number	Plant Height (cm)	Tiller Number (per plant)	Kernels/ Spike	Kernel Weight (g/1000)	Grain Yield (g/plant)	Grain Protein (%)
			B_1 (PMV/Newton//PMV)			
26101-2	63	22	63	23.5	13.2	17.47
26101-3	55	22	46	18.1	10.2	17.60
26105-5	67	21	47	16.0	11.4	19.87
26105-7	64	19	51	19.1	13.1	17.87
26123-3	63	17	52	23.0	11.0	18.53
26130-5	60	17	39	19.0	10.8	19.90
26130-6	64	18	47	20.0	11.4	18.43
26135-4	65	18	61	20.0	10.7	18.03
26135-6	67	18	52	18.8	10.1	18.57
26135-7	65	19	43	18.5	12.3	18.03
26142-2	62	19	42	26.1	12.5	17.33
26142-6	65	20	68	20.6	12.9	17.47
26149-1	65	22	56	22.2	16.3	18.83
26149-2	71	16	58	23.6	11.9	18.03
Mean	--	--	--	--	10.0	17.28
			B_2 (PMV/Newton//Newton)			
26103-4	68	18	51	23.4	11.3	17.73
26103-6	78	21	54	17.5	13.6	18.00
26112-1	70	18	64	19.0	10.6	17.47
26112-2	66	21	77	20.2	15.5	18.27
26112-5	67	21	48	18.8	12.5	18.27
26112-7	76	13	55	22.1	11.8	17.87
26128-5	66	18	61	22.7	12.4	17.23
26128-7	67	21	60	16.8	12.9	17.37
26132-1	77	19	65	18.0	11.6	18.70
26132-2	71	14	63	21.0	10.7	17.90
26148-1	69	20	53	17.0	10.6	18.03
26148-6	67	19	55	22.1	12.2	19.10
26154-6	67	19	60	17.4	11.4	17.20
26154-7	73	23	47	17.6	11.4	17.33
Mean	--	--	--	--	10.4	17.17

TABLE XII

INDIVIDUAL F_2 PLANTS EXCEEDING THE MEANS FOR GRAIN YIELD AND GRAIN PROTEIN IN POPULATION 3 (PMV/PAYNE)

Plant Number	Plant Height (cm)	Tiller Number (per plant)	Kernels/ Spike	Kernel Weight (g/1000)	Grain Yield (g/plant)	Grain Protein (%)
26202-1	78	19	61	25.7	15.3	16.53
26202-4	72	23	46	21.1	13.8	17.73
26202-5	67	25	58	20.4	15.8	17.47
26203-4	72	18	64	26.1	20.1	17.87
26203-6	72	36	61	21.4	24.1	17.33
26203-7	73	31	60	23.7	18.0	16.93
26205-3	65	21	50	21.1	14.1	17.47
26205-6	70	24	52	19.0	14.0	16.67
26205-7	67	25	48	18.8	13.4	16.80
26211-4	61	19	46	23.1	13.0	16.67
26211-7	69	19	57	22.5	15.3	17.87
26214-3	78	20	63	24.3	19.4	16.80
26215-4	60	41	60	25.3	19.7	16.93
26215-5	67	23	50	23.3	15.8	17.07
26215-6	67	15	53	24.4	12.7	18.27
26221-3	67	26	64	23.4	18.4	17.07
26228-1	68	17	58	24.4	13.7	18.27
26230-1	68	30	48	25.3	20.6	17.33
26230-3	62	18	51	26.3	15.7	16.93
26230-5	72	30	57	30.2	28.7	17.20
26230-7	69	22	61	24.6	22.0	17.47
26233-3	70	21	56	22.4	14.1	17.07
26243-7	68	18	48	20.7	12.6	17.33
26244-1	68	27	59	24.7	20.1	16.93
26244-5	73	24	57	26.2	21.4	17.73
26251-3	65	21	56	20.6	15.8	16.80
26253-2	74	20	60	25.1	16.3	17.07
26253-6	71	19	49	27.7	16.8	17.20
Mean	--	--	--	--	12.1	16.50

TABLE XIII

INDIVIDUAL BACKCROSS PLANTS EXCEEDING THE MEANS FOR GRAIN YIELD AND GRAIN PROTEIN IN POPULATION 3 (PMV/PAYNE)

Plant Number	Plant Height	Tiller Number	Kernels/ Spike	Kernel Weight	Grain Yield	Grain Protein
	(cm)	(per plant)		(g/1000)	(g/plant)	%
			B_1 (PMV/Payne//PMV)			
26204-1	70	20	55	22.6	14.8	17.33
26204-4	59	25	39	21.6	15.2	17.20
26209-4	64	19	50	20.4	10.3	18.53
26213-2	61	27	51	20.6	16.2	17.87
26213-5	63	27	62	27.9	20.9	17.47
26227-3	65	24	55	22.6	20.2	17.87
26232-1	63	17	56	25.2	12.5	18.00
26245-6	62	20	58	22.5	13.4	17.33
26252-4	67	18	56	22.9	14.8	17.20
26252-6	66	19	56	25.2	15.6	17.60
26255-1	66	15	48	23.5	11.1	17.33
26255-2	65	18	53	23.5	11.1	18.00
26255-7	64	15	58	20.1	11.2	18.13
Mean	--	--	--	--	10.1	17.12
			B_2 (PMV/Payne//Payne)			
26201-1	64	29	43	22.8	23.8	16.27
26206-1	74	23	64	22.9	19.1	16.53
26206-4	70	25	57	26.1	25.4	16.13
26208-2	72	25	47	19.3	24.1	16.53
26208-7	69	19	58	22.6	16.8	17.33
26222-4	68	28	43	23.8	17.7	16.40
26223-6	63	26	60	26.8	21.7	16.53
26254-5	70	20	61	28.3	19.3	16.27
Mean	--	--	--	--	16.2	16.01

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