INHERITANCE OF PROTEIN, LYSINE, AND SELECTED TRAITS IN FOUR SPRING WHEAT CROSSES

by

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INHERITANCE OF PROTEIN, LYSINE, AND SELECTED TRAITS IN FOUR SPRING WHEAT CROSSES

Steven Kuhr

INTRODUCTION

Although emphasis on yield continues to be one of the most important aspects of crop improvement, an increasing awareness of the nutritional imbalance in cereal protein has stimulated much recent research on protein quality.

The yield potential of wheat and other cereal crops has been increased both by selective breeding and improved cultural techniques. The advent of dwarf wheat varieties has led to increased yields in many areas of the world. These short-statured varieties possess lodging resistance even under irrigation and nitrogen fertilization. Thus, maximum yield expression is possible over a wide range of environments.

Wheat protein has an insufficient amount of the amino acid, lysine (19, 22). Studies to improve the protein content of wheat have shown that lysine as a percent of kernel protein is negatively correlated with protein (19, 27). This has stimulated search for high protein wheat with a high lysine/protein percentage. Systematic analysis of wheat varieties in the World Collection maintained by the United States Department of Agriculture

(13, 15, 33) identified the Indian spring wheat variety NapHal, P.I. 176217, as having consistently high grain protein percentage in combination with high lysine/protein percentage. NapHal is, therefore, of obvious interest to those breeders concerned with transferring higher protein and lysine potential to agronomically acceptable adapted varieties.

Many of the currently available high protein wheat varieties are too tall. For commercial acceptability, it will be necessary to transfer the trait to shorter plant types. McNeal et al (23) suggested that short plants are generally less able to translocate nitrogen from the foliage into the grain than tall plants. In their study, short plant height was found to be positively correlated with low grain protein content. A contradictory observation was made by Johnson et al (16) who found a significant correlation of -0.24 between plant height and grain protein in a cross of NapHal with C.I. 13449. If high protein content can be expressed in short plants, then high yield in combination with better nutritional qualities can be expected in future wheat varieties.

This study was conducted to further evaluate the behavior of protein-lysine inheritance of NapHal as influenced by plant height, other agronomic traits, and environments.

LITERATURE REVIEW

Grain Protein

Grain protein is generally considered to be negatively correlated with yield and seed weight (6, 7, 9, 10). Since seed weight and seed plumpness are highly correlated (34), a significant negative correlation would be expected between seed weight and protein content. Kernel size in itself has little influence on protein or lysine levels (14, 16). No significant differences in protein or lysine were found between small plump kernels and large plump kernels. There was, however, a marked increase in protein content in seeds which were wrinkled. Seed shriveling tends to be caused by a reduction of the starchy endosperm (19, 29).

Lawrence et al (19) found the endosperm of wheat to be lower in protein content than the bran and germ components of the wheat kernel. Johnson et al (14) reported that the non-endosperm proteins tended to be higher in lysine (over 4%) than the endosperm proteins which had about 2%. However, while a reduction of the endosperm increased the percentage of protein, the lysine level and lysine percentage of protein were not significantly changed.

The protein content in wheat grain has also been shown to be sensitive to soil fertility and environmental factors. Haunold et al (6) suggested that the higher protein content of the grain of some wheats resulted from a more efficient translocation of nitrogenous compounds through the plant. It was postulated that an internal protein-fixing threshold

was operative in wheat varieties. The threshold represents the genetic potential for kernel protein content. With adequate nitrogen levels in the soil, a variety with a high threshold will be expected to deposit more protein in its seeds than one with a lower threshold. The protein threshold for Atlas 66 in the study was about 3 percentage points higher than that of Wichita.

McNeal et al (23) reported that the amount of top growth in the wheat plant regulates the amount of nutrients taken up and translocated to the grain. In a fertilizer study involving short, medium, and normal height in the variety Centana, the protein content of grain from the short selection was found to be less than that of the other selections. Also, there was a higher percentage of protein remaining in the straw of the short selection at harvest. This was interpreted as a lower protein translocation capacity in the short Centana selection.

Terman et al (31) also studied the effects of nitrogen fertilization on wheat. They found that the applied N would increase total yield if adequate water was available. Moisture supply was found to be the chief factor influencing response to applied N. When moisture levels were low, the chief effect of added N was to increase the protein content of the grain. Fertilization with N was found to increase the total protein yield per acre in all cases.

Evidence of moisture effects and geographical influences were reported by Pisarev (26) and Waldron (34).

Waldron observed that wheat grain protein is higher in dry years. Pisarev found that the protein level of wheat varied from 14-15% in wet years to 20% in dry years. A reduction in kernel protein was also observed from dry warm geographical areas toward cooler and moister areas.

Hojjati (8) reported an inverse relationship between applied N and lysine as a percent of protein. This might be expected from reported inverse protein-lysine correlations (13, 14, 27, 32). Hojjati found potassium to increase lysine expressed as a percent of protein. Increasing K from 0 to 100 kg/ha increased the lysine content of the protein by about 29% with no added N. When N was applied at high levels, the effectiveness of K on lysine was reduced. Khera et al (17) found that wheat grown on soil with available phosphorus of 12.5 ppm or more had higher lysine levels in its grain protein, and higher yields, but the protein percent of the grain was decreased.

The yield-protein question was somewhat clarified when the high protein variety, Atlas 66, was determined to maintain its high grain protein percentage without significant yield reductions over many environments (12, 24). The high protein of Atlas 66 has been transferred to other wheats with heritability values for proteins approaching 82% (9, 11). Some of the high protein lines were demonstrated to be highly productive.

Genetic studies involving Wichita and Atlas 66 (5, 30) produced evidence that protein was under polygenic control

with no dominant genes for either high or low protein levels. Heritability values for grain protein in those studies ranged from 68 to 83%.

Chapman and McNeal (2) studied five crosses in which Frontiera was a common parent. No significant epistatic effects were detected for grain protein inheritance in any cross. Additive genetic effects were found to be significant in all crosses of the study. One cross, in which NapHal (P.I. 176217) was the second parent, demonstrated a significant dominance effect for low protein from Frontiera.

Hsu and Sosulski (7) made diallel crosses among four hard red spring wheat varieties Thatcher, Selkirk, Gabo, and Prairie Pride to study protein inheritance. Thatcher exhibited nearly all of the dominant genes for protein among the four varieties. Gabo showed predominantly recessive genes, while Selkirk and Prairie Pride had both dominant and recessive genes for protein expression. The recessive genes in Selkirk were favorable for high protein expression as were the dominant genes of Thatcher.

The Indian spring wheat variety NapHal is of particular value to breeding programs due to the superior lysine content of its protein (12, 14). The very high protein content of NapHal also is relatively stable. NapHal was crossed with a Korean wheat variety, Yang Kwang, and with the Nebraska variety Lancer (14). All NapHal parental values for protein exceeded 20 percent. The mean of Yang Kwang was about 17.4%,

and that of Lancer 16.4%. High protein in these crosses appeared to be partially dominant, since, in each, the F_2 frequency distribution had a modal class of 18 percent and a range from 16 to 21 percent.

NapHal x Atlas 66 crosses at Nebraska (15) exhibited transgressive segregation for both high and low protein. Interpretation of this leads to speculation that different protein genes exist in the two varieties. Mean lysine values of the F_2 populations were intermediate to the parents. The NapHal level of lysine was recovered in some segregates.

In another study by Johnson et al (15), NapHal was crossed with C.I. 13449. C.I. 13449 is a short-statured variety which has the highest value of lysine percent of protein in the World Collection (11, 14, 15, 33). The mean value of lysine adjusted to a common protein level and expressed as a percent of protein for NapHal was 3.23%. C.I. 13449 had 3.35% adjusted lysine. Eleven percent of the F_2 progeny bulks grown in the F_3 generation were found to have adjusted lysine levels outside the parental range. The results of the study suggested transgressive segregation for lysine inheritance. In the same study (15) the protein values ranged from 12 to 21 percent.

The relationship between protein and lysine expressed as a percent of protein has been shown to be curvilinear and negative (14, 15, 33). The inverse relationship between grain protein and lysine expressed as percent of protein is significant for wheats with less than 15% protein, while

it is non-significant for wheats with more than 15% protein.

Identification of genes for high lysine in wheat requires that the effect of protein be eliminated to avoid overlooking potentially high lysine wheats which also have high protein. Johnson et al (14, 15) have searched common wheats from the World Collection for possible high lysine material. In a report by Vogel et al (33), protein levels from analysis of 12,613 common wheats ranged from 6.90 to 22.0% with a mean of 12.97%. Lysine values expressed as percent of protein were adjusted to the mean protein level of the 12,613 wheats sampled, so that unbiased comparisons of lysine levels could be made between them. Lysine expressed as a percent of protein ranged from 2.25 to 4.26 with a mean of 3.16. The adjusted lysine values ranged from 2.28 to 3.71 percent of protein.

Because of the curvilinearity of the relationship, a third degree polynomial was used to determine the regression of lysine percent of protein on percent protein. The coefficient of determination for that regression was 0.5231. Therefore, about 52% of the variation in lysine percent of protein could be attributed to variation in the protein content.

Five hundred wheat varieties were found to have protein contents of 17 percent or more (33). These represent potential genetic sources for high protein. The best sources for high lysine also were identified and ranked. The variety C.I. 13449 was shown to possess the highest adjusted lysine value of 3.71%.

Plant Height

Studies of plant height in wheat have led to similar but by no means identical results (1, 3, 11, 25, 28). Plant height in wheat has been shown to be an expression of both multigenic and major gene effects. Anwar and Chowdhry (1) reported that plant height is a complexly inherited character. In their study involving F_1, F_2, and backcross populations from four spring wheat varieties of tall and short stature, plant height as well as yield behaved as quantitatively inherited traits. Heterosis also occurred for height, since each of the F_1's was taller than its tall parent.

Chapman and McNeal (3) reported an environmental influence on gene expression. In 1967 a cross between Henry and Lemhi 53 produced dominance and dominance x dominance epistatic effects for plant height and yield. The F_1's were taller than the parents. In 1968 the epistatic effects were not shown, since the F_1's were within the parental range.

Johnson et al (11) obtained evidence that plant height inheritance was largely through accumulative additive effects. In a cross between Seu Seun 27, a short variety, and Bluejacket, a tall variety, there was indication that additive, dominance, and additive x additive epistasis were involved in plant height inheritance. Partial dominance was indicated by an F_1 mean larger than the mid-parent value. The bimodal frequency distribution of the F_2 in the study suggested the

operation of a small number of genes. This was further supported by study of the F_3 rows. Since the average variation in plant height between plants within parental rows was 15 cm., F_3 rows having a height variation of 15 cms or less were considered to be homozygous. The proportion of F_3 rows classified as homozygous was 12.1%. This percentage was then used to arrive at a 3-gene pair model for the expression of plant height.

Similar findings were reported by Novoa (25). In an analysis of population means and frequency distributions involving the parents, F_1, and F_2 of a cross between La Molina 60 and a dwarf variety, Novoa found evidence of the operation of more than one type of gene action. Additive gene action was suggested from F_1 and F_2 means that approximated the mid-parent values. The F_2 frequency distribution was slightly bimodal with major groupings in the 68 and 98 cm classes. This bimodal effect, similar to that observed by Johnson et al (11), again suggested a small number of genes for plant height expression.

Heritability values for plant height are generally high. Values computed by Anwar and Chowdhry (1) show a narrow sense range of from 21 to 40%, and a broad sense range from 50 to 66%. Johnson et al (11) computed a narrow sense heritability of 45.3% and broad sense value of 60.8%. Reddi (28) measured culm lengths in two populations involving Norin 10 x adapted varieties. He determined heritability values for culm length of 63 and 81%. He

also found a strong correlation between culm length and seed weight. The short culm was associated with low kernel weight. Johnson et al (11) also measured significant positive correlation values between plant height, kernel weight, and yield. Similar results also were reported by Knott and Talukdar (18) from a study involving Selkirk and Thatcher.

MATERIALS AND METHODS

Plant Materials-

Five spring wheat varieties were selected as parental material for this study. The variety NapHal, P.I. 176217, was used as a common female parent in crosses to the other varieties. NapHal has medium plant height but lacks yield and desirable kernel morphology traits. NapHal has been shown to possess combined high grain protein content and high lysine (percent of protein) value (14, 33). The other varieties used in the study were C.B. No. 113, Justin, Pitic 62, and Selkirk.

C.B. No. 113 (Ciano S x Chris 23583-10M-6Y-100M-300Y) is a Mexican semi-dwarf line which was not released as a commercial variety. It has short straw, but does not yield as well as some other semi-dwarfs.

Justin (Thatcher-Kenya Farmer Lee-Mida x Conley) is a tall hard red spring wheat variety developed in North Dakota. It is moderately resistant to leaf rust, loose smut, bunt, and black chaff. It has been the leading variety in northern states in recent years. Justin yields well and has a higher-than-average protein content.

Pitic 62, (Yaktana 54 x Norin 10-Brevor 26-1C-7064-1Y-1H-1R-2M) was the first Mexican semi-dwarf released as a commercial variety. It is a high yielding variety, but has a low test weight and is susceptible to many strains of rust.

Selkirk (McMurachy-Exchange x Redman[3]) was developed in Canada. It also has good rust and loose smut resistance. Prior to Justin, it was the leading hard red spring wheat in the United States. It is relatively tall but does not yield as well as Justin. It produces fewer kernels per unit area which have higher test weight than Justin.

Experimental Procedure

The study was initiated as a portion of the thesis research in 1970 of Charles Lay, then a graduate student at the University of Nebraska. The populations utilized in the study were developed in a greenhouse at Lincoln, Nebraska in 1969-70 and 1970-71.

The field experiments were organized in a split-plot design with groups comprising the main plots and generations the sub-plots. Groups consisted of four adjacent single rows of parental, F_1 and F_2 populations of a cross. The rows were randomized within groups, and groups were randomized within replications. Three replications were grown in 1971 at each of two locations, Ft. Collins, Colorado, and Bozeman, Montana.

At each location the rows were planted 12 inches apart and seeds were spaced 3 inches apart within the rows. Thirty seeds were planted in each row except in the case of some of the F_1's, particularly NapHal x C.B. No. 113. Nicking disparity in the greenhouse resulted in a low number of F_1 seeds.

Rows were bordered at each end with two durum plants so that a total of 34 seeds were planted per row. The durum plants were discarded at harvest. In addition, durum border rows were planted at the ends of each replication. Durum plants were also substituted in the rows which had less than 30 seeds at planting. This was done to reduce border and population density effects.

The experiment at Ft. Collins was planted on April 5 and harvested on August 5, 1971. Individual plants were pulled at Ft. Collins at harvest time. The plants were individually bagged in paper sacks to avoid loss of seed during shipment to Lincoln, Nebraska where all data measurements were taken.

The trial at Bozeman was planted on May 12, and harvested on September 8, 1971. Plants were measured for height at the time of harvest. The spikes of each plant were then removed and placed in paper sacks for shipment to Lincoln.

The following data were obtained for each plant:

Grain Protein Content - The amount of protein expressed as a percent of dry grain weight.

Adjusted Lysine - Lysine expressed as a percent of grain protein adjusted to a common level of 13% protein.

Plant Height - The height in centimeters measured from the crown of the plant to the tip of the tallest tiller, excluding awns.

Grain Yield - The weight of the grain obtained from each plant expressed to the nearest one-tenth of a gram.

Twenty-seed Weight - The weight of twenty seeds randomly selected from each plant measured to the nearest one-hundredth of a gram.

Number of Heads per Plant - The number of seed-bearing heads from each plant.

Plant Weight (Ft. Collins only) - The weight of top growth of each plant measured to the nearest one-tenth of a gram.

Protein analyses were made using the Kjeldahl method of nitrogen determination. Protein values were computed by multiplying the percent nitrogen by a factor of 5.7.

Lysine values were obtained from an automatic amino acid analyzer which operated on the principle of ion exchange chromatography. The size, weight, and charge of the amino acid molecules determine the rate at which they will flow through the column. The greater the affinity of the acid for the resin, the slower the acid will move. Each amino acid thus has a characteristic time-order phase in traversing the length of the column. The amino acids are reacted with ninhydrin, and the color intensity is automatically measured in a colorimeter. A recorder scribes a peak for each acid, the position of which identifies the amino acid and the area beneath a peak which is proportional to the amount of that amino acid.

Lysine expressed as a percent of protein was adjusted to a common protein level. The protein level used was 13%, which represents the mean protein percentage of 12,613 common wheats analyzed from the World Collection. A computer program utilizing a third degree regression polynomial was utilized to obtain the adjusted values.

Data from plants which produced highly shriveled seed or less than the amount necessary for protein and lysine determinations were not used in the statistical analyses. Two rows identified as NapHal at Ft. Collins also were eliminated from the statistical analyses. They were determined not to be NapHal based on agronomic characters and lysine analyses. These rows were treated as missing data in computing analysis of variance tables according to Cochran and Cox (4).

Means, variances, and standard deviations were computed for the traits in each population over replications. The variances of the traits are pooled row variances. Analyses of variance were complicated by variable numbers of plants in rows. The F_1 between NapHal and C.B. No. 113 had only 11 plants at Bozeman and 13 at Ft. Collins. The analyses were therefore based on row means. Comparisons were made within groups between parents, parents and F_1's, parents and F_2's, and between F_2's and the average of the parents with F_1's. In some cases the error b (populations within groups) mean square was larger than the error a, (among groups and replications) mean square. In those instances, a pooled

error variance was used in computing the F ratios.

Frequency distributions were constructed to graphically illustrate the variability of plant height, protein content, and adjusted lysine values within families. Linear correlation coefficients were computed so that relationships between characters could be quantified and compared.

Broad sense heritability values (ratio of total genetic variance to the phenotypic variance) were computed by three methods. The first method employs the F_1 as the measure of environmental variance. However, since some F_1 populations were represented by only a few plants, a second method utilizing the geometric mean of the parental variances, after Mahmud (21), was used as an estimate of the environmental variance. The second method was not applicable in situations where the variances of the parents were shown to be non-homogeneous by Bartlett's test. Seed from F_2 plants grown at Ft. Collins was advanced to the F_3 generation at Mead, Nebraska in 1972. A third heritability estimate was thus provided by correlating the F_3 and F_2 values as suggested by Frey and Horner (5). This method was used only for protein and adjusted lysine values.

EXPERIMENTAL RESULTS

Since there was primary emphasis on grain protein, adjusted lysine, and plant height, results of statistical analyses for those traits consequently received more thorough examination than other traits. Since NapHal was the common female parent, F_1 and F_2 populations will often be identified by the male parent; i.e., the NapHal/Justin F_1 is referred to as the F_1 of the Justin group.

Protein

Means

Means, variances, and coefficients of variation for grain protein are recorded in Table 1. The highest mean grain protein content at Ft. Collins was recorded for Justin. Its value of 19.0% was significantly higher than the other three male parents. F_1 means were intermediate to the parents except in the Justin group in which the F_1 mean was not significantly different from NapHal.

F_2 protein means at Ft. Collins did not differ significantly from F_1 means, except in the Pitic 62 group. The F_2 protein means of the C.B. No. 113 and Pitic 62 groups were significantly larger than their respective male parents. None of the F_2 means for grain protein differed significantly from the mean of NapHal.

Bozeman protein means were consistently higher than those observed at Ft. Collins. The highest mean for grain protein at Bozeman again was in Justin. Its mean value of

Table 1. Means, variances, and coefficients of variation for grain protein in parental, F_1 and F_2 populations of four spring wheat crosses grown at Ft. Collins, Colorado and Bozeman, Montana in 1971.

Population	Ft. Collins				Bozeman			
	No. of Plants	$\bar{x}$ %	s^2	c.v.	No. of Plants	$\bar{x}$ %	s^2	c.v.
NapHal	260	18.3	0.82	5.0	222	19.2	1.18	5.7
C.B. No. 113	79	17.0	0.67	4.8	51	17.8	0.29	3.0
NapHal/C.B. No. 113 F_1	13	18.0	0.35	3.3	11	18.7	0.67	4.4
NapHal/C.B. No. 113 F_2	79	18.5	2.94	9.3	79	19.4	2.60	8.3
Justin	78	19.0	0.67	4.3	75	20.0	0.32	2.8
NapHal/Justin F_1	57	18.1	0.38	3.4	63	19.0	0.42	3.4
NapHal/Justin F_2	75	18.7	1.43	6.4	73	19.5	1.51	6.3
Pitic 62	72	14.9	1.60	8.5	87	16.6	0.54	4.4
NapHal/Pitic 62 F_1	22	16.7	0.72	5.1	29	18.3	1.00	5.5
NapHal/Pitic 62 F_2	73	18.0	2.36	8.6	75	18.6	1.17	5.8
Selkirk	75	17.9	0.74	4.8	66	18.2	0.41	3.5
NapHal/Selkirk F_1	74	18.0	0.70	4.6	79	18.8	0.60	4.1
NapHal/Selkirk F_2	76	17.9	1.75	7.4	69	19.5	1.72	6.8
LSD at .05		0.6				0.4		

20.0% was significantly larger than the means of all other populations. The mean of NapHal, 19.2%, was significantly larger than the means of the male parents other than Justin. The F_1 mean of the Justin group was significantly lower than the mean of Justin but not different from NapHal. The F_1 means of the other groups were intermediate to the parental values.

The F_2 mean of the Pitic 62 group was significantly lower than the mean of NapHal. Other F_2 means were not different from the mean of NapHal. F_2 populations were generally higher in protein than their male parents and F_1's.

Variances

Pitic 62 exhibited the largest protein variation among parental populations at Ft. Collins, (Table 1). Its variance was significantly greater than the variances of other parent varieties. F_1 variances were less than parental variances in all groups.

All F_2 populations at Ft. Collins had significantly larger variances than their corresponding F_1 populations. F_2 variances also exceeded parental values. These differences were significant in all but the Pitic 62 group in which the F_2 variance was significantly larger than the variance of NapHal, but non-significantly different from the variance of Pitic 62.

At Bozeman, the NapHal protein variance was significantly larger than those of the male parents. F_2 protein variances

were larger than F_1 variances, being significantly larger in all but the Pitic 62 group. The variances of the F_2 populations were all significantly larger than the variances of their corresponding male parents. Only the F_2 populations of the C.B. No. 113 and Selkirk groups had significantly larger protein variances than the NapHal parent.

Frequency Distributions

The F_2 population of the C.B. No. 113 group had the widest distribution for grain protein (Tables 2 and 3). At both locations, high protein segregants contributed to the high mean protein value of the F_2 population. The F_2 distributions of the Justin group exhibited slight bimodality at both locations.

The distribution of the Pitic 62 parent grown at Ft. Collins differed markedly from that of Bozeman. At Ft. Collins, Pitic 62 was highly variable for protein, while at Bozeman it exhibited much less variability.

Adjusted Lysine

Means

Means, variances, and coefficients of variation for adjusted lysine are recorded in Table 4. At Ft. Collins, the highest mean value for adjusted lysine was 3.2% for NapHal. The lowest lysine value among the male parents was 3.0% for Justin. The means of all male parents were significantly lower than NapHal at the 5% level. All F_1 means for lysine were higher than their respective male parents

Table 2. Frequency distribution of grain protein expressed as percent of p

Population	No. of Plants	11.2	11.7	12.2	12.7	13.2	13.7	14
NapHal	260							
C.B. No. 113	79							
NapHal/C.B. No. 113 F_1	13							
NapHal/C.B. No. 113 F_2	79							
Justin	78							
NapHal/Justin F_1	57							
NapHal/Justin F_2	75							
Pitic 62	72	1		1	1	7	17	2
NapHal/Pitic 62 F_1	22						5	
NapHal/Pitic 62 F_2	73							
Selkirk	75							
NapHal/Selkirk F_1	74							
NapHal/Selkirk F_2	76							

rcent of population for parental, F_1 and F_2 populations of four spring wheat crosses (

Class Midpoints (%)											
13.7	14.2	14.7	15.2	15.7	16.2	16.7	17.2	17.7	18.2	18.7	19.2
			1	2	2	3	5	13	28	27	15
		1		9	15	22	30	13	6	1	
							23	15	38	23	
	1		1	5	3	8	11	10	18	5	13
								4	19	40	10
						2	7	33	30	21	4
					1	7	11	12	11	20	12
17	22	4	7	17	7	6	6	1	1	1	
5				14	18	23	18	14	5		5
	1	1	3	4	5	10	10	18	11	12	10
			1		3	8	19	23	28	7	5
			1			4	9	34	34	7	5
	1		1	5	11	4	12	12	20	14	8

.ng wheat crosses grown at Ft. Collins, Colorado in 1971.

18.7	19.2	19.7	20.2	20.7	21.2	21.7	22.2	22.7	$\bar{x}$
27	15	2	1						18.3
1		1	1						17.0
23									18.0
5	13	6	4	6	5	1	1	1	18.5
40	10	15	5	3	1	3			19.0
21	4		4						18.1
20	12	13	8	3		3			18.7
1									14.9
	5								16.7
12	10	5	3	3	3			1	18.0
7	5	4	1	1					17.9
7	5	1	1	3					18.0
14	8	5	3	3	1				17.9

Table 3. Frequency distribution of grain protein expressed as percent of pop
crosses grown at Bozeman, Montana in 1971.

Population	No. of Plants	14.2	15.7	16.2	16.7	17.3	17.7	18.3	Class 18.7
NapHal	222		1		1		4	19	19
C.B. No. 113	51				8	22	37	20	14
NapHal/C.B. No. 113 F_1	11							64	9
NapHal/C.B. No. 113 F_2	79		1		3	3	6	18	22
Justin	75								1
NapHal/Justin F_1	63						2	16	40
NapHal/Justin F_2	73						4	12	26
Pitic 62	87	1	20	25	25	16	8	3	1
NapHal/Pitic 62 F_1	29					17	28	17	31
NapHal/Pitic 62 F_2	75		1	1	3	5	19	13	31
Selkirk	66				5	9	15	42	24
NapHal/Selkirk F_1	79					1	8	19	51
NapHal/Selkirk F_2	69					7	6	16	20

percent of population for parental, F_1 and F_2 populations of four spring wheat

		Class Midpoints (%)											
.7	18.3	18.7	19.3	19.7	20.3	20.7	21.3	21.7	22.3	22.7	23.3	23.7	$\bar{x}$
4	19	19	21	14	7	6	4	2					19.2
37	20	14											17.8
	64	9	9	9		9							18.6
6	18	22	6	10	6	5	8	4	3	4	3		19.4
		1	12	37	29	11	7	1		1			20.0
2	16	40	22	16	2		3						19.0
4	12	26	19	12	1	12	7		3	1	1		19.5
8	3	1											16.6
28	17	31		3					3				18.3
19	13	31	12	5	4	3	1			1			18.6
15	42	24		2	3								18.2
8	19	51	9	5	3	3	1		1				18.8
6	16	20	9	14	10	4	6	3	4				19.3

Table 4. Means, variances, and coefficients of variation for adjusted lysine in parental, F_1 and F_2 populations of four spring wheat crosses grown at Ft. Collins, Colorado and Bozeman, Montana in 1971.

Populations	Ft. Collins			Bozeman		
	$\bar{x}$ %	s^2	c.v.	$\bar{x}$ %	s^2	c.v.
NapHal	3.2	0.009	3.0	3.3	0.010	3.1
C.B. No. 113	3.0	0.002	1.6	3.0	0.005	2.4
NapHal/C.B. No. 113 F_1	3.1	0.004	2.0	3.1	0.011	3.4
NapHal/C.B. No. 113 F_2	3.0	0.010	3.2	3.1	0.007	2.7
Justin	3.0	0.006	2.6	2.9	0.005	2.5
NapHal/Justin F_1	3.1	0.005	2.3	3.2	0.030	5.5
NapHal/Justin F_2	3.0	0.010	3.3	3.1	0.009	3.0
Pitic 62	3.0	0.013	3.8	3.0	0.006	2.5
NapHal/Pitic 62 F_1	3.1	0.004	2.1	3.1	0.006	2.6
NapHal/Pitic 62 F_2	3.1	0.015	3.9	3.1	0.010	3.2
Selkirk	3.0	0.005	2.2	3.0	0.006	2.6
NapHal/Selkirk F_1	3.1	0.006	2.6	3.0	0.005	2.3
NapHal/Selkirk F_2	3.0	0.009	3.2	3.0	0.013	3.8
LSD at .05	0.10			0.08		

and equal to the mid-parent value for adjusted lysine.

The F_2 lysine values at Ft. Collins were not significantly different from their respective male parents except in the Pitic 62 group. The F_2 means, except in the Pitic 62 group, were generally lower than the F_1 means.

At Bozeman, the highest mean adjusted lysine value, 3.3% was also for NapHal. This value was significantly higher than the means of all the male parents, F_1's, and F_2's. Among the male parents, Justin produced the lowest mean adjusted lysine of 2.9%.

The means of the F_2 populations were not significantly different from the means of their respective F_1 populations. Only the mean of the NapHal/Justin F_2 population was significantly larger than the mean of its male parent.

Variances

The most variable parental population in adjusted lysine at both locations was Pitic 62 (Table 4). At Ft. Collins, NapHal had a significantly larger lysine variance than the male parents at Bozeman.

F_1 variances were comparable to or smaller than parental variances at Ft. Collins. Only the F_2's of the Justin and Pitic 62 groups had variances significantly greater than their F_1 variances for adjusted lysine.

The F_2 variances for adjusted lysine at Bozeman were larger than the variances of the male parents. The F_2 variances of the Justin and C.B. No. 113 groups were smaller

than the F_1 variances for these groups. At Bozeman only the F_2 variance of the Selkirk group was significantly larger than the F_1 variance.

Frequency Distributions

The adjusted lysine distributions for parents, F_1 and F_2 populations are shown for Ft. Collins in Table 5 and for Bozeman in Table 6. With exception of the Pitic 62 group F_2 at Ft. Collins and the Selkirk group F_2 at Bozeman which exhibited some evidence of genetic segregation, F_2 populations were not generally more variable than the parents and F_1's.

Plant Height

Means

Means, variances, and coefficients of variation for plant height are recorded in Table 7. At. Ft. Collins, the largest mean for plant height was for Justin at 101 cm. The shortest parent was C.B. No. 113 which had a mean of only 64 cm. At Bozeman, the largest mean for plant height was in the F_1 of the Justin group. C.B. No. 113 again was the shortest population, having a mean value of only 62 cm. C.B. No. 113 was significantly shorter, while Justin and Selkirk were significantly taller than NapHal.

All F_1's at both locations were approximately as tall or significantly taller than their tall parent. F_2 means for plant height were consistently less than the means of the F_1's, and generally intermediate to the parental means.

Table 5. Frequency distribution of adjusted lysine expressed as percent of population for parental, F_1 and F_2 populations of four spring wheat crosses grown at Ft. Collins, Colorado in 1971.

Population	No. of Plants	Class Midpoints (%)										
		2.6	2.7	2.8	2.9	3.0	3.1	3.2	3.3	3.4	3.5	$\bar{x}$
NapHal	260				3	9	22	38	23	3	2	3.2
C.B. No. 113	79				11	68	19	1				3.0
NapHal/C.B. No. 113 F_1	13				8	8	38	38	8			3.1
NapHal/C.B. No. 113 F_2	79		3		17	27	41	13				3.0
Justin	78			8	23	47	21		1			3.0
NapHal/Justin F_1	57					14	65	16	4	2		3.1
NapHal/Justin F_2	75		1	3	9	39	33	12	1	1		3.0
Pitic 62	72			8	10	24	42	12	3	1		3.0
NapHal/Pitic 62 F_1	22				5	14	55	27				3.1
NapHal/Pitic 62 F_2	73	1	3		5	21	48	12	4	4	1	3.1
Selkirk	75			3	9	48	33	7				3.0
NapHal/Selkirk F_1	74		1		5	38	45	7	4			3.1
NapHal/Selkirk F_2	76		1	5	12	38	36	8				3.0

Table 6. Frequency distribution of adjusted lysine expressed as percent of population for parental, F_1 and F_2 populations of four spring wheat crosses grown at Bozeman, Montana in 1971.

Population	No. of Plants	Class Midpoints (%)										$\bar{x}$
		2.6	2.7	2.8	2.9	3.0	3.1	3.2	3.3	3.4	3.5	
NapHal	222				1	2	8	19	42	20	7	3.3
C.B. No. 113	51				24	55	16	6				3.0
NapHal/C.B. No. 113 F_1	11					36	27	27		9		3.1
NapHal/C.B. No. 113 F_2	79			3	8	37	32	15	5	1		3.1
Justin	75		1	13	44	36	5					2.9
NapHal/Justin F_1	63				3	15	35	42	2		2	3.2
NapHal/Justin F_2	73			1	1	29	27	29	10	3		3.1
Pitic 62	87				10	38	39	10	1	1		3.0
NapHal/Pitic 62 F_1	29				7	24	41	21	3	3		3.1
NapHal/Pitic 62 F_2	75			1	4	25	37	24	8			3.1
Selkirk	66			2	24	44	24	5	2			3.0
NapHal/Selkirk F_1	79			1	11	44	37	6				3.0
NapHal/Selkirk F_2	69	1	3	12	33	28	16	3	3	1		3.0

Table 7. Means, variances, and coefficients of variation for plant height in parental, F_1 and F_2 populations of four spring wheat crosses grown at Ft. Collins, Colorado and Bozeman, Montana in 1971.

Population	Ft. Collins			Bozeman		
	$\bar{x}$	s^2	c.v.	$\bar{x}$	s^2	c.v.
	cm			cm		
NapHal	77	18.6	5.6	81	41.8	7.9
C.B. No. 113	64	5.7	3.7	62	10.1	5.1
NapHal/C.B. No. 113 F_1	82	3.0	2.1	80	63.7	10.0
NapHal/C.B. No. 113 F_2	73	66.3	11.2	74	102.9	13.7
Justin	101	45.8	6.7	99	34.6	6.0
NapHal/Justin F_1	99	20.8	4.6	100	53.4	7.3
NapHal/Justin F_2	95	91.6	10.1	96	59.9	8.0
Pitic 62	78	13.0	4.6	78	22.5	6.1
NapHal/Pitic 62 F_1	85	25.4	6.0	88	16.2	4.6
NapHal/Pitic 62 F_2	80	86.4	11.6	85	111.8	12.5
Selkirk	95	40.3	6.7	95	139.1	12.4
NapHal/Selkirk F_1	96	20.3	4.7	95	104.1	10.8
NapHal/Selkirk F_2	91	69.8	9.2	90	143.6	13.3
LSD at .05	3			4		

Variances

The largest parental variance for plant height at Ft. Collins was in Justin (Table 7). The least variability for height occurred in the C.B. No. 113 parent and F_1. F_1 variances for height generally were less than parental variances. The F_2 variances for plant height were significantly greater than their parental and F_1 variances.

All height variances were much larger at Bozeman than at Ft. Collins. At Bozeman, Selkirk had the highest parental variation for height. The variances of Selkirk and NapHal at Ft. Collins were 40.27 and 18.64 respectively, while at Bozeman the variances were 139.10 and 41.80 respectively. F_2 variances were larger than the parental and F_1 variances.

Frequency Distributions

Distribution data for plant height at Ft. Collins and Bozeman are recorded in Tables 8 and 9 respectively. The distribution of NapHal was approximately normally distributed at both locations. The NapHal/Justin F_2 distribution contained few plants within the NapHal height range indicating strong dominance for height from Justin. Pitic 62 and NapHal were nearly equal in height with similar distributions.

Other Traits

Means

Means, variances, and coefficients of variation for yield and twenty-seed weight are recorded in Table 10; number of heads per plant and plant weight in Table 11. NapHal had the

Table 8. Frequency distribution of plant height expressed as percent of population for parental, F_1 and F_2 populations of four spring wheat crosses grown at Ft. Collins, Colorado in 1971.

Population	No. of Plants	Class Midpoints (%)												$\bar{x}$
		57	63	67	73	77	83	87	93	97	103	107	113	
NapHal	260			4	23	42	27	4						77
C.B. No. 113	79	3	47	51										64
NapHal/C.B. No. 113 F_1	13					8	85	8						82
NapHal/C.B. No. 113 F_2	79	5	9	24	22	19	14	4	4					73
Justin	78								6	15	56	21	1	101
NapHal/Justin F_1	57					2			9	39	44	5	2	99
NapHal/Justin F_2	75			3	1		5	20	19	17	16	13	5	95
Pitic 62	72				19	49	28	4						78
NapHal/Pitic 62 F_1	22			5		5	36	41	14					85
NapHal/Pitic 62 F_2	73		3	12	12	22	19	18	10	1	3			80
Selkirk	75					3	3	11	29	32	16	3	4	95
NapHal/Selkirk F_1	74						1	9	24	39	24	1		96
NapHal/Selkirk F_2	76			1	1	5	14	25	24	14	9	4	1	91

Table 9. Frequency distribution of plant height expressed as percent of population for parental, F_1 and F_2 populations of four spring wheat crosses grown at Bozeman, Montana in 1971.

Population	No. of Plants	Class Midpoints (%) 53	57	63	67	73	77	83	87	93	97	103	107	113	117	$\bar{x}$
NapHal	222			3	3	5	21	40	19	7	1					81
C.B. No. 113	51		25	55	20											62
NapHal/C.B. No. 113 F_1	11				9	18	9	27	36							80
NapHal/C.B. No. 113 F_2	79	3	4	11	16	16	18	18	9	4		1				74
Justin	75						1	4		8	36	45	4	1		99
NapHal/Justin F_1	63					2		6	3	5	11	51	19	3		100
NapHal/Justin F_2	73					1		7	12	14	32	19	10	4	1	96
Pitic 62	87			3	3	13	40	31	8			1				78
NapHal/Pitic 62 F_1	29					3		10	41	45						88
NapHal/Pitic 62 F_2	75			3	9	7	9	13	17	27	7	8				85
Selkirk	66			3	2	6	3	5	3	11	23	29	14	3		95
NapHal/Selkirk F_1	79		1	1	1	5	4	1	5	13	32	23	10	4		95
NapHal/Selkirk F_2	69		3	1	3	3	10	7	19	20	10	6	14	3		90

Table 10. Means, variances, and coefficients of variation for grain yield and twenty-seed weight in parental, F_1 and F_2 populations of four spring wheat crosses grown at Ft. Collins, Colorado and Bozeman, Montana in 1971.

Population	Grain Yield						Twenty-seed Weight					
	Ft. Collins			Bozeman			Ft. Collins			Bozeman		
	$\bar{x}$	s^2	c.v.	$\bar{x}$	s^2	c.v.	$\bar{x}$	s^2	c.v.	$\bar{x}$	s^2	c.v.
	g			g			g			g		
NapHal	8.8	6.7	29	6.3	3.5	30	0.51	0.002	9.0	0.42	0.003	13.9
C.B. No. 113	7.7	5.5	31	5.3	1.6	24	0.66	0.003	7.8	0.59	0.001	5.8
NapHal/C.B. No. 113 F_1	13.6	11.4	25	7.8	3.5	24	0.69	0.006	11.2	0.60	0.002	8.3
NapHal/C.B. No. 113 F_2	9.0	13.6	41	6.5	4.2	32	0.62	0.005	10.9	0.56	0.006	13.7
Justin	10.1	10.8	32	6.7	3.3	27	0.74	0.006	10.1	0.65	0.002	7.1
NapHal/Justin F_1	13.9	15.1	28	8.6	6.9	31	0.78	0.005	8.7	0.63	0.004	9.6
NapHal/Justin F_2	11.7	20.5	39	7.4	5.7	32	0.67	0.004	9.8	0.58	0.006	12.9
Pitic 62	14.7	37.8	42	11.6	14.4	33	0.73	0.005	9.8	0.72	0.005	10.1
NapHal/Pitic 62 F_1	16.5	18.2	26	11.2	11.0	30	0.66	0.003	7.7	0.65	0.006	12.0
NapHal/Pitic 62 F_2	11.3	28.4	47	9.4	15.1	41	0.61	0.011	17.1	0.56	0.007	15.0
Selkirk	10.0	9.8	31	6.7	4.5	32	0.78	0.002	6.0	0.67	0.003	8.2
NapHal/Selkirk F_1	13.1	18.0	32	8.1	4.9	27	0.74	0.002	6.6	0.63	0.004	10.6
NapHal/Selkirk F_2	10.8	16.7	38	7.3	6.6	35	0.66	0.007	12.4	0.57	0.004	11.7

Table 11. Means, variances, and coefficients of variation for number of heads and plant weight in parental, F_1 and F_2 populations of four spring wheat crosses grown at Ft. Collins, Colorado and Bozeman, Montana in 1971.

Population	Number of Heads						Plant Weight		
	Ft. Collins			Bozeman			Ft. Collins		
	$\bar{x}$	s^2	c.v.	$\bar{x}$	s^2	c.v.	$\bar{x}$	s^2	c.v.
							g		
NapHal	9	4.25	23	7	2.72	25	19.5	31.7	29.0
C.B. No. 113	9	4.18	24	6	1.31	21	15.0	21.0	30.5
NapHal/C.B. No. 113 F_1	11	7.20	24	6	1.52	20	27.3	44.0	24.3
NapHal/C.B. No. 113 F_2	9	6.37	28	6	2.52	25	19.3	58.9	39.8
Justin	9	5.64	27	6	3.00	28	25.9	67.2	31.6
NapHal/Justin F_1	11	6.95	25	6	3.04	28	31.4	72.9	27.2
NapHal/Justin F_2	10	9.51	31	7	3.73	29	27.0	96.3	36.3
Pitic 62	9	9.58	33	7	3.90	30	30.0	140.5	39.5
NapHal/Pitic 62 F_1	11	5.18	20	8	3.22	23	33.8	75.0	25.6
NapHal/Pitic 62 F_2	9	9.56	34	7	4.07	29	25.3	115.5	42.4
Selkirk	9	6.10	28	6	3.45	33	24.7	60.0	31.3
NapHal/Selkirk F_1	11	8.36	27	7	2.85	26	28.7	84.4	32.0
NapHal/Selkirk F_2	10	6.83	26	7	3.48	27	25.6	89.4	37.0
LSD at .05	2			1			5.1		

lowest seed weight at both locations. At Ft. Collins, Selkirk had the highest seed weight, while Pitic 62 had the heaviest grain at Bozeman. At both locations, seed weight means of F_2 populations were lower than those of their male parents and F_1's, but higher than the mean of NapHal.

The highest yielding population at Ft. Collins was the F_1 of the Pitic 62 group. Pitic 62 also was the highest yielding parent. C.B. No. 113 had the lowest mean for grain yield. All F_1 populations exceeded their parents in grain yield. F_2 means generally were larger than the means of the parents.

Pitic 62 was the population with the highest yield at Bozeman. C.B. No. 113 again had the lowest mean yield. With the exception of the Pitic 62 group, F_1's exceeded their parental values. F_2 means with exception of the Pitic 62 group were smaller than the F_1 means, but larger than the parental means.

Means for number of heads per plant at Ft. Collins (Table 11) were largest for F_1 populations. F_2 means also were generally larger than parental mean values. Parental values were approximately equal to each other.

Bozeman means for number of heads were considerably lower than those from Ft. Collins. F_1 and F_2 populations had somewhat larger means than did the male parents. F_2 mean values were larger than the F_1 values in all but the Pitic 62 group.

Plant weight means from Ft. Collins data indicated the heaviest plants to be in the NapHal/Pitic 62 F_1 population. All F_1 populations were higher in plant weight than parental and F_2 populations. F_2 means exceeded parental values except in the C.B. No. 113 group where the F_2 mean was slightly less than the mean of NapHal.

Variances

Variances for number of heads per plant and grain yield were generally larger at Ft. Collins than at Bozeman (Tables 10 and 11). At Ft. Collins the largest variance in number of heads was 9.58 in Pitic 62. The largest variance at Bozeman was 4.07 in the F_2 population of the Pitic 62 group.

The largest variance for grain yield at Ft. Collins was 37.8 in the Pitic 62 population. Pitic 62 also had the most variation in plant weight at Ft. Collins. The largest grain yield variance at Bozeman was recorded for the F_2 population of the Selkirk group.

Correlations

Correlation coefficients between grain protein and other measured data are recorded in Table 12. Correlation coefficients involving protein were generally low, except in relation to lysine. Coefficient values under 0.30 were observed for most comparisons, while coefficient values in excess of 0.50 frequently occurred between protein and lysine.

Grain protein was negatively correlated with adjusted lysine in most of the populations at both locations. The

Table 12. Correlation coefficients among seven traits in parental, F_1 and F_2 populations of four spring wheat crosses grown in Ft. Collins, Colorado and Bozeman, Montana in 1971.

Population	Unadjusted Lysine	Adjusted Lysine	Plant Height	Grain Yield	20-seed Weight	Number of Heads	Plant Weight
			Ft. Collins				
Grain Protein							
NapHal	-0.41**	-0.40**	0.07	-0.00	0.01	0.01	0.06
C.B. No. 113	-0.40**	-0.27*	-0.13	-0.01	0.18	0.07	0.04
NapHal/C.B. No. 113 F_1	-0.70**	-0.69**	-0.16	-0.25	-0.11	0.02	-0.15
NapHal/C.B. No. 113 F_2	-0.64**	-0.63**	0.22*	-0.16	-0.06	0.03	0.03
Justin	-0.44**	-0.51**	-0.05	-0.14	-0.49**	0.06	-0.05
NapHal/Justin F_1	0.15	0.12	0.02	-0.34**	-0.29*	-0.23	-0.25
NapHal/Justin F_2	-0.54**	-0.58**	0.19	-0.30**	-0.21	-0.28*	-0.27*
Pitic 62	-0.44**	-0.01	0.11	-0.15	-0.44**	0.04	-0.01
NapHal/Pitic 62 F_1	0.27	0.51*	-0.12	0.05	-0.24	0.26	0.10
NapHal/Pitic 62 F_2	-0.28	-0.25*	-0.01	-0.36**	-0.26*	-0.17	-0.27*
Selkirk	-0.56**	-0.54**	0.22	-0.02	0.21	-0.04	0.10
NapHal/Selkirk F_1	-0.50**	-0.49**	-0.32**	0.02	0.07	0.03	0.06
NapHal/Selkirk F_2	-0.53**	-0.46**	-0.16	-0.14	-0.22	-0.00	-0.01

Table 12. (cont.)

Population	Unadjusted Lysine	Adjusted Lysine	Plant Height	Grain Yield	20-seed Weight	Number of Heads
			Bozeman			
Grain Protein						
NapHal	-0.18**	-0.24**	-0.14*	-0.33**	-0.34**	-0.06
C.B. No. 113	-0.32*	-0.29*	-0.30*	-0.58**	0.01	-0.45**
NapHal/C.B. No. 113 F_1	-0.29	-0.34	-0.56	-0.69(	-0.09	-0.19
NapHal/C.B. No. 113 F_2	-0.20	-0.30**	0.26*	-0.23*	-0.06	-0.04
Justin	-0.58**	-0.64**	-0.19	-0.27*	-0.33**	-0.30**
NapHal/Justin F_1	-0.47**	-0.50**	-0.46*	-0.42**	-0.16	-0.31*
NapHal/Justin F_2	-0.10	-0.20	-0.07	-0.18	-0.21	0.11
Pitic 62	-0.45**	-0.34**	0.04	-0.21*	-0.08	-0.09
NapHal/Pitic 62 F_1	-0.09	-0.14	-0.09	-0.33	-0.48**	0.01
NapHal/Pitic 62 F_2	0.10	0.06	-0.03	-0.35**	-0.27*	-0.11
Selkirk	-0.44**	-0.44**	0.46**	-0.00	-0.10	-0.25*
NapHal/Selkirk F_1	-0.44**	-0.51**	-0.18	-0.13	-0.27	0.04
NapHal/Selkirk F_2	-0.31**	-0.38**	-0.10	-0.28*	0.08	-0.23

* Indicates significance at the 5% level.
** Indicates significance at the 1% level.

adjustment of lysine was designed to eliminate the negative influence of protein on lysine percent of protein. However, as was shown by Johnson et al (15) the curvilinear relationship between protein and lysine percent of protein becomes negligible at about the 15% protein level. Grain samples with protein values greater than 15% consequently receive less adjustment than samples with lower protein. Correlation values between protein and unadjusted lysine percent of protein were comparable to those using the adjusted values.

Few significant coefficients were observed between protein and the other traits except at Bozeman where there was significant negative correlation with grain yield in 9 populations. At Ft. Collins (Table 12), protein correlations with plant height were positive for the NapHal/C.B. No. 113 F_2 population, and negative for the NapHal/Selkirk F_1 population. Two statistically significant negative coefficients were found in comparing protein with plant weight at Ft. Collins.

At Bozeman, protein correlations with plant height were negative for NapHal, C.B. No. 113, and the NapHal/Justin F_1 populations. Positive correlations were computed for Selkirk and the F_2 population of the C.B. No. 113 group. The majority of coefficients resulting from comparisons of protein with number of heads, and twenty-seed weight were small and negative at both locations.

Although not shown in Table 12, plant height was positively correlated with yield, number of heads, and twenty-seed

weight at both locations. These correlation values were all very large and statistically significant. Positive values also were observed among the yield components.

Heritability Estimates

Heritability estimates from Ft. Collins and Bozeman are listed in Tables 13 and 14 respectively. Three methods of computation were utilized. Method a utilized the F_1 as an estimate of the environmental variance. Method b had as estimates of the environmental variance, geometric means of the parental variances after Mahmud and Kramer (21). Method c utilized the correlation between F_3 and F_2 values according to Frey and Horner (5). The latter method was used only for values of protein and adjusted lysine from Ft. Collins.

Results using method b were omitted from the table if the parental variances were not shown to be homogeneous through use of Bartlett's test. Parental variances which did not show homogeneity could not be used as representatives of the same environmental variance.

The results were variable and inconsistent. Both positive and negative estimates of heritability were observed. On the average, the estimates computed from Ft. Collins data were larger than those from Bozeman.

Estimates of heritability for adjusted lysine averaged about 27%. Results from method c alone averaged about 11%. Protein heritability estimates were generally higher than those for adjusted lysine. The estimates for protein were

Table 13. Broad sense heritability estimates for seven traits in four spring wheat crosses. Parental, F_1 and F_2 populations were grown at Ft. Collins, Colorado in 1971; F_3 populations at Mead, Nebraska in 1972.

Cross	Method of Computation	Protein	Adjusted Lysine	Plant Height	Yield	20-seed Weight	Number of Heads	Plant Weight
NapHal/C.B. No. 113	a	88%	59%	95%	17%	-30%	-13%	25%
	b	75			55	51	34	56
	c	51	7					
NapHal/Justin	a	74	38	77	26	- 7	27	24
	b	48	24				49	
	c	64	14					
NapHal/Pitic 62	a	69	71	71	36	76	46	35
	b		25	82				
	c	24	-12					
NapHal/Selkirk	a	60	29	71	- 7	65	-22	6
	b	55			52	67	26	
	c	45	13					

Method of computation:

(a) $$h^2 = \frac{VF_2 - VF_1}{VF_2} \times 100$$

(b) $$h^2 = \frac{VF_2 - (VP_1 \times VP_2)^{1/2}}{VF_2} \times 100$$

(c) $$h^2 = \frac{\Sigma (F_3 - \bar{F}_3)(F_2 - \bar{F}_2)}{[\Sigma (F_3 - \bar{F}_3)^2 \times \Sigma (F_2 - \bar{F}_2)^2]^{1/2}}$$

Table 14. Broad sense heritability estimates for six traits in four spring wheat crosses grown at Bozeman, Montana in 1971.

Cross	Method of Computation	Protein	Adjusted Lysine	Plant Height	Yield	20-seed Weight	Number of Heads
NapHal/C.B. No. 113	a	74%	- 67%	38%	16%	57%	40%
	b						
NapHal/Justin	a	72	-231	11	-21	34	19
	b			37	41	53	24
NapHal/Pitic 62	a	15	32	86	27	13	21
	b	32	18		53	40	20
NapHal/Selkirk	a	65	61	28	26	0	18
	b	59	38	47	40	30	12

Method of computation:

(a) $h^2 = \frac{VF_2 - VF_1}{VF_2} \times 100$

(b) $h^2 + \frac{VF_2 - (VP_1 \times VP_2)^{1/2}}{VF_2} \times 100$

about 70% in the C.B. No. 113 group, 60% in the Justin group, 32% in the Pitic 62 group, and 56% in the Selkirk group.

Plant height heritabilities were generally larger at Ft. Collins than at Bozeman. Only the Pitic 62 group had high estimates at both sites. Heritability values were about 67% in the C.B. No. 113 group, 40% in the Justin group, 80% in the Pitic 62 group, and 48% in the Selkirk group. An average heritability estimate for plant weight was about 25%. Overall, heritability estimates were for number of heads per plant about 27%, for yield about 35%, and for twenty-seed weight about 49%.

DISCUSSION

The study was designed to investigate the inheritance of protein and lysine in the spring wheat variety, NapHal, which produces a higher level of kernel protein with higher lysine content than other wheat varieties. Also, the influence of plant height on protein was examined. To insure height differences, two semi-dwarf and two tall varieties were used as male parents.

Protein

NapHal produces small and often times shriveled seed. Studies previously cited as well as results of this study show seed plumpness and protein content to be related. Adjusted lysine to a lesser degree was also related to seed weight, probably because of its association with protein.

At Ft. Collins, the F_1 protein means did not differ significantly from the mid-parent means. The F_1 means of the Justin and Selkirk groups were somewhat smaller than the mid-parent means, while those of the C.B. No. 113 and Pitic 62 groups were somewhat larger. Additive gene action therefore is indicated, but slight dominance from NapHal may exist. Dominance was also reported by Johnson et al (14).

Environmental effects at Bozeman caused the populations to have lower yields and higher protein values than they did at Ft. Collins. This is in agreement with previous studies involving yield-protein relationships. At Bozeman, all F_1 protein means except the Justin group were larger than

the mid-parent mean. Since none were significantly larger than the mid-parent value, additive effects were again indicated with possible slight dominance from NapHal.

Justin had the highest mean protein and the lowest mean adjusted lysine levels at both locations. The F_1 progeny showed a marked reduction in protein and an increase in adjusted lysine over that of Justin. The NapHal/Justin F_1 means for protein were lower at both sites than the NapHal means. Since NapHal was, in this case, the lower protein parent, dominance from NapHal was again shown. Chapman and McNeal (2) reported similar but opposite results in a cross between NapHal and Frontiera. Dominance in that cross was for low protein from Frontiera.

The NapHal/C.B. No. 113 F_1 protein means were not significantly different from the mid-parent means, indicating additive effects, and possible slight dominance from NapHal. This was observed at both locations. The F_2 means however, were larger than the mean of NapHal. At Ft. Collins the mid-parent value was 17.6%, the F_1 was 18.0%, the F_2 was 18.5%, and the F_3 grown at Mead, Nebraska had 19.5% protein. This may reflect inter-allelic interaction and possible additive fixation or accumulation. Since the F_3 mean was based on a population grown in a different environment it cannot be validly compared with the F_2 and F_1 data.

At Ft. Collins all F_2 variances were significantly larger than the pooled parental variances, indicating segregation for protein had occurred. Bozeman results were

similar, except that the NapHal/Pitic 62 F_2 variance was not significantly different from the pooled parental variance. The distribution of the C.B. No. 113 F_2 populations revealed many high protein progeny at both locations. High protein selections, therefore, should readily be obtained from these populations.

Adjusted Lysine

On the whole, F_1 means for adjusted lysine were lower than their mid-parent means. Since these differences were not significant, either or both additive and dominant gene action could have been functioning for lysine.

At Bozeman, the NapHal/C.B. No. 113 F_2 population and the F_1 and F_2 populations of the Selkirk group showed dominance for low lysine, as the means were significantly lower than the mid-parent values. The NapHal/Justin F_1 population displayed additive and possibly dominance gene action for high lysine since the F_1 means were higher than the mid-parent value. F_2 values for lysine were essentially equal to those of the male parents at both sites.

If NapHal possesses genes for lysine which are different from those of the other varieties, one might expect increased F_2 variances from segregants combining the lysine genes of both parents which also could be observed in the lysine distribution range.

F_1 variances for adjusted lysine were less than the pooled parental variances at Ft. Collins, with the differences

in the Justin and Pitic 62 groups being significant. The NapHal/Pitic 62 F_2 population was the only one which significantly exceeded the pooled parental variance at Ft. Collins. The frequency distribution showed values in that population to range from the highest to the lowest parental values. There were no F_2 values higher than the highest NapHal values indicating that no transgressive segregation occurred. Since the Pitic 62 group progeny also yielded well, useful selections should be possible from these populations. At Bozeman, none of the F_2 population variances differed significantly from the pooled parental variance. Any segregation for lysine was masked by the very large variances of the parents.

Whether a few or many genes are involved in the inheritance of protein and lysine cannot be determined from this study. Measurements on quantitative traits are all subject to experimental error, and continued evaluation in advanced generations would be necessary for greater reliability.

Cytogenetic analyses would be valuable in locating the protein and lysine genes, studying their dosage effects, and perhaps establishing substitution lines involving whole chromosomes if favorable linkage groups exist.

Whether the genes for high protein-lysine influence seed size or vice versa, seed size almost invariably decreased with generations. The F_2 populations had smaller seeds than the F_1's, which were in turn generally smaller than the male parent seeds.

Yield, on the contrary, exhibited a great deal of heterosis. With one exception, F_1 populations consistently had larger yields than parents and F_2's. F_2's also had higher yields than parents, except in the Pitic 62 group. The yields were influenced by the number of heads per plant. Head fertility also may have been a factor, but it was not measured.

Heterosis was generally shown for plant height and plant weight, since F_1 means exceeded the larger parental means. Generally, plant height was inherited additively with dominance from the tall parent. Plant height was not shown to be consistently correlated with grain protein content. Short plant height should, therefore, not prevent high grain protein content from occurring. This is important if desirable shorter strawed wheats with high protein contents are to be developed.

Adjusted lysine was negatively correlated with protein in this study. The adjustment was based on the method used to compare wheats in the World Collection, which utilized a common 13% level of protein. Adjustments are necessary to permit comparisons of lysine as percents of protein among populations which differ in protein content. This is necessary because of the relationship between the two traits.

The protein-lysine relationships in these populations grown in the Ft. Collins and Bozeman environments may be different from that exhibited by the World Collection. If such is the case, a more specialized adjustment might be

needed to more thoroughly remove the protein-lysine influence.

Environmental influences at a location are assumed to be equal in all populations whether segregating or non-segregating. This was supported by the lack of significance in the ANOV for replications (Appendix tables). Genetic variance is that part of the variability between plants which can be attributed to genotypic differences. This is generally estimated by subtracting the variance of a homogeneous population from the variance of a non-homogeneous segregating population.

Broad sense heritability estimates give the genetic variance as a percentage of the total variance, and thus may be used as indicators of trait inheritance. Parental populations were non-homogeneous in many instances. This may reflect environmental interactions, or possible variability within the parental populations.

Heritability values should be positive, and less than 100%. Negative estimates were obtained, however, in several instances. These can be interpreted as values of zero. Adjusted lysine estimates therefore ranged from 0 to 71% (Tables 13 and 14). Plant height and protein demonstrated the most uniform heritability estimates over locations and methods of computation. The highest heritability for protein was 88% in the C.B. No. 113 group. High protein heritability values have also been observed by others (5, 11, 26).

Probably the best high lysine selections could be made from the Pitic 62 group, while the C.B. No. 113 and Justin

groups represent sources for selection of high protein lines. These, of course, are within the confines of this study and do not preclude the chances of other varieties and crosses from being better.

SUMMARY

The Indian spring wheat variety NapHal, P.I. 176217, was crossed with two Mexican semi-dwarfs, C.B. No. 113 and Pitic 62, and to two taller wheats Selkirk and Justin. NapHal was the common female parent in crosses with the other varieties. Both short and tall male varieties were utilized to determine whether plant height has an influence on protein inheritance.

Parents, F_1 and F_2 populations were grown at Ft. Collins, Colorado and Bozeman, Montana in 1971. F_3 populations derived from the Ft. Collins trial were grown at Mead, Nebraska in 1972.

Data were taken on the agronomic traits plant weight, plant height, number of heads per plant, yield, and twenty-seed weight and the quality traits grain protein and adjusted lysine. Adjusted lysine represents the lysine component of protein as a percent of the total grain protein adjusted to a common protein level.

NapHal produced the highest adjusted lysine values of 3.2% and 3.3% at Ft. Collins and Bozeman respectively. Protein values for NapHal were 18.3% and 19.2% respectively.

Protein values were consistently higher at Bozeman than at Ft. Collins. Yields were higher at Ft. Collins, however. The variety which had the highest protein values at both locations also had the lowest adjusted lysine values.

Negative correlations were detected between protein and several agronomic traits. Plant height was not significantly correlated with grain protein except in two populations, one value of which was positive and the other negative. Protein was negatively correlated with lysine adjusted to a 13% protein level.

Plant height appeared to be inherited as a combination of additive with dominance effects from the tall parent. Inheritance of lysine was largely additive, with some dominance from the low lysine parents. Protein inheritance was by additive and dominance gene action. Dominance for protein was apparent in NapHal.

In the C.B. No. 113 group, additive and epistatic action may have been expressed. This was evidenced from the increased protein means of each succeeding generation.

Heritability estimates were highly variable, with the most uniform values obtained for grain protein and plant height. The highest estimate for adjusted lysine was 71%, for protein 88%, and plant height 95%.

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Appendix Table 1. Analysis of variance mean squares and F ratios for grain protein and adjusted lysine for all populations grown at Ft. Collins in 1971.

Source	d.f.	Grain Protein		Adjusted Lysine	
		M.S.	F	M.S.	F
Total	45				
Families	3	5.2473	12.1889**	0.0046	1.3143
Reps	2	0.8258	1.9182	0.0060	1.7143
Error (a)	6	0.4305		0.0015	
Within Family 1	3	1.1695	9.5469**	0.0139	3.9714*
NapHal vs CB No. 113	1	1.3824	11.2849**	0.0294	8.4000**
$P_1 + P_2$ vs F_1	1	0.6498	5.3045*	0.0032	0.9143
$P_1 + P_2$ vs F_2	1	2.0000	16.3265**	0.0050	1.4286
$P_1 + P_2 + F_1$ vs F_2	1	1.4762	12.0506**	0.0090	2.5714
Within Family 2	3	0.4039	3.2971*	0.0098	2.8000
NapHal vs Justin	1	0.1536	1.2539	0.0204	5.8286*
$P_1 + P_3$ vs F_1	1	1.0561	8.6212**	0.0084	2.4000
$P_1 + P_3$ vs F_2	1	0.0910	0.7429	0.0000	0.0000
$P_1 + P_3 + F_1$ vs F_2	1	0.0019	0.0155	0.0006	0.1714
Within Family 3	3	7.3143	59.7086**	0.0116	3.3143*
NapHal vs Pitic 62	1	18.4802	150.8588**	0.0308	8.8000**
$P_1 + P_4$ vs F_1	1	0.0280	0.2286	0.0024	0.6857
$P_1 + P_4$ vs F_2	1	3.2513	26.5412**	0.0029	0.8286
$P_1 + P_4 + F_1$ vs F_2	1	3.4348	28.0392**	0.0016	0.4571
Within Family 4	3	0.0668	0.5433	0.0263	7.5143**
NapHal vs Selkirk	1	0.1700	1.3878	0.0580	16.5714**
$P_1 + P_5$ vs F_1	1	0.0009	0.0073	0.0068	1.9429
$P_1 + P_5$ vs F_2	1	0.0296	0.2416	0.0193	5.5143*
$P_1 + P_5 + F_1$ vs F_2	1	0.0295	0.2408	0.0140	4.0000
Error (b)	22	0.1225		0.0040	
Pooled error	28			0.0035	

* Indicates significance at the 5% level.
** Indicates significance at the 1% level.

Appendix Table 2. Analysis of variance mean squares and F-ratios for grain protein and adjusted lysine for all populations grown at Bozeman, Montana in 1971.

Source	d.f.	Grain Protein		Adjusted Lysine	
		M.S.	F	M.S.	F
Total	47				
Families	3	3.0905	32.8427**	0.0144	2.9388
Reps	2	0.0316	0.3358	0.0075	1.5306
Error (a)	6	0.0941		0.0049	
Within Family 1	3	1.7287	30.4885**	0.0456	19.0000**
NapHal vs CB No. 113	1	3.4961	61.6596**	0.1262	52.5833**
$P_1 + P_2$ vs F_1	1	0.0174	0.3069	0.0029	1.2083
$P_1 + P_2$ vs F_2	1	1.5961	28.1499**	0.0103	4.2917*
$P_1 + P_2 + F_1$ vs F_2	1	1.6727	29.5009**	0.0078	3.2500
Within Family 2	3	0.6777	11.9524**	0.0730	30.4167**
NapHal vs Justin	1	1.3538	23.8765**	0.2166	90.2500**
$P_1 + P_3$ vs F_1	1	0.6612	11.6614**	0.0022	0.9167
$P_1 + P_3$ vs F_2	1	0.0207	0.3651	0.0000	0.0000
$P_1 + P_3 + F_1$ vs F_2	1	0.0182	0.3210	0.0001	0.0417
Within Family 3	3	3.7801	66.6684**	0.0391	16.2917**
NapHal vs Pitic 62	1	10.4808	184.8466**	0.0963	40.1250**
$P_1 + P_4$ vs F_1	1	0.2664	4.6984*	0.0128	5.3333*
$P_1 + P_4$ vs F_2	1	0.8064	14.2222**	0.0150	6.2500*
$P_1 + P_4 + F_1$ vs F_2	1	0.5929	10.4568**	0.0081	3.3750
Within Family 4	3	0.6912	12.1905**	0.0445	18.5417**
NapHal vs Selkirk	1	1.2513	22.0688**	0.0794	33.0833**
$P_1 + P_5$ vs F_1	1	0.0392	0.6914	0.0181	7.5417*
$P_1 + P_5$ vs F_2	1	0.8107	14.2981	0.0501	20.8750**
$P_1 + P_5 + F_1$ vs F_2	1	0.7832	13.8131**	0.0361	15.0417**
Error (b)	24	0.0567		0.0024	
Pooled error	30				

* Indicates significance at the 5% level.
** Indicates significance at the 1% level.

Appendix Table 3. Analysis of variance mean squares and F-ratios for plant weight, plant height, and number of heads per plant for all parental, F_1 and F_2 populations grown at Ft. Collins, Colorado in 1971.

Source	d.f.	Plant Weight		Plant Height		Number of Heads	
		M.S.	F	M.S.	F	M.S.	F
Total	45						
Families	3	110.2258	11.9103**	955.3759	206.9302**	0.1140	0.1075
Reps	2	2.8934	0.3126	23.4746	5.0845	0.9534	0.8987
Error (a)	6	6.3899		4.6169		0.4923	
Within Family 1	3	81.3515	8.7903**	170.5946	66.9576**	4.9409	4.6573**
NapHal vs CB No. 113	1	28.8643	3.1189	248.4554	97.5176**	0.3700	0.3488
$P_1 + P_2$ vs F_1	1	211.0828	22.8082**	255.7568	100.3834**	12.8524	12.1146**
$P_1 + P_2$ vs F_2	1	8.5974	0.9290	7.4884	2.9392	0.0000	0.0000
$P_1 + P_2 + F_1$ vs F_2	1	4.1074	0.4438	7.5717	2.9719	1.6002	1.5083
Within Family 2	3	74.8255	8.0851**	320.7920	125.9094**	2.4199	2.2810
NapHal vs Justin	1	67.6033	7.3048*	775.8888	304.5328**	0.0038	0.0036
$P_1 + P_3$ vs F_1	1	152.1931	16.4450**	176.9080	69.4356**	6.5643	6.1875*
$P_1 + P_3$ vs F_2	1	37.8450	4.0893	54.0453	21.2125**	2.6835	2.5295
$P_1 + P_3 + F_1$ vs F_2	1	4.6800	0.5057	9.5790	3.7597	0.6917	0.6520
Within Family 3	3	144.4549	15.6088**	34.4213	13.5102**	5.4265	5.1150**
NapHal vs Pitic 62	1	191.4220	20.6838**	1.1793	0.4629	0.7142	0.6732
$P_1 + P_4$ vs F_1	1	229.6224	24.8114**	102.0544	40.0559**	14.6340	13.7939**
$P_1 + P_4$ vs F_2	1	3.0340	0.3278	12.4667	4.8931*	0.1335	0.1258
$P_1 + P_4 + F_1$ vs F_2	1	12.3201	1.3312	0.0300	0.0118	0.9312	0.8777

Appendix Table 3. (cont.)

Source	d.f.	Plant Weight		Plant Height		Number of Heads	
		M.S.	F	M.S.	F	M.S.	F
Within Family 4	3	31.3105	3.3832*	217.8684	85.5124**	1.6783	1.5820
NapHal vs Selkirk	1	21.2440	2.2955	474.7262	186.3279**	0.5104	0.4811
$P_1 + P_5$ vs F_1	1	71.0829	7.6807**	175.2816	68.7972**	4.2729	4.0276
$P_1 + P_5$ vs F_2	1	16.0367	1.7328	38.4564	15.0940**	1.3503	1.2728
$P_1 + P_5 + F_1$ vs F_2	1	1.6044	0.1734	3.5973	1.4119	0.2517	0.2373
Error (b)	22	10.0360		2.5478		1.2160	
Pooled error	28	9.2547				1.0609	

* Indicates significance at the 5% level.
** Indicates significance at the 1% level.

Appendix Table 4. Analysis of variance mean squares and F-ratios for plant height and number of heads per plant for all populations grown at Bozeman, Montana in 1971.

Source	d.f.	Plant Height		Number of Heads	
		M.S.	F	M.S.	F
Total	47				
Families	3	957.6060	69.2582**	1.3289	1.9679
Reps	2	36.2282	2.6202	1.4756	2.1851
Error (a)	6	13.8266		0.6753	
Within Family 1	3	226.2762	32.1836**	0.7332	2.3350
NapHal vs CB No. 113	1	539.9811	76.8022**	2.0534	6.5395*
$P_1 + P_2$ vs F_1	1	138.3339	19.6754**	0.0007	0.0022
$P_1 + P_2$ vs F_2	1	21.1250	3.0046	0.1233	0.3927
$P_1 + P_2 + F_1$ vs F_2	1	0.5136	0.0731	0.1457	0.4640
Within Family 2	3	199.9575	28.4402**	0.2641	0.8411
NapHal vs Justin	1	396.4188	56.3832**	0.5104	1.6255
$P_1 + P_3$ vs F_1	1	186.4381	26.5173**	0.0983	0.3131
$P_1 + P_3$ vs F_2	1	71.2420	10.1328**	0.0896	0.2854
$P_1 + P_3 + F_1$ vs F_2	1	17.0156	2.4202	0.1835	0.5844
Within Family 3	3	54.0583	7.6888**	0.7794	2.4822
NapHal vs Pitic 62	1	8.8331	1.2563	0.0794	0.2529
$P_1 + P_4$ vs F_1	1	138.0014	19.6281**	2.2543	7.1793*
$P_1 + P_4$ vs F_2	1	57.8880	8.2336**	0.1901	0.6054
$P_1 + P_4 + F_1$ vs F_2	1	15.3403	2.1335	0.0047	0.0150
Within Family 4	3	122.3619	17.4748**	0.7451	2.3729
NapHal vs Selkirk	1	277.8482	39.5187**	0.6338	2.1140
$P_1 + P_5$ vs F_1	1	90.4513	12.8650**	0.5305	1.6895
$P_1 + P_5$ vs F_2	1	7.1064	1.0108	1.4849	4.7290*
$P_1 + P_5 + F_1$ vs F_2	1	0.2862	0.0407	1.0712	3.4115
Error (b)	24	7.0308		0.3140	
Pooled error	30				

* Indicates significance at the 5% level.
** Indicates significance at the 1% level.

Appendix Table 5. Analysis of variance mean squares and F-ratios for grain yield and twenty-seed weight for all populations grown at Ft. Collins in 1971.

Source	d.f.	Grain Yield		Twenty-seed Weight	
		M.S.	F	M.S.	F
Total	45				
Families	3	19.5665	7.5331**	0.0099	11.0000**
Reps	2	0.2950	0.1136	0.0074	8.2222**
Error (a)	6	2.0773		0.0005	
Within Family 1	3	20.9784	8.0767**	0.0175	19.4444**
NapHal vs CB No. 113	1	2.8982	1.1158	0.0323	35.8889**
$P_1 + P_2$ vs F_1	1	57.4235	22.1081**	0.0200	22.2222**
$P_1 + P_2$ vs F_2	1	1.0035	0.3865	0.0032	3.5556
$P_1 + P_2 + F_1$ vs F_2	1	2.6136	1.0062	0.0001	0.1111
Within Family 2	3	15.7713	6.0720**	0.0436	48.4444**
NapHal vs Justin	1	3.9366	1.5156	0.0817	90.7778**
$P_1 + P_3$ vs F_1	1	41.7089	16.0579**	0.0491	54.5556**
$P_1 + P_3$ vs F_2	1	11.3606	4.3738*	0.0050	5.5556*
$P_1 + P_3 + F_1$ vs F_2	1	1.6684	0.6423	0.0000	0.0000
Within Family 3	3	43.1226	16.6022**	0.0300	33.3333**
NapHal vs Pitic 62	1	58.9067	22.6791**	0.0864	96.0000**
$P_1 + P_4$ vs F_1	1	61.5310	23.6895**	0.0032	3.5556
$P_1 + P_4$ vs F_2	1	0.0411	0.0158	0.0000	0.0000
$P_1 + P_4 + F_1$ vs F_2	1	8.9301	3.4381	0.0004	0.4444
Within Family 4	3	7.3417	2.8266	0.0387	43.0000**
NapHal vs Selkirk	1	0.1536	0.0591	0.0988	109.7778**
$P_1 + P_5$ vs F_1	1	21.8681	8.4192**	0.0168	18.6667**
$P_1 + P_5$ vs F_2	1	2.2614	0.8706	0.0007	0.7778
$P_1 + P_5 + F_1$ vs F_2	1	0.0034	0.0013	0.0003	0.3333
Error (b)	22	2.7392		0.0010	
Pooled error	28	2.5974		0.0009	

* Indicates significance at the 5% level.
** Indicates significance at the 1% level.

Appendix Table 6. Analysis of variance mean squares and F-ratios for grain yield and twenty-seed weight for all populations grown at Bozeman, Montana in 1971.

Source	d.f.	Grain Yield		Twenty-seed Weight	
		M.S.	F	M.S.	F
Total	47				
Families	3	21.2234	36.8015**	0.0046	4.1818
Reps	2	1.4478	2.5105	0.0004	0.3636
Error (a)	6	0.4161		0.0011	
Within Family 1	3	3.3044	5.7298**	0.0210	30.0000**
NapHal vs CB No. 113	1	2.6401	4.5779*	0.0451	64.4286**
$P_1 + P_2$ vs F_1	1	7.2454	12.5636**	0.0174	24.8571**
$P_1 + P_2$ vs F_2	1	0.5478	0.9499	0.0044	6.2857*
$P_1 + P_2 + F_1$ vs F_2	1	0.0278	0.0482	0.0005	0.7143
Within Family 2	3	2.7898	4.8375**	0.0350	50.0000**
NapHal vs Justin	1	0.1014	0.1758	0.0840	120.0000**
$P_1 + P_3$ vs F_1	1	8.1878	14.1977**	0.0207	29.5714**
$P_1 + P_3$ vs F_2	1	1.4907	2.5849	0.0047	6.7143*
$P_1 + P_3 + F_1$ vs F_2	1	0.0803	0.1392	0.0005	0.7143
Within Family 3	3	20.1878	35.0057**	0.0511	73.0000**
NapHal vs Pitic 62	1	49.5363	85.8961**	0.1350	192.8571**
$P_1 + P_4$ vs F_1	1	10.9824	19.0435**	0.0162	23.1429**
$P_1 + P_4$ vs F_2	1	0.8192	1.4205	0.0000	0.0000
$P_1 + P_4 + F_1$ vs F_2	1	0.0448	0.0777	0.0020	2.8571
Within Family 4	3	2.6970	4.6766**	0.0309	44.1429**
NapHal vs Selkirk	1	0.7994	1.3862	0.0817	116.7143**
$P_1 + P_5$ vs F_1	1	6.8821	11.9336	0.0108	15.4286**
$P_1 + P_5$ vs F_2	1	0.3483	0.6040	0.0006	0.8571
$P_1 + P_5 + F_1$ vs F_2	1	0.4096	0.7102	0.0001	0.1429
Error (b)	24	0.6169		0.0007	
Pooled error	30	0.5767			

* Indicates significance at the 5% level.
** Indicates significance at the 1% level.