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Title: HERITABILITY ESTIMATES AND ASSOCIATIONS FOR PROTEIN CONTENT AND GRAIN YIELD INVOLVING FOUR WINTER WHEAT CROSSES (*TRITICUM AESTIVUM* VILL., HOST)

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Four agronomically and genetically diverse winter wheat parents were utilized as the experimental organisms. Atlas 66 and NB 68513 were selected as cultivars with a high and stable protein content when grown under different environmental condidtions. They are intermediate for grain yield when grown in the Pacific Northwest. Yamhill and Hyslop represented low protein, high yielding cultivars adapted to the Pacific Northwest.

Data were obtained from crosses between the two high protein cultivars and the two low protein cultivars based on the performance of the parents and the $F_1$ and $F_2$ generations. These experimental populations were grown in 1971 at the Pendleton Experiment Station and the Central Oregon Experimental site at Madras, Oregon.

Measurements were made on an individual plant basis for protein content, grain yield, 50 kernel weight, kernels per spike, tillers per plant and plant height.

Differences among and within crosses were determined by the analysis of variance. Information concerning the nature of inheritance was obtained by comparing the $F_1$ and $F_2$ means in relation to performance of the parents; the frequency distribution of the generations for protein content; and by determining broad and narrow sense heritability estimates for the six characters studied. The existence of possible phenotypic associations among the six characters studied was determined by using correlation coefficients. In order to evaluate the possible direct and indirect effects of grain yield and the components of yield on protein content, path coefficient analyses were employed.

Significant differences were observed among and within crosses at both the Pendleton and Madras sites for most characters measured.

The $F_1$ and $F_2$ mean values were found to be near the mid-parent of the two parents in all four crosses for plant height, 50 kernel weight and kernels per spike. There were several exceptions depending on the particular cross and specific character. Protein content mean values were also intermediate between the two parents for the $F_1$ and $F_2$ generations. In crosses involving Hyslop, the mean values tended to be near the highest parent. Little or no transgressive segregation was noted in the $F_2$ generation.

Evidence of non additive gene action was noted both for grain yield and tiller number in the $F_1$ and $F_2$ generations with the mean values exceeding the highest parent in all crosses for grain yield at the Pendleton site. Tillers per plant at Pendleton and both tillers per plant and grain yield at Madras also showed some degree of hybrid vigor, but the magnitude depended on the particular cross.

The high broad and narrow sense heritability estimates obtained both at Pendleton and Madras for all traits suggested that there was a large amount of genetic variation present for the characters studied. The narrow sense estimates further suggested that a high percentage of the total genetic variation was due to genes which function in an additive manner.

Significant negative correlations were noted between protein content and grain yield including some of the components of yield. In evaluating the direct and indirect effects with path coefficient analysis, these negative associations resulted from the large negative indirect effects of 50 kernel weight and kernels per spike on protein content via grain yield at the Madras site. At the Pendleton site, where moisture became a limiting factor, the negative association resulted largely as the indirect effect of 50 kernel weight on protein content through grain yield.

The large environmental influence on protein content was particularly striking at the Pendleton site. With the spring application of nitrogen, a delay in maturity for Hyslop and Yamhill was noted and with the subsequent loss of moisture, shriveled grain resulted and hence a higher protein content with lower grain yield. This resulted in the grain protein of Hyslop and Yamhill being higher than that of Atlas 66 and NB 68513.

The results of this study suggest that it may be necessary to compromise in attempting to develop high protein lines with maximum yield. However, it should be possible to increase the protein content two to three percent and still maintain the yielding ability of Hyslop and Yamhill.

# Heritability Estimates and Associations for Protein Content and Grain Yield Involving Four Winter Wheat Crosses (*Triticum aestivum* Vill., Host)

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Typed by Susie Kozlik for Polat Solen

In dedication to my mother and father

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# HERITABILITY ESTIMATES AND ASSOCIATIONS FOR PROTEIN CONTENT AND GRAIN YIELD INVOLVING FOUR WINTER WHEAT CROSSES (*TRITICUM AESTIVUM* VILL., HOST)

## INTRODUCTION

Mankind in today's world faces not only the threat of inadequate food supplies, but also the likelihood that increased sources of food may be inferior in nutritional properties. Cereal grains and particularly wheat are widely adapted to many areas of the world and currently are the staple food for many of the developing countries. If through plant breeding, new cultivars of wheat can be developed which combine high grain yield with increased protein content, a major contribution can be achieved. Should increases in protein quantity be realized, it will then be necessary to evaluate the quality aspects of this increased protein content in later studies.

Plant breeders rely on genetic variability for the improvement of plant species to better meet his needs. In the past, breeders have been very successful in utilizing such variability to increase the production of cereal grains. The recent dramatic increase in wheat yields with the development of the semi-dwarf cultivars is an excellent example of how genetic variability can be explored.

Grain protein is influenced both by genetic and environmental factors as are other plant characters and may account in part for the lack of success in developing high protein cultivars. There is also the possibility that grain yield and protein content may be negatively associated. Therefore, in order to make progress selecting for both high grain yield and also acceptable protein levels in wheat, the plant breeder must know how much of the total variation observed in segregating populations is due to genetic factors. Also he must be aware of any possible negative associations which might exist between yield and protein content.

The major objectives of this study were to determine the nature of inheritance influencing protein content, grain yield and the components of yield; to investigate the possible associations of these characters including the possible direct and indirect associations which may exist; and to evaluate how much the environment may influence the efficiency of selection at two diverse locations.

# LITERATURE REVIEW

Many research workers have been interested in the protein content of wheat grain, particularly because protein is one of the major factors determining bread quality. Perhaps of even more importance is that wheat flour in some form is a major source of protein in the diet of millions of people. If the protein content of wheat could be increased, it might improve the nutritional aspects of wheat as a food. Therefore, if plant breeders could combine high grain yields with increased protein, a major contribution could be achieved. Unfortunately, many investigators have noted that a negative relationship exists between grain protein and grain yield in some wheat populations.

Information concerning the inheritance, the relationship between grain yield and its components and the influence of environment on protein content is needed if plant breeders are to develop high yielding, high protein cultivars and perhaps avoid, to a degree, the reported negative relationship between yield and protein content.

## Nature of Inheritance Influencing Protein

The genetic variability for protein content in wheat was clearly demonstrated in 1954 by Middleton *et al*. (26). Protein content of thirteen soft red winter wheat cultivars were compared in a series of tests during a three year period. Large varietal differences were observed with Atlas 50 and Atlas 66 being superior in yield and protein content. In a similar study significant differences were found in protein content among cultivars Atlas 50, Atlas 66, Wichita and Comanche (12).

Recent studies in Mexico (43) showed that the protein content of grain can vary from 11.63% to 18.67% with an average of 15.25% in 489 wheat lines grown under the same environmental conditions. In 1970, 7,000 wheat cultivars from the world collection were screened for protein by Johnson et al. (14). There were great varietal differences in protein content of wheat cultivars, varying from 6% up to 22%.

Inheritance of protein in wheat has been studied in an effort to better understand the nature of this character. Several investigators (18, 19, 35) have attempted to study the number of genetic factors involved in the inheritance of protein content in wheat. Normal distribution of $F_2$ segregating populations have been reported by Stuber et al. (35) and Johnson et al. (18). They concluded that there was more than one major gene conditioning high protein content in the populations studied. Most inheritance studies have considered protein content as a quantitatively inherited character.

Davis et al. (4) determined broad sense heritability estimates for protein content in four crosses of winter wheat in which Atlas 66 was used as the high protein progenitor. The heritability estimates ranged from 54% to 69% depending upon the cross. High heritability values indicated the presence of considerable genetic variability for protein content, and hence selection for high and low protein content would be effective depending upon the particular cross.

Kaul and Sosulski (20) studied a cross between Selkirk X Gabo, and Hsu and Sosulski (13) used a four parent diallel cross of spring wheat for evaluation of protein content. In both studies high broad sense heritability estimates were obtained. The heritability values ranged from 42 % to 71% and 79% to 82%, respectively.

In 1962 Haunold et al. (11) calculated the narrow sense heritability estimates for grain protein in wheat by using standard unit method ( a modification of parent progeny regression method by coding data in standard units) and the regression of $F_3$ on $F_2$. Larger heritability estimates were obtained from the standard unit method. With heritability values ranging from 58% for Atlas 66 X Wichita and 41% for Atlas 66 X Comanche the values obtained from the regression method were 36% and 25%, respectively.

Lofgren et al. (24) calculated narrow sense heritabilities for protein content in wheat using the regression and standard unit method. Information was obtained on four crosses involving Atlas 50, Atlas 66, Triumph and Kaw utilizing the regression of $F_4$ on $F_3$ and $F_5$ on $F_4$ generations for two consecutive years. The values obtained by the standard unit method ranged from 16% to 73% for the four crosses, whereas values obtained by the regression method ranged from 24% to 68%.

In general, values were larger where the standard unit method was used.

Schlehuber et al. (30) studied the narrow sense heritability values for protein content by regressing the $F_5$ on $F_4$ in a Triumph X CI 12406 cross. The narrow sense heritability estimate for protein was 47%.

Parental and early generation populations from the cross PI 56219 X Conley were evaluated for a number of baking quality properties involving protein (23). Narrow sense heritability values were determined by regression of $F_5$ and $F_6$ generation means on $F_2$ line values. The values for protein content were 37% and 70%, respectively. They concluded that great differences for heritabilities were an indication of environment X genotype interaction which could reduce effectiveness of early generation selection for this trait under certain conditions.

Also Stuber et al. (35) calculated broad and narrow sense heritability estimates for protein content and other agronomic characters in wheat. The average of $P_1$, $P_2$, and $F_1$ variances was used as a measure of the nonheritable variances in obtaining broad sense heritabilities. The broad sense heritability estimates were based on $F_2$ and the backcross variances. The narrow sense heritability estimate for protein content (82%) was as large as broad sense heritability values. In fact, some of the narrow sense heritability estimates for other agronomic characters were larger than broad sense heritability values.

Interrelationships between grain protein content and other quality characters of wheat were studied in $F_2$ and $F_3$ generations of Itana X Atlas 66 cross (37). The narrow and broad sense heritability estimates were low. The values for protein content obtained utilizing the regression method of $F_3$ on $F_2$ and the components of variance were 15% and 24% respectively.

Dokic et al. (6) found largely a non additive influence on protein content in several crosses of wheat. They reported that there was no additive effect of genes on protein content in these crosses. In another study Hsu and Sosulski (13) found a slight over-dominance intraallelic gene action for protein content, and that both dominant and recessive genetic factors were contributing to the expression of this trait.

In 1972 eight wheat cultivars were evaluated for combining ability with regard to protein content (2). Both specific and general combining ability were significant. However, specific combining ability was more important than general combining ability for this trait.

Five spring wheat crosses were evaluated on the basis of gene action for grain protein by Chapman and McNeal (3). There was no epistatic effect for the inheritance of protein content. Two crosses out of five showed significant dominant type gene action. In all crosses under investigation, the additive genetic effect was highly significant.

Transgressive segregation for protein content in wheat has also been reported by several investigators (9, 13, 35).

## Relationship Between Protein, Grain Yield and Some Components of Grain Yield

Association between yield and protein content has been investigated by many research workers. Some investigators reported that increased protein content in the hybrid progeny was not associated with a decrease in grain production (6, 10, 16, 17, 26). However, results from the majority of studies suggest that depending on the populations evaluated and the environmental factors present during the growing season, negative associations between these two characters were generally observed.

Four cultivars were utilized to determine the possible relationship between yield and protein content over a two year period by Haunold et al. (12). The relationship between yield and protein content was not consistent and depended upon the year and variety. The correlation between yield and protein in Atlas 50 and Atlas 66 in 1958 was low and negative but statistically not significant. In 1959 a highly significant negative correlation was found for Atlas 66 and Comanche.

Davis et al. (4) evaluated four crosses between Atlas 66, Leap, Malakoff - Nittany - 3 and Chancellor to determine the inheritance of protein, texture and grain yield. Genotypic and phenotypic correlations were determined for these characters. A negative relationship between percent protein and yield was observed in three out of four populations.

Terman and others (39) studied yield and protein relationships in wheat as affected by nitrogen and moisture. They found a highly significant negative relationship between yield and protein at each level of nitrogen applied. Kivi (21) also found a negative relationship between grain yield and protein content of 42 spring wheat cultivars. There was a wide variation in protein content among cultivars producing medium yield, and selection could have increased protein content without reducing yield excessively.

A significant negative association was also observed between yield and protein in both $F_2$ and $F_3$ generations involving a cross between Itana X Atlas 66 (37). Johnson _et_ _al_. (18) also reported that yield and protein tended to be negatively associated.

McNeal and others (25) studied grain and plant nitrogen relationships in crosses of eight spring wheat cultivars. They selected high and low protein lines from the extraneous of the $F_3$ distribution. Bulk populations of high and low protein lines were seeded at three locations. A significant negative association was observed between grain yield and grain nitrogen content.

Duffield et al. (8) found that a negative relation existed between yield and protein content in segregating populations of NB 65579 X OK 60111 cross. By selecting simultaneously for both high protein and high yield, improvements could be made for both traits.

Since protein analysis is expensive and time consuming, plant breeders have been interested in determining if protein content might be associated with other more easily identified agronomic characters that might help in the selection process.

Haunold et al. (12) and Johnson et al. (19) found that a gene for high protein content from Atlas 66 was closely associated with mature plant resistance to leaf rust. Haunold et al. (12) also reported that shriveled kernels were higher in protein content. It was, however, not known if the higher protein content of shriveled grain was due to the presence of more or less carbohydrate (10).

Haunold (10) studied the relationship between grain protein content and yield, tiller number per plant and grain yield per tiller in four wheats grown in the greenhouse. Grain yield was significantly and negatively correlated with the protein content in the cultivars Comanche and Wichita. Grain per tiller was significantly and negatively correlated in all cultivars studied. In one out of four cultivars, number of tillers per plant was found to be negatively correlated with the protein content. Most correlations among characters studied were negative but low in magnitude.

In 1962 Stuber et al. (35) reported both phenotypic and genotypic correlation coefficients between grain protein and other plant and seed characteristics in $F_2$ generation of a Wichita X Atlas 66 cross. The genotypic correlation was greater than phenotypic correlation values. The correlation coefficients between protein content and plant height, number of tillers per plant, grain per spike and grain yield per plant were highly significant and negative. Grain protein content had a highly significant positive correlation with flowering data. All phenotypic correlations were low. Therefore, selection could not be effective for high protein content based on seed and plant characteristics. Genotypic correlation of grain protein content with plant height was high in magnitude. Thus selection for high protein based on plant height may be effective if environmental effects could be reduced.

The simple correlations among 14 quality and four agronomic characters were evaluated for 112 $F_4$ lines in a Triumph X CI 12406 cross (30). Correlation coefficients were low and statistically nonsignificant between protein content and grain yield, test weight, height and heading date.

## Influence of Environment on Protein Content

Environmental factors have been shown to have a major influence in determining protein content in wheat. Austin and Kumari (1) studied the influence of several environment factors on the protein content of several Indian wheat cultivars. They observed a highly significant environmental effect with the varietal effect being much smaller. The mean protein content for 13 New Puso wheats tested ranged from 11.75% to 12.39%. Some varieties were consistent with respect to protein content regardless of the environment in which they were grown.

Terman et al. (39) studied yield and protein relationships in wheat as effected by nitrogen and moisture at several locations. Protein content of hard red winter wheat cultivars varied more widely between locations than among varieties at each location. Similar findings have been reported by other investigators (29, 31).

Johnson et al. (16, 19) reported that a single wheat genotype could produce grain protein varying from 8 to 18 percent depending upon the environment in which it is grown and the particular cultivars. Due to this strong influence of the environment on protein content, the genetic differences among the cultivars for protein content have not been easily separated (19, 23).

The effect of environment and rate and type of nitrogen application on protein and lysine was determined on the content of six spring wheat cultivars when grown at four locations (38). Both protein and lysine were greatly influenced by environmental factors, nitrogen content ranged from 3.7% to 5.1% depending upon variety and location.

Hence the influence of environment should be considered when evaluating genotypes collected from different locations for this trait.

The International Winter Wheat Performance Nursery (IWWPN) was established to determine the influence of the environment on several characters of wheat (33). According to the results obtained from 21 sites in 1970, the Frondoso derivatives, Atlas 66, Purdue 4930 A6-28-2-1 and NB 67730 consistently had a higher protein content than other varieties tested. However, the protein content of these cultivars varied between 14.2% to 21.5% for Atlas 66, 14.3% to 19.5% for Purdue 4930 A6-28-2-1 and 13.6% to 20.5% for NB 67730 depending on the locations. The results were similar to those reported from the 1971 International Winter Wheat Performance Nursery (34).

The intraplant and interplant variation for grain protein content in Atlas 66 x Wichita and the $F_1$ progeny resulting from this cross was determined (36). Variations were found to exist between plants of the same cultivar as well as within portions of individual spikes. In the same study the environmental effect was found to be more pronounced among high protein cultivars than low protein cultivars. Significant correlations were not found between yield and protein or flowering date and protein. Therefore, variation among plants resulting from the high protein parent Atlas 66 could not be attributed to those characters noted.

The vegetative parts of plants were analyzed by Seth et al. (32) at different stages of development for nitrogen content to determine the nitrogen utilization of high and low protein cultivars of wheat. There was no significant difference in total nitrogen content of vegetative parts of high and low protein cultivars before heading. Later a rapid increase in nitrogen content in the spikes of the high protein cultivars was observed.

Swaninathan and others (38) observed a gradual increase in protein content with an increasing rate of nitrogen. The average protein content of six spring wheat cultivars was 16.88% when 200 kg/ha of nitrogen was added and 13.66% average protein content for the control plots. Similar findings have been reported by a number of investigators (22, 28, 29, 31, 42).

Finlay and Shepherd (9) reviewed the literature and concluded that high protein was the result of efficient and complete translocation of nitrogen from plant to grain.

Johnson et al. (15, 16, 18) investigated several wheat cultivars and five experimental high protein lines to evaluate possible relationships between plant nitrogen and the protein content of the grain. Differences in nitrogen content of these vegetative parts of the plant and the protein content of the grain were noted, but these differences were not found to be associated. Actually they found that low protein lines were higher in nitrogen than high protein lines, but these differences were not significant. Therefore, the nitrogen uptake and the translocation of nitrogen were separate and independent physiological systems in the wheat plant.

Different results were obtained in another study when selected high and low protein $F_3$ bulk populations of eight spring wheat crosses were analyzed (25). Both high and low protein levels of the $F_3$ bulk populations produced the same amount of above ground plant nitrogen and each translocated the same percentage of nitrogen to the grain. However, grain nitrogen content of high protein $F_3$ bulk populations was significantly higher than lower protein lines but they were lower in yield. A possible explanation was that the high grain nitrogen content in these high protein populations resulted in the distribution of the same amount of nitrogen to a smaller amount of grain yield.

Most of the research workers have agreed that correlations between protein and other agronomic characters were usually too low to be predictive. Also, due to the strong influence of environment on protein content, the genetic differences among cultivars have not been easily separated.

# MATERIALS AND METHODS

Four agronomic and genetic diverse winter wheat parents were used as the experimental organisms. The parental lines were Yamhill (CI 14563), Hyslop (CI 14564), Atlas 66 (CI 12561) and NB 68513 (CI 10574). These four parents will be referred to as $P_1$, $P_2$, $P_3$ and $P_4$, respectively. A detailed pedigree for each line is given in the Appendix.

Hyslop and Yamhill are low protein,soft white, winter, high yielding cultivars adapted to the Pacific Northwest. Atlas 66 and NB 68513 are high protein, red, winter cultivars which are intermediate for grain yield when grown in the Pacific Northwest.

Crosses were made in 1970 and 1971 with the $F_1$ generation grown for $F_2$ seed production in 1971. In the fall of 1971, $F_1$ and $F_2$ generations, along with the parents were planted in a split plot design with crosses being the main plots and generations the sub plots. Parents were planted with each group of crosses resulting in sixteen entries per replication with four replications. Individual plots consisted of 25 plants for the parents and $F_1$ plants and $F_2$ entires consisted of 4 rows with 25 plants per row. In order to provide uniform competition, parents, $F_1$ and $F_2$ populations were blended with a semi-dwarf brown chaffed experimental line and planted as a solid seeding. Plots were established at the Pendleton Experiment Station and Central

Oregon Experiment Station site located at Madras, Oregon. Soil type, rainfall during growing season, fertility and weed control procedures are listed in Table 1 in the Appendix. In order to minimize any possibility of moisture stress at Madras, the experiment was irrigated seven times with a total of 356 mm of water applied during the growing season.

Protein content was determined by the Udy dye binding capacity method (27, 41). The amount of protein was expressed as a percent of dry matter (a 0.5 g/sample from an individual plant). Forty samples were subjected to both Udy and Kjeldahl determinations with similar protein values observed for both methods. Periodical checks with samples of known protein content were used during the protein analysis to ensure consistent results.

Plant height was obtained by measuring the distance between the secondary crown and the tip of the tallest tiller, excluding awns. Grain yield was obtained by weighing the grain from each plant and fifty kernel weights from each plant were noted. Tiller number was determined by counting the number of tiller bearing spikes. Number of kernels per spike was determined by the following formula:

$$\text{Kernels per spike} = \frac{\text{50 x grain yield/50 kernel weight}}{\text{tillers per plant}}$$

Measurements were made on a single plant basis for the parents, $F_1$'s

$F_2$'s. Ten plants representing parents and $F_1$ and 50 $F_2$ plants per replication were sampled.

Data for the six characters from each location were analyzed separately. Each cross was considered as one group in the analysis of variance. The general error term (entries x replication) was used to test differences among crosses and within crosses. The mean values of the parents, $F_1$ and $F_2$ generation of each cross were compared using Duncan Multiple Range Test at the five percent level.

Broad and narrow sense heritability values were calculated for each character. Broad sense heritability estimates were obtained from the analysis of variance using the formula suggested by Thomas and Kernkamp (40).

Narrow sense heritability estimates were calculated by the standard unit method using the $F_1$'s means on the means of the mid-parent, and $F_2$'s means on the means of $F_1$'s.

All possible phenotypic correlations among the six characters were computed at two locations. The simple correlations for the four crosses were further analysed by path coefficient analysis (5). By this method, direct and indirect relationships were determined between protein and other characters studied. The path coefficient (P = standard partial regression coefficient) was determined by the following formula:

$$b' = b \frac{S_i}{S_y}$$

where $b'$ = standard partial regression coefficient, $b$ = regression coefficient, $S_i$ = standard deviation of $i^{th}$ independent variable, and $S_y$ = standard deviation of dependent variable.

# EXPERIMENTAL RESULTS

## Analysis of Variance

Differences among all 16 entries were highly significant for the six characters at both locations (Tables 1 and 2). When each cross was considered as a group, differences among crosses were also significant ($p=0.01$) for tillers per plant, protein content, 50 kernel weight and kernels per spike at both locations. The differences among crosses for grain yield were highly significant only at the Pendleton site. There were significant differences ($p=0.05$) among crosses for plant height at Madras, but similar differences were not observed in height at Pendleton.

Differences within crosses (among $F_1$, $F_2$ generations and the parents of a given cross) were partitioned for each cross. For generations within each cross, significant differences ($p=0.01$) were observed for plant height, protein content, 50 kernel weight and kernels per spike at both locations. Grain yield was also found to be significantly different for generations at the Pendleton site. At Madras, the crosses $P_1 \times P_3$ and $P_2 \times P_3$ were significantly greater for grain yield while there were no significant differences within generations for the other crosses. For tillers per plant, significant differences were observed at Pendleton only for generations within $P_1 \times P_3$ and $P_2 \times P_3$. Opposite results were obtained at Madras where generations

Table 1. Summary of the observed mean squares from analysis of variance for protein content, yield per plant, 50 kernel weight, kernels per spike, tillers per plant, and plant height obtained at Pendleton, Oregon.

| Source of Variation | D. F | Observed mean squares | | | | | |
|---|---|---|---|---|---|---|---|
| | | Protein content | Yield per plant | 50 kernel weight | Kernels per spike | Tillers per plant | Plant height |
| Replication | 3 | 4.97** | 2.14 | .080** | 7.27 | .58 | 3.50 |
| Entries | 15 | 9.04** | 13.46** | .120** | 57.69** | 1.76** | 523.02** |
| Among crosses | 3 | 10.37** | 8.56** | .060** | 50.27** | 2.21** | 1.09 |
| Within crosses | 12 | 8.70** | 14.67** | .140** | 59.55** | 1.65** | 6.26 |
| Within $P_1$ x $P_3$ | 3 | 2.89** | 14.79** | .090** | 33.82** | 2.37** | 499.61** |
| Within $P_1$ x $P_4$ | 3 | 9.05** | 10.88** | .200** | 98.33** | .67 | 317.07** |
| Within $P_2$ x $P_3$ | 3 | 6.44** | 24.63** | .160** | 36.23** | 3.30** | 975.37** |
| Within $P_2$ x $P_4$ | 3 | 16.44** | 8.34** | .120** | 69.80** | .25 | 713.67** |
| Replication x Entries | 45 | .46 | .83 | .008 | 4.60 | .22 | 3.61 |
| Total | 63 | --- | --- | --- | --- | --- | --- |
| Coefficient of variation | | 5.10 | 13.17 | 5.24 | 5.96 | 8.67 | 1.62 |

* Significant at the 5% level
** Significant at the 1% level

Table 2. Summary of the observed mean squares from analysis of variance for protein content, yield per plant, 50 kernel weight kernels per spike, tillers per plant, and plant height obtained at Madras, Oregon.

| Source of Variation | D. F | Observed mean squares | | | | | |
|---|---|---|---|---|---|---|---|
| | | Protein content | Yield per plant | 50 kernel weight | Kernels per spike | Tillers per plant | Plant height |
| Replication | 3 | .53 | 9.63** | .070** | 134.24** | .19 | 372.58** |
| Entries | 15 | 16.83** | 2.41** | .121** | 93.15** | 1.33** | 194.49** |
| Among crosses | 3 | 5.30** | .80 | .020** | 32.13** | 2.70** | 36.68** |
| Within crosses | 12 | 19.72** | 2.82** | .147** | 108.40** | .99** | 231.45** |
| Within $P_1$ x $P_3$ | 3 | 22.87** | 3.72** | .086** | 101.72** | .10 | 205.17** |
| Within $P_1$ x $P_4$ | 3 | 26.64** | 1.66 | .268** | 162.44** | 2.13** | 152.93** |
| Within $P_2$ x $P_3$ | 3 | 12.74** | 4.38** | .069** | 59.32** | .22 | 362.36** |
| Within $P_2$ x $P_4$ | 3 | 16.61** | 1.51 | .160** | 110.11** | 1.51** | 205.25** |
| Replication x Entries | 45 | .24 | .73 | .003 | 5.07 | .21 | 5.51 |
| Total | 63 | --- | --- | --- | --- | --- | --- |
| Coefficient of variation | | 3.17 | 16.75 | 2.43 | 7.20 | 12.76 | 2.66 |

* Significant at the 5% level

** Significant at the 1% level

within the crosses $P_1$ x $P_4$ and $P_2$ x $P_4$ were significantly different for tillers per plant.

The coefficients of variation were high for grain yield and number of tillers per plant at both locations (Tables 1 and 2): 13.2 and 16.8 percent for grain yield and 8.67 and 12.76 percent for tillers per plant at Pendleton and Madras, respectively. However, for other characters the values were quite low ranging from 1.62 to 7.20 percent depending on the character studied and the location.

## Nature of Inheritance

At the Pendleton site (Table 3) there were significant differences for plant height ($p=0.05$) between the respective parents in every cross; however, other significant differences between parents depended upon the cross and specific character. Significant differences were noted for grain yield in crosses $P_1$ x $P_4$ and $P_2$ x $P_3$; tillers per plant ($P_1$ x $P_3$); protein content ($P_1$ x $P_4$, $P_2$ x $P_3$ and $P_2$ x $P_4$); 50 kernel weight ($P_2$ x $P_4$); and for kernels per spike ($P_1$ x $P_3$, $P_1$ x $P_4$ and $P_2$ x $P_4$). The mean values for the $F_1$ populations were intermediate between the two parents for plant height in all crosses. The $F_1$ means exceeded the highest parent for yield per plant, tillers per plant, and 50 kernel weight in all crosses. Values for protein content in the $F_1$ were lower than the lowest parent in all crosses while kernels per spike tended to be intermediate or higher than the highest parent

Table 3. Mean values for protein content, yield per plant, 50 kernel weight, kernels per spike, tillers per plant and plant height obtained at Pendleton, Oregon.

| | Mean Values | | | | | |
|---|---|---|---|---|---|---|
| | Protein content (%) | Yield per plant (gm) | 50 kernel weight (gm) | Kernels per spike | Tillers per plant | Plant height (cm) |
| Yamhill ($P_1$) | 15.27a* | 6.17b | 1.60bc | 40.47a | 4.71c | 103.11d |
| Atlas 66 ($P_3$) | 14.70ab | 5.89b | 1.51c | 34.41b | 5.45b | 128.00a |
| $F_1$ | 13.30b | 10.08a | 1.86a | 40.38a | 6.58a | 125.18b |
| $F_2$ | 14.02b | 6.97b | 1.68b | 37.13b | 5.48b | 120.85c |
| Yamhill ($P_1$) | 15.27a | 6.17b | 1.60cd | 40.47a | 4.71b | 103.11c |
| NB 68513 ($P_4$) | 12.34b | 4.52c | 1.54c | 29.18d | 4.90ab | 122.29a |
| $F_1$ | 12.02b | 8.39a | 2.03a | 36.86b | 5.53a | 121.59a |
| $F_2$ | 12.50b | 5.45b | 1.79b | 32.40c | 4.62b | 116.93b |
| Hyslop ($P_2$) | 15.70a | 4.85c | 1.41c | 35.29b | 4.91b | 93.33d |
| Atlas 66 ($P_3$) | 14.70b | 5.89b | 1.51c | 34.41b | 5.45b | 128.00a |
| $F_1$ | 12.74c | 10.49a | 1.85a | 40.38a | 7.00a | 124.54b |
| $F_2$ | 13.84bc | 6.29b | 1.70b | 33.78b | 5.39b | 117.06c |
| Hyslop ($P_2$) | 15.70a | 4.85b | 1.41c | 35.29b | 4.91a | 93.33c |
| NB 68513 ($P_4$) | 12.34b | 4.52b | 1.54b | 29.18c | 4.90a | 122.29a |
| $F_1$ | 11.00c | 7.73a | 1.82a | 39.08a | 5.41a | 120.50a |
| $F_2$ | 12.12b | 5.47b | 1.66b | 32.71b | 4.90a | 115.45b |

* Ranking of the mean values using Duncan Multiple Range Test at the 5% level.

depending on the cross. The $F_2$ mean values were generally lower than the $F_1$ values and intermediate between the two parents. There were exceptions with protein content where the $F_2$ consistently exceeded the $F_1$ for all crosses. Also, $F_2$ mean values for 50 kernel weight exceeded the highest parent in all crosses.

At Madras (Table 4) the parents were significantly different for most traits involving all four crosses. The only exceptions were tillers per plant for the crosses $P_1$ x $P_3$ and $P_2$ x $P_3$ and for grain yield in the cross $P_2$ x $P_4$. The $F_1$ mean values tended to be intermediate between the two parents; however, there were examples where the $F_1$ exceeded the highest parent (50 kernel weight). This latter situation was not as prevalent at the Madras site when compared with the Pendleton location, particularly for grain yield and tillers per plant. The $F_2$ mean values were observed to be intermediate or near the top parent and usually less than the $F_1$ mean values. This depended on the cross and the particular character with a number of exceptions being observed.

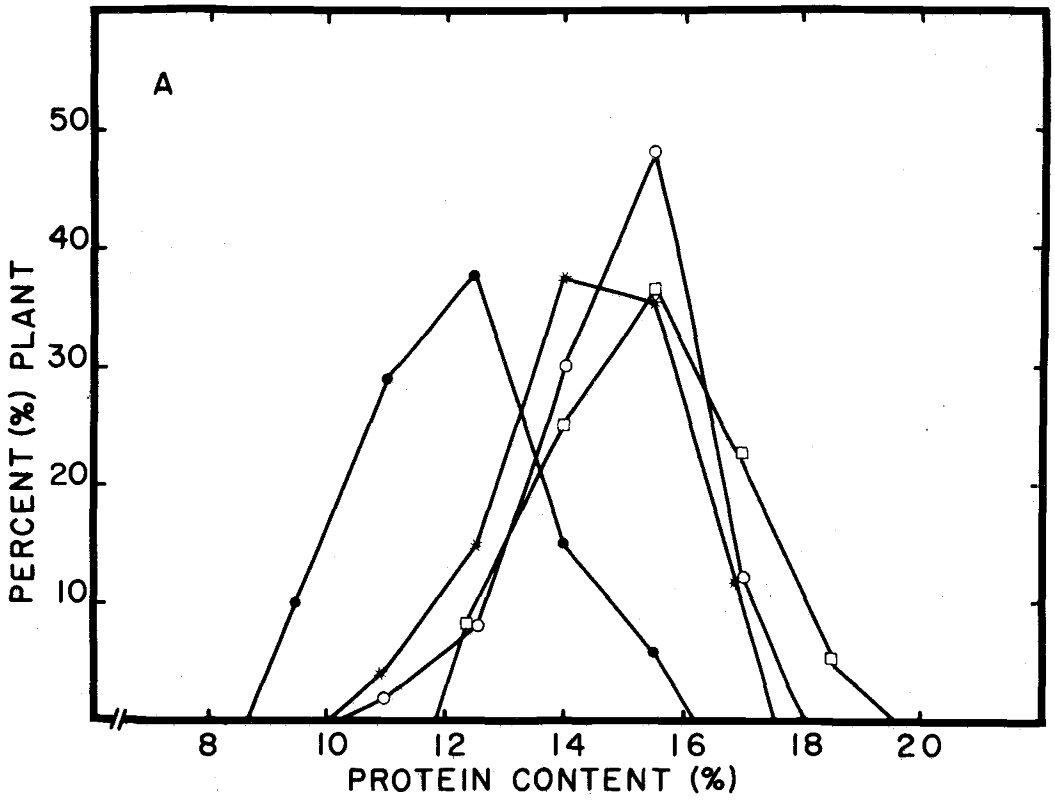
To further understand the nature of inheritance and environmental influence on protein in wheat grain, frequency distributions for the parents are presented for the Pendleton and Madras sites (Figure 1-A and B). A large environmental effect was noted at the Pendleton site (Figure 1-A). The varieties overlapped one another with the mean values of Yamhill and Hyslop exceeding those of Atlas 66 and

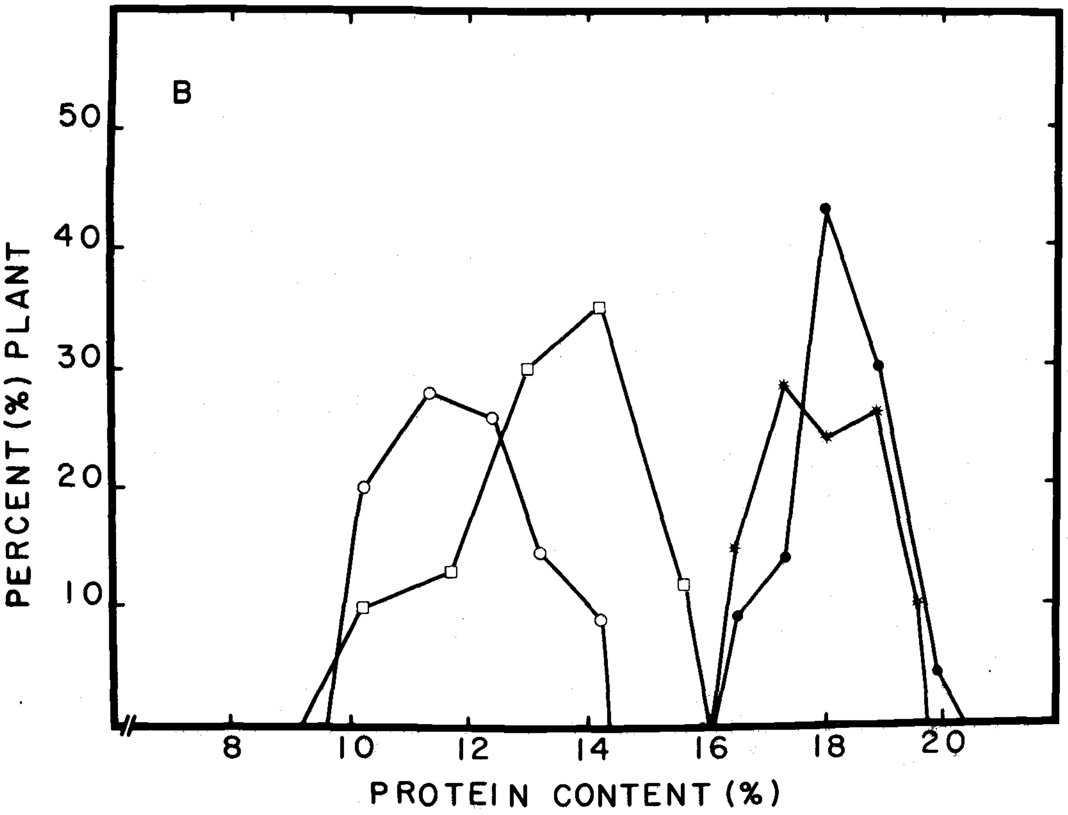
Table 4. Mean values for protein content, yield per plant, 50 kernel weight, kernels per spike, tillers per plant and plant height obtained at Madras, Oregon.

| | Mean Values | | | | | |
|---|---|---|---|---|---|---|
| | Protein content (%) | Yield per plant (gm) | 50 kernel weight (gm) | Kernels per spike | Tillers per plant | Plant height (cm) |
| Yamhill ($P_1$) | 11.94c* | 5.72a | 2.34ab | 39.41a | 3.06a | 77.78b |
| Atlas 66 ($P_3$) | 17.76a | 3.58bc | 2.05c | 27.34c | 3.15a | 93.50a |
| $F_1$ | 15.38b | 5.26ab | 2.37a | 31.81b | 3.27a | 92.33a |
| $F_2$ | 15.28b | 4.28b | 2.26b | 31.31b | 3.01a | 88.77a |
| Yamhill ($P_1$) | 11.94c | 5.72a | 2.34b | 39.41a | 3.06b | 77.78b |
| NB 68513 ($P_4$) | 18.25a | 4.28b | 1.88c | 23.88c | 4.77a | 88.57a |
| $F_1$ | 14.96b | 5.56ab | 2.46a | 31.77b | 3.59b | 91.41a |
| $F_2$ | 14.77b | 5.20ab | 2.37b | 30.39b | 3.52b | 89.81a |
| Hyslop ($P_2$) | 13.40c | 5.56ab | 2.26b | 36.50a | 3.33a | 74.07c |
| Atlas 66 ($P_3$) | 17.76a | 3.58c | 2.05c | 27.34c | 3.15a | 93.50a |
| $F_1$ | 15.23b | 5.97a | 2.35a | 33.76ab | 3.70a | 94.86a |
| $F_2$ | 15.50b | 4.95ab | 2.27ab | 32.01b | 3.35a | 88.72b |
| Hyslop ($P_2$) | 13.40c | 5.56a | 2.26ab | 36.50a | 3.30c | 74.07b |
| NB 68513 ($P_4$) | 18.25a | 4.28a | 1.88c | 23.88c | 4.77a | 88.57a |
| $F_1$ | 16.74b | 5.29a | 2.33a | 28.12b | 3.98b | 87.14a |
| $F_2$ | 16.60b | 5.59a | 2.23b | 29.21b | 4.28ab | 89.17a |

* Ranking of the mean values using Duncan Multiple Range Test at the 5% level.

Figure 1. Frequency distribution of four parent populations for protein content: Yamhill (open circle); Hyslop (open square); Atlas 66 (asterix); and NB 68513 (solid circle). A) Pendleton, Oregon, B) Madras, Oregon.


A
PERCENT (%) PLANT
50
40
30
20
10
8
10
12
14
16
18
20
PROTEIN CONTENT (%)


B
PERCENT (%) PLANT
50
40
30
20
10
8
10
12
14
16
18
20
PROTEIN CONTENT (%)

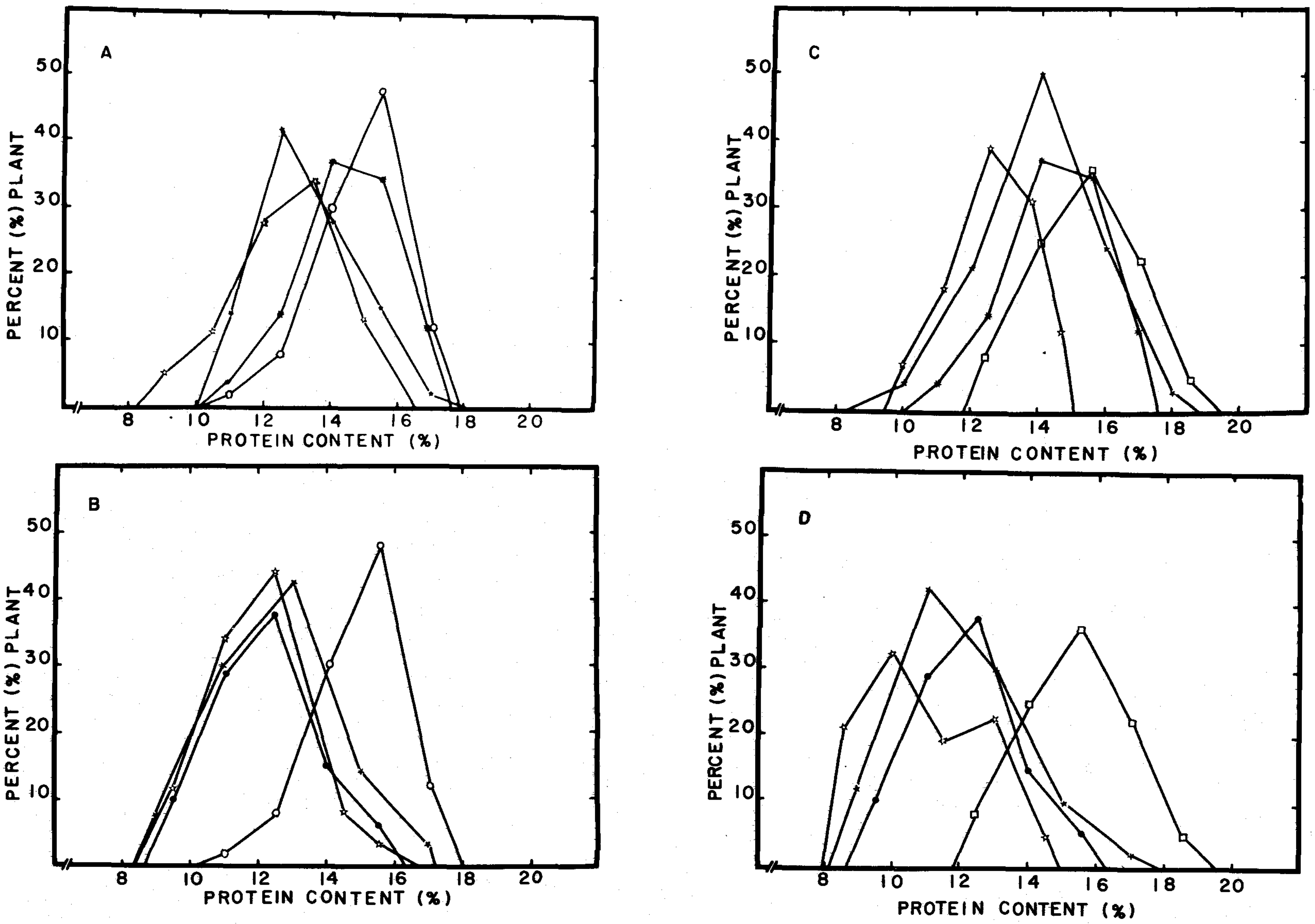
NB 68513. This was contrary to previous results where the protein levels of Yamhill and Hyslop were generally between 9 and 10 percent protein at this site. With such a high degree of environmental variation any genetic interpretation would be difficult.

The four parents grown at the Madras site tended to form two distinct classes (Figure 1-B). NB 68513 and Atlas 66 represent the higher protein class which ranged on an individual plant basis between 16.08 and 18.25 percent protein. Yamhill and Hyslop protein percentages varied from 9.63 to 13.40 percent.

Figures 2-A, B, C, and D represent the parents, $F_1$ and $F_2$ frequency distribution observed at the Pendleton site for protein content. As noted before, the large environmental effect precludes an accurate evaluation of the nature of inheritance. This can be noted for the respective parents and $F_1$ populations in all four crosses. In all crosses, the mean value of the $F_1$ was lower than the means of the parents and $F_2$ populations. The $F_2$ generation tended to have greater variation than either the parents or $F_1$'s; however, in none of the crosses does the $F_2$ population exceed the highest percent for the high parent.

At Madras, the parents were distinctively different in all crosses with no overlapping between the low and high classes (Figure 1-B). In all crosses, the $F_1$ frequency distribution tended to span both the high and low parent distributions but did not exceed the high parent

Figure 2. Frequency distribution of parents, $F_1$ and $F_2$ populations for protein content at Pendleton, Oregon: (A) Yamhill x Atlas 66; (B) Yamhill x NB 68513; (C) Hyslop x Atlas 66; (D) Hyslop x NB 68513: Yamhill (open circle); Hyslop (open square); Atlas 66 (asterix); NB 68513 (solid circle); $F_1$ (open star); and $F_2$ (solid star).

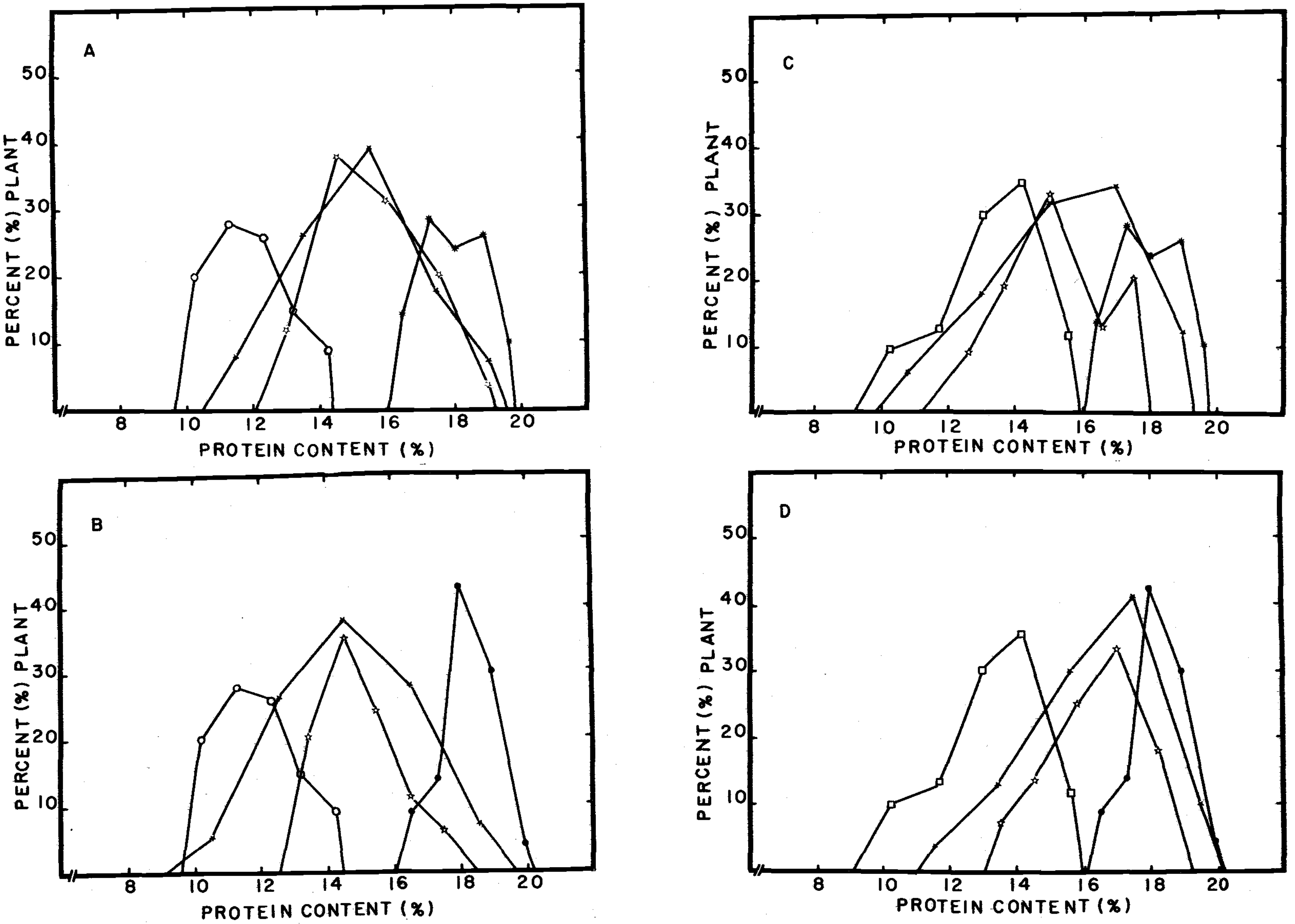

A
B
C
D
PERCENT (%) PLANT
10
20
30
40
50
PROTEIN CONTENT (%)
8
10
12
14
16
18
20

(Figure 3-A, B, C, and D). In the cross Yamhill and NB 68513, the $F_2$ distribution did exceed the low parent distribution (Figure 3-B). In the crosses Hyslop x Atlas 66 and Hyslop x NB 68513, the $F_2$ population tended to be skewed toward the distribution of the highest parent (Figure 3-C and D). This is also true for the $F_1$ in the cross between Hyslop and NB 68513 (Figure 3-C) and to a lesser degree with the cross between Hyslop and Atlas 66 (Figure 3-D).

Both broad and narrow sense heritability estimates were calculated to obtain additional information regarding the nature of gene action controlling the six measured characters. High broad sense heritability estimates ranging from 63% for tillers per plant to 97% for plant height were obtained for each character at the Pendleton site (Table 5). At Madras, however, the broad sense heritability values for plant height (89%), protein content (92%), 50 kernel weight (91%) and kernels per spike (74%) were quite high while yield per plant (37%) and tillers per plant (47%) were lower (Table 5).

The narrow sense heritability estimates were calculated utilizing the standard unit method for both $F_1$ on mid-parent and $F_2$ on $F_1$ for both locations. In general, the narrow sense heritability estimates of $F_2$ on $F_1$ were larger than those obtained from using the $F_1$ on mid-parent estimates (Table 5). The narrow sense heritability estimates were high and consistent for protein content and plant height at both locations while estimates for the other characters were not as

Figure 3. Frequency distribution of parents, $F_1$ and $F_2$ populations for protein content at Madras, Oregon: (A) Yamhill x Atlas 66; (B) Yamhill x NB 68513; (C) Hyslop x Atlas 66; (D) Hyslop x NB 68513: Yamhill (open circle); Hyslop (open square); Atlas 66 (asterix); NB 68513 (solid circle); $F_1$ (open star); and $F_2$ (solid star).


A
PERCENT (%) PLANT
50
40
30
20
10
8
10
12
14
16
18
20
PROTEIN CONTENT (%)
B
PERCENT (%) PLANT
50
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10
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12
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18
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PROTEIN CONTENT (%)
C
PERCENT (%) PLANT
50
40
30
20
10
8
10
12
14
16
18
20
PROTEIN CONTENT (%)
D
PERCENT (%) PLANT
50
40
30
20
10
8
10
12
14
16
18
20
PROTEIN CONTENT (%)

consistent. In some comparisons the narrow sense heritability estimates exceeded those determined for the broad sense heritability values.

Table 5. Broad and narrow sense heritability estimates for protein content, yield per plant, 50 kernel weight, kernels per spike, tillers per plant and plant height obtained at Pendleton and Madras, Oregon.

| | Pendleton | | | Madras | | |
|---|---|---|---|---|---|---|
| | Broad sense (%) | $F_1$ on midparent (%) | $F_2$ on $F_1$ (%) | Broad sense (%) | $F_1$ on midparent (%) | $F_2$ on $F_1$ (%) |
| Protein content | 82 | 78 | 95 | 92 | 68 | 95 |
| Yield per plant | 79 | 73 | 85 | 37 | 41 | 07 |
| 50 kernel weight | 78 | 73 | 89 | 91 | 02 | 93 |
| Kernels per spike | 74 | 32 | 69 | 81 | 43 | 90 |
| Tillers per plant | 63 | 17 | 10 | 47 | 70 | 91 |
| Plant height | 97 | 65 | 80 | 89 | 76 | 40 |

## Associations

The existence of possible phenotypic relationships between the six characters studied were examined by determining all possible correlation coefficients using the mean values for the parents, $F_1$ and $F_2$ populations. There were significant positive correlations between yield per plant and tillers per plant, 50 kernel weight and kernels per spike at the Pendleton location (Table 6). Plant height was found to be positively associated with tillers per plant and negatively associated with protein content. Tillers per plant and 50 kernel weight were positively associated. Of particular interest is the large negative association between protein content and 50 kernel weight. Even though not significant, a negative association was found between yield per plant and protein content.

Significant positive associations were observed between plant height and protein content, yield per plant with 50 kernel weight and kernels per spike, and between tillers per plant and protein and 50 kernel weight and kernels per spike at the Madras location (Table 7). There were significant negative correlations between plant height and kernels per spike, tillers per plant with 50 kernel weight and kernels per spike and with protein content and 50 kernel weight and kernels per spike. A large negative correlation was also detected between protein content and yield per plant.

Direct and indirect effects of the five measured characters on total grain protein for the 16 entries grown for each location were determined. At Pendleton (Table 8), a significant negative correlation between protein content and plant height (r=-0.61) was largely the result of a negative indirect effect by the way of grain yield (-1.21). The negative direct and indirect effects were cancelled somewhat by the positive indirect effect of number of tillers per plant (0.89).

The relationship between yield per plant and protein content (r=-0.29) was not significant even though a large negative direct effect (-2.97) was observed. The indirect effect of tillers per plant (1.49)

Table 6. Phenotypic correlation coefficients among six characters: protein content, yield per plant, 50 kernel weight, kernels per spike, tillers per plant and plant height obtained at Pendleton, Oregon.

| | Yield per plant | 50 kernel weight | Kernels per spike | Tillers per plant | Plant height |
|---|---|---|---|---|---|
| Protein content | -0.29 | -0.67** | 0.23 | -0.22 | -0.61** |
| Yield per plant | | 0.78** | 0.72** | 0.87** | 0.41 |
| 50 kernel weight | | | 0.39 | 0.52* | 0.47 |
| Kernels per spike | | | | 0.47 | 0.17 |
| Tillers per plant | | | | | -0.53* |

* Significant at the 5% level.
** Significant at the 1% level.

Table 7. Phenotypic correlation coefficients among six characters: protein content, yield per plant, 50 kernel weight, kernels per spike, tillers per plant and plant height obtained at Madras, Oregon.

| | Yield per plant | 50 kernel weight | Kernels per spike | Tillers per plant | Plant height |
|---|---|---|---|---|---|
| Protein content | -0.73** | -0.71** | -0.97** | 0.62** | 0.71** |
| Yield per plant | | 0.75* | 0.71** | -0.08 | -0.45 |
| 50 kernel weight | | | 0.70** | 0.54* | -0.17 |
| Kernels per spike | | | | -0.68** | -0.68** |
| Tillers per plant | | | | | -0.25 |

* Significant at the 5% level.
** Significant at the 1% level.

Table 8. Direct and indirect interrelationships of grain yield and some components of yield influencing total protein content at Pendleton, Oregon.

| | | | |
|---|---|---|---|
| Protein (%) and yield per plant | | | |
| Direct effect | (P) -2.97600 | | |
| via plant height | | -0.07002 | |
| via tillers per plant | | 1.49223 | |
| via 50 kernel weight | | 0.21917 | |
| via kernels per spike | | 1.03703 | |
| | TOTAL (r) | | -0.2925 |
| Protein (%) and 50 kernel weight | | | |
| Direct effect | (P) 0.28219 | | |
| via plant height | | -0.08125 | |
| via yield per plant | | -2.31134 | |
| via tillers per plant | | 0.88159 | |
| via kernels per spike | | 0.56573 | |
| | TOTAL (r) | | -0.66503 |
| Protein (%) and kernels per spike | | | |
| Direct effect | (P) 1.44612 | | |
| via plant height | | 0.02877 | |
| via yield per plant | | -2.13651 | |
| via tillers per plant | | 0.78429 | |
| via 50 kernel weight | | 0.11002 | |
| | TOTAL (r) | | 0.23269 |
| Protein (%) and tillers per plant | | | |
| Direct effect | (P) 1.68374 | | |
| via plant height | | -0.08125 | |
| via yield per plant | | -2.63375 | |
| via 50 kernel weight | | 0.14781 | |
| via kernels per spike | | 0.67360 | |
| | TOTAL (r) | | -0.21902 |
| Protein (%) and plant height | | | |
| Direct effect | (P) -0.17156 | | |
| via yield per plant | | -1.21457 | |
| via tillers per plant | | 0.88738 | |
| via 50 kernel weight | | 0.13364 | |
| via kernels per spike | | -0.24252 | |
| | TOTAL (r) | | -0.60764 |

Correlation (r)

$R^2 = 0.98883$

Residual = 0.01117

and kernels per spike (1.04) were similar in value while the direct effect of yield per plant on protein content was negative.

The negative correlation between protein content and tillers per plant (r=-0.22)resulted from a large indirect negative effect of grain yield (-2.63). The positive direct effect of tillers per plant (1.68) and indirect positive effect of kernels per spike (0.67) tended to cancel the large portion of the indirect negative effect of yield on protein.

The significant negative relationship between protein content and 50 kernel weight (r=-0.67) was mainly due to the negative indirect effect of grain yield (-2.31). Some portion of this negative effect is cancelled by indirect positive effects of tillers per plant (0.88) and kernels per spike (0.57).

The positive correlation between protein content and number of kernels per spike (r=0.23) was attributed to the cancellation of the indirect negative effect of grain yield (-2.14) by direct positive effect of tillers per plant (0.78). The small residual effect indicated that the five traits studied accounted for 98.8% of the total variation in protein content in those populations.

At Madras, a significant positive correlation between protein content and plant height (r=0.72) was the result of a large positive indirect effect via kernels per spike (1.07)(Table 9). This large positive effect was reduced by negative indirect effects of grain yield per plant (-0.42) and tillers per plant (-0.20). The relationship between

Table 9. Direct and indirect interrelationships of grain yield and some components of yield influencing total protein content at Madras, Oregon.

| | | | |
|---|---|---|---|
| Protein (%) and yield per plant | | | |
| Direct effect | (P) 0.93210 | | |
| via plant height | | -0.06269 | |
| via tillers per plant | | 0.06618 | |
| via 50 kernel weight | | -0.54441 | |
| via kernels per spike | | -1.12061 | |
| | TOTAL (r) | | 0.72943 |
| Protein (%) and 50 kernel weight | | | |
| Direct effect | (P) -0.72539 | | |
| via plant height | | -0.02173 | |
| via yield per plant | | 0.69955 | |
| via tillers per plant | | 0.43791 | |
| via kernels per spike | | -0.10132 | |
| | TOTAL (r) | | -0.71098 |
| Protein (%) and kernels per spike | | | |
| Direct effect | (P) -1.58234 | | |
| via plant height | | -0.09414 | |
| via yield per plant | | 0.66011 | |
| via tillers per plant | | 0.54679 | |
| via 50 kernel weight | | -0.50488 | |
| | TOTAL (r) | | -0.97446 |
| Protein (%) and tillers per plant | | | |
| Direct effect | (P) -0.80747 | | |
| via plant height | | 0.03441 | |
| via yield per plant | | -0.07640 | |
| via 50 kernel weight | | 0.39403 | |
| via kernels per spike | | 1.07148 | |
| | TOTAL (r) | | 0.61605 |
| Protein (%) and plant height | | | |
| Direct effect | (P) 0.13902 | | |
| via yield per plant | | -0.42034 | |
| via tillers per plant | | -0.19787 | |
| via 50 kernel weight | | 0.12042 | |
| via kernels per spike | | 1.07381 | |
| | TOTAL (r) | | 0.71504 |

Correlation (r)

$R^2 = 0.98112$

Residual = 0.01888

grain yield and protein content (r=-0.23) was significant and negative, even though the direct effect (0.93) was large and positive. The indirect negative effects of 50 kernel weight (-0.54) and kernels per spike (-1.12) cancelled the direct positive effect of grain yield on protein. The significant positive correlation between protein content and tillers per plant (0.62) resulted from the negative direct effect of tillers per plant on protein (-0.81). This, in turn, resulted from a large positive indirect effect of 50 kernel weight (0.89) and kernels per spike (1.07) which cancelled the large negative direct effect of tillers per plant.

The significant negative relationship between protein content and 50 kernel weight (r=-0.71) was attributed to the direct effect of 50 kernel weight on protein (-0.73) and the negative indirect effect of kernels per spike (-1.10). A portion of these negative effects was reduced by the positive indirect effects of grain yield and tillers per plant. The highly significant negative correlation between protein content and kernels per spike (r=-0.97) was due to the direct effect (-1.58) and the indirect effect of 50 kernel weight (-0.50). These large negative direct and indirect effects were reduced by the positive indirect effects of grain yield (0.66) and tillers per plant (-0.50). The small residual effect indicated that the five characters studied accounted for 98.1% of the total variation in protein content.

# DISCUSSION

The expression of a character in a plant population is influenced by differences among genotypes, environment and the genotype-environment interactions. Plant breeders rely upon the genetic variability for improvements of the plant species through breeding. Such improvements can be accomplished more efficiently if the plant breeder can base his selection on a knowledge of the inheritance, relationship with the other characters and the influence of environment on the agronomic and quality characters.

Wheat, being one of the most widely adapted cereal grains, offers perhaps the greatest potential in many developing countries for providing an adequate food supply. The two most important characters which will determine the success of wheat in removing the food deficit are grain yield and protein content. Much has been written concerning the "Green Revolution" and the major breakthrough in grain yields; however, the question is now being raised if in addition to being an energy source, wheat might also become a better source of protein.

Concern has been expressed and supported by some research data that a negative relationship exists between grain yield and protein content. If such a relationship does exist then it may be difficult for the plant breeder to increase both yield and protein content in a single cultivar. In approaching this problem, the breeder first needs to evaluate how much genetic variability he has present in the population for grain yield and protein content. Secondly, does indeed a negative association exist between these two characters and if so what is the basis of this negative relationship? Also, to what extent does the environment influence the expression of protein in the wheat kernel?

Broad sense heritability estimates derived from the components of variance ranged from 37% to 97% depending upon the character and the location. The estimates obtained at Pendleton for grain yield and protein content were 79% and 82%, respectively. At the Madras site, estimates were somewhat lower for grain yield (37%) and higher for protein content (92%). These values suggested that considerable genetic variation existed for both traits within these populations and the plant breeder should be able to make considerable improvement in increasing grain yield and protein content. The broad sense heritability estimates obtained in this study for protein content were similar to those reported by Davis *et al*. (4), Kaul and Sosulski (20) and Hsu and Sosulski (13). However, the estimates for grain yield were generally higher than those reported in the literature, particularly at the Pendleton site.

The breeder of self-pollinating species such as wheat can only utilize the additive type of gene action. Therefore, narrow sense heritability estimates provide more accurate predictions as to how the total genetic variation can be used in the improvement of a particular trait. With protein content, it would be very desirable if the narrow sense heritability estimates are high since it is very time consuming to run chemical analyses on a large number of segregating progeny. In this study, narrow sense estimates for protein content calculated by regression of the $F_1$ means on the mid-parents and the $F_2$ means on the $F_1$ were very high. The estimates for the two generations were 78% and 95% at the Pendleton site and 68% and 95%, respectively, at Madras. High estimates were also noted at Pendleton for grain yeild (73% and 85%), but much lower values particularly when $F_2$ means were regressed on $F_1$ (7.0%) were obtained at Madras.

Both high broad and narrow sense heritability estimates were noted for those traits other than protein content and grain yield. However, a number of inconsistent results were noted, particularly the narrow sense heritability estimates for the two generations involving grain yield and 50 kernel weights at the Madras site where there were large differences between the two estimates. Also, several narrow sense heritability estimates were higher than those obtained for the broad sense estimates (Table 5).

Several workers have reported that the mean values for protein content of $F_1$ and $F_2$ populations were similar to the mid parent of the two parents (3, 13, 20, 35). This situation would suggest that protein content was controlled largely by additive gene action. The observations noted in this study from the Madras site would support the conclusion that protein content in wheat is controlled largely by additive gene action as the mean values for the $F_1$ and $F_2$ were similar in magnitude to the mid-parents in three crosses. In the cross between Hyslop and NB 68513, the $F_1$ and $F_2$ mean values were skewed toward the high protein parent. Also, in this same cross several of the $F_2$ progeny appeared to exceed the highest parent; however, due to the limits imposed by the protein analysis, values above 20% were questionable so such data were recorded as being 20%. Progeny in the $F_2$ exceeded the lowest parent in the cross between Yamhill and NB 68513.

Due to the large environmental effect noted at Pendleton, any attempt to determine the nature of the gene action would be difficult; however, it was observed that the $F_1$ and $F_2$ means were skewed toward the low protein parents which at this site were Atlas 66 and NB 68513. The fact that Yamhill and Hyslop had the higher protein content at this site further suggests a strong environmental effect which makes any genetic interpretations impossible.

When grain yield is considered, the $F_1$ means exceeded the highest parent in all four crosses at Pendleton suggesting that non-additive gene action greatly influenced the expression of grain yield. The $F_2$ means were less than the $F_1$ means indicating that inbreeding depression was a factor in subsequent generations. Even in the $F_2$'s, the mean values exceeded the highest parent suggesting that considerable nonadditive gene action existed in this generation. There may also have been an interaction of the $F_1$ and $F_2$ generations with the environment which tended to inflate these mean values. This latter conclusion is based on the nature of gene action observed in the $F_1$ and $F_2$ populations at Madras. Only in one cross (Hyslop x Atlas 66) did the $F_1$ exceed the highest parent with the others being very close to the highest parent. The $F_2$ mean values varied depending on the cross. In the Hyslop x NB 68513 cross, the $F_2$ mean exceeded the $F_1$ and the highest parent. Yamhill x NB 68513 and Hyslop x Atlas 66 crosses showed the $F_2$ means were close to the highest parent whereas in the Yamhill x Atlas 66 cross the $F_2$ mean was near the mid-parent of the two parents. It would appear that there was less nonadditive gene action at the Madras site; however, the large environmental effects noted at the Pendleton site may be biasing the gene action estimates.

If a negative relationship should exist between protein content and grain yield in wheat, the degree of selection pressure applied to either or both of these two characters may have to be compromised. Several investigators have reported that protein content and grain yield are independent and that it should be possible to maximize both factors by selecting simultaneously (6, 10, 16, 17, 26). This finding is not in agreement with the results of most protein studies in wheat where a significant negative correlation between these two characters has been reported (4, 8, 12, 13, 18, 21, 35, 37, 39). This apparent discrepancy could result if different wheat populations were utilized and particularly if the environmental conditions under which the various studies were conducted were greatly different. In previous studies of possible associations using the simple correlation coefficients, no attempt was made to determine possible direct and indirect effects of other chracters.

In the present study r values were determined between protein content, grain yield and several components of yield. At Pendleton, the r values were negative with the exception of protein content and kernels per spike. When the direct and indirect effects were determined utilizing path coefficient analysis, several very interesting relationships became apparent. The negative r value between grain yield and protein content was due mainly to the direct effect while the large negative r value between protein content and 50 kernel weight was due to the negative indirect effect of 50 kernel weight via yield per plant. Even though the r value between protein content and kernels per spike was positive, it was observed that a large negative effect was expressed indirectly through yield per plant. Since kernel number and kernel weight are the primary components of yield, it may be difficult to achieve high grain yield and high protein content through selection at the Pendleton site. The low protein parents, Hyslop and Yamhill, were higher in protein than either Atlas 66 and NB 68513 and this was attributed to kernel weight. Hyslop and Yamhill are later maturing varieties than either Atlas 66 or NB 68513. With the spring application of nitrogen, a further delay in maturity resulted coupled with a loss in moisture which shriveled the kernel of these varieties. This was reflected in lower 50 kernel weights and hence lower grain yield. The shriveling caused the starch component of the kernel to be reduced resulting in a higher percentage of total protein. This large environmental influence did not provide a reliable expression of the characters studied.

The Madras site was irrigated throughout the growing season so the moisture stress experienced at Pendleton did not occur. Even so, a negative correlation was obtained between protein content and grain yield; however, unlike Pendleton, that significant negative correlation was not due to the direct effect of grain yield, but to the indirect negative effects of kernels per spike and 50 kernel weight. These latter two components also had large direct negative effects on grain protein. It would appear that even at the Madras site it would be difficult to select for maximum yield and protein content at the same time.

From the results obtained for the wheat populations evaluated in this study, it is apparent that progress can be made to develop wheat cultivars which combine high yields with acceptable levels of grain protein.

The high heritability estimates indicated that there was a large amount of genetic variation present in these populations for the six characters measured. Genetic variation associated with protein content was largely additive which should enable the plant breeder to practice efficient selection in the $F_2$ generation. A similar situation was true for plant height, 50 kernel weight and kernels per spike. This was in contrast to grain yield and tillers per plant where much of the genetic variation in the $F_1$ and $F_2$ was attributed to non additive gene action. Since this latter form of genetic variation cannot be utilized in self-pollinated species and frequently masks the additive effects, selection for these characters should be delayed until the $F_3$ and possibly the $F_4$ generations.

A second factor which will influence the rate of progress in developing high yielding, high protein lines is the negative association noted between these characters at both experimental sites. Upon examining this negative relationship in more detail, this association was expressed as the result of a large negative direct effect of the yield components, kernel weight and kernel number on protein content. Since these were the two primary components of yield, the plant breeder must compromise and evaluate resulting progeny as to what levels of yield can be achieved with acceptable protein content. Based on the performance of the mean values observed in the $F_2$ generation in this study, it would appear that protein percentages can be raised, through breeding by two or three percent without greatly influencing grain yield. This increase would greatly assist the protein deficient areas in the developing countries; however, it must be emphasized that this increase involves protein quantity and not quality. More detailed studies involving the nutritional properties of this protein will be required before its food value can be assessed.

Also, certain cultural practices particularly rate and date of nitrogen application can greatly influence protein content. In Pendleton, where a spring application of nitrogen was applied to ensure the expression of protein the usually low protein lines, Hyslop and Yamhill responded by exceeding the protein level of Atlas 66 and NB 68513. The latter two lines did not appear to respond as their protein levels were actually lower at Pendleton than at the irrigated site at Madras. The large increase in protein content of Hyslop and Yamhill was due to a delay in maturity and a loss of moisture which resulted in shriveling of the grain in both varieties. Atlas 66 and NB 68513, both earlier maturing lines, were not influenced to the same degree.

Another approach for producing high yielding and high protein wheat cultivars may be $F_1$ hybrids. At the Madras site yields of $F_1$'s were close to or exceeded the highest parent while the protein content of $F_1$'s was near the mid-parent or close to the highest parent. If $F_1$'s can be economically produced then the wheat breeder can utilize both additive and non additive gene action for increasing protein content and yield in wheat.

# SUMMARY

Crosses were made between high protein cultivars (Atlas 66 and NB 68513) and low protein cultivars (Hyslop and Yamhill) and the performance of these parents as well as the $F_1$ and $F_2$ generations were studied at two locations in Oregon: Pendleton Experiment Station and Central Oregon experimental site at Madras. Data were obtained for protein content, grain yield, 50 kernel weight, kernels per spike, tillers per plant, along with plant height.

Significant differences were observed among and within crosses at both the Pendleton and Madras sites for most characters measured. The $F_1$ and $F_2$ mean values were found to be near the mid-parent of the two parents in all four crosses for plant height, 50 kernel weight and kernels per spike. There were several exceptions depending on the particular cross for tillers per plant and grain yield. Protein content mean values were also intermediate between the two parents for the $F_1$ and $F_2$ generations. In crosses involving Hyslop, the mean values tended to be near the highest parent. Little or no transgressive segregation was noted in the $F_2$ generation.

Evidence for non additive gene action was noted both for grain yield and tiller number in the $F_1$ and $F_2$ generations with the mean values exceeding the highest parent in all crosses for grain yield at the Pendleton site. Both tillers per plant and grain yield at Pendleton

also showed some degree of non additive gene action, but was dependent on the cross.

The high broad and narrow sense heritability estimates obtained both at Pendleton and Madras for all traits suggested that there is a large amount of genetic variation present for the characters studied. The narrow sense estimates further suggest that a high percentage of the total genetic variation was due to additive gene action.

Significant negative correlations were noted between protein content and grain yield including some of the components of yield. In evaluating the direct and indirect effects with path coefficient analysis, these negative associations were the result of the large negative indirect effects of 50 kernel weight and kernels per spike on protein content via grain yield at the Madras site. At the Pendleton site where moisture became a limiting factor, the negative association resulted largely as the indirect effect of 50 kernel weight on protein content through grain yield.

The large environmental influence on protein content was particularly striking at the Pendleton site. With the spring application of nitrogen, a delay in maturity of Hyslop and Yamhill was noted. With the subsequent loss of moisture, shriveled grain with a higher protein content resulted and hence a lower grain yield was realized.

Based on the performance of the mean values observed in the $F_2$ generations at the Madras site, yields were close to the highest parent whereas the protein content was near the mid-parent. Even though there was a negative relationship between protein content and grain yield at this location, it would appear that protein percentages can be increased by two to three percent through breeding without greatly influencing yield.

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# APPENDIX

# APPENDIX I

## Pedigrees and Descriptions of the Four Parental Lines

1. Yamhill (CI 14563) is a soft white, winter wheat developed from the cross 'Heines VIII'/Alba' (Redmond) at the Oregon Agricultural Experimental Station. It is mid-tall, stiff straw, high yielding cultivar with low grain protein content when grown under recommended cultural practices.

2. Hyslop (CI 14564) is a soft white winter wheat developed at the Oregon Agricultural Experimental Station from a cross between 'Nord Desprez' and Pullman Selection 101 (CI 13438) with an additional back cross to Pullman Selection 101. It is a semi-dwarf, stiff straw, high yielding cultivar with low grain protein content when grown under recommended cultural practices.

3. Atlas 66 (CI 12561) is an intermediate wheat developed from the cross Frondoso x (Redhart 3 x Noll 28) at North Carolina Agricultural Experiment Station. It is a tall, intermediate in yield cultivar with a stable protein content when grown under different environmental conditions.

4. NB 68513 (CI 10574) is a hard red winter wheat from the cross Warrior/Atlas 66/3/Comanche/CI 13348. It is a tall, intermediate in yield cultivar with high stable protein content when grown under different environmental conditions. It was developed at the Nebraska Agricultural Experiment Station.

Appendix Table 1. Some environmental factors associated with the two experimental sites.

| Location | Soil Type | Rainfall | Nitrogen Application | | Weed Control |
|---|---|---|---|---|---|
| Pendleton | Walla Walla silt loam | 474 mm | 60(1)* | 25(3)*** | Karmex .27 kg/ha |
| Madras | Madras loam | irrigated | 100(2)** | 40(3) | 2-4. D 1. 1 kg/ha |

* Fertilizer applied at planting time
** Fertilizer applied during tillering
*** Fertilizer applied at late boot stage

Appendix Table 2. Mean values of all entries at two locations for six characters.

| Character | Location | |
|---|---|---|
| | Pendleton | Madras |
| Plant height (cm) | 116.98 | 88.01 |
| Tillers per plant | 5.40 | 3.59 |
| Yield per plant (gm) | 6.86 | 5.10 |
| Protein content (%) | 13.29 | 15.48 |
| 50 kernel weight (gm) | 1.70 | 2.26 |
| Kernels per plant | 36.00 | 31.29 |