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Title : Possible Association Between Grain Protein Content and Yield as Influenced by Harvest Index and Biological Yield in Selected Hard Red Winter Wheat (*Triticum aestivum* L.) Crosses

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Grain yield and grain protein are often negatively associated in wheat. When yield increases and grain protein decreases, there can be an adverse effect on the milling and baking quality if the desired end product is bread flour. It has been suggested that this inverse association is the result of selecting for a higher harvest index (ratio of grain yield to total biomass), to enhance grain yield.

Parents, F1, F2, and F3 generations of three crosses and reciprocal backcrosses of one cross were space-planted to study the association of grain protein content with grain and biological yields, harvest index, and related traits. Selection P5221, a high protein selection, was a common parent in crosses with three different genotypes.

Differences were observed among generations within crosses for biological yield, grain yield, harvest index, grain protein content,

grain hardness, and protein yield. The coefficients of variation for the measured traits were low for the three crosses.

No associations between grain protein content and grain yield were observed in the populations studied. The largest association detected was between harvest index and grain protein. The r values ranged from -0.39 to -0.46, and rho was not different from -0.50 in two of the crosses. Path coefficient analyses revealed that this association was mostly due to the direct effect of harvest index on grain protein content, with little direct or indirect effect via other plant traits. In the cross P5221/ORCR 8313, biological yield exhibited a moderately large (0.64) direct effect on grain protein content; however this was offset by the negative indirect effect of tiller number. The R^2 of the path analyses were relatively small for the three crosses, indicating that most of the variation in grain protein content was not explained by the variables included in the analyses.

A possible negative association between grain protein content and harvest index, although moderate, suggests that selection for high yield should not be based on further increases of harvest index because grain protein could decrease.

POSSIBLE ASSOCIATION BETWEEN GRAIN PROTEIN CONTENT AND YIELD AS INFLUENCED BY HARVEST INDEX AND BIOLOGICAL YIELD IN SELECTED HARD RED WINTER WHEAT (*Triticum aestivum* L.) CROSSES

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Typed by Jose M. Costa

Dedicated to

my wife,

Gillian

my children,

Emilia and Daniel

and my father,

Jose Maria

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INTRODUCTION

Wheat growers in the Pacific Northwest region of the United States have historically grown predominantly soft white winter wheat cultivars. In this environment, grain yields are high and grain protein is low. The low protein content and other baking and milling properties of the resulting flour are excellent for end use products such as pastries. However, low grain protein adversely affects both the milling and baking properties of the wheat flour if bread is the desired end product.

Developing high yielding cultivars with acceptable bread-making quality is an objective of the Oregon State University wheat breeding and genetics program. If successful, it would provide the wheat growers in the region with an alternative to produce more than one market class of wheat. Thus becoming more competitive in both domestic and export markets.

It has frequently been suggested that the negative relation between grain yield and protein is in part the result of developing semi-dwarf wheat cultivars which have an increased harvest index. The objective of this investigation was to determine if there are associations between harvest index, biological yield, and other plant traits, with grain protein content in Hard Red Winter Wheat populations when grown in Oregon.

Results from this study would be useful in determining breeding strategies to develop cultivars which combine high grain yield and acceptable protein levels for bread flour when grown in this region.

REVIEW OF LITERATURE

Source of grain protein

Nitrogen (N) is absorbed through the roots mostly in the form of nitrate (NO_3^-) and to a lesser extent as ammonium ion (NH_4^+). Nitrate is reduced first to nitrite and then to ammonium in the presence of nitrate and nitrite reductase. The ammonium ion reacts with glutamic acid and Adenosine triphosphate (ATP) to form glutamine and Adenosine diphosphate (ADP). Then, glutamine reacts with α-ketoglutaric acid to form two glutamic acid molecules. One molecule of glutamic acid is used to form an amino-acid. While the other molecule of glutamic acid reacts with more ammonium ions. The amino-acids formed are later used for the synthesis of proteins at the ribosomes (Salisbury and Ross, 1985).

Almost 50% of the total leaf protein is Ribulose diphosphate (RUBP) carboxylase, which is responsible for CO_2 fixation in photosynthesis. When leaves senesce, leaf proteins are broken down by proteases into their constituent amino-acids which are then translocated to the grain (Dalling et al., 1976).

Storage proteins account for most of the endosperm proteins (70 to 80%), according to Forde and Mifflin (1983). The major storage proteins in wheat are the alcohol-soluble prolamins which are deposited in the starchy endosperm in protein bodies (Mifflin et al., 1983). The prolamins can be further subdivided into gliadins and glutenins. These are the main constituents responsible for the bread baking quality of wheat flour (Finney et al., 1987).

Influence of the environment on grain protein concentration

The environment usually causes the largest variation in grain protein (Kramer, 1979; McNeal, 1982). Main environmental factors are: a) fertilizer, b) water availability, and c) temperature (Campbell and Davidson, 1979).

High yield and high protein, can be obtained with high nutrient availability as shown by Morris and Paulsen (1985) and Spiertz and Ellen (1978). At very low fertility levels, grain yields increase linearly with added N and protein remains unchanged. With added N, grain yields level off, but a higher grain protein percentage is achieved (Kramer,1979).

Nitrogen fertilization usually affects the percentage of grain protein indirectly by increasing grain yield. A larger grain biomass produces a "dilution" effect on the amount of N assimilated, thus lowering grain protein content (Campbell and Davidson, 1979).

Terman et al. (1969) observed that the effect of applied N with adequate moisture was to increase grain yield, but when water was limited the main effect of N was to increase protein content. They also noted that in dryland experiments, both yield and protein increased in response to applied N. When no grain yield response occurred, added N increased protein content. The effect of soil moisture stress depends on the stage of growth and relative level of N and temperature. After anthesis, water stress increased grain protein by reducing grain yield (Campbell and Davidson, 1979). Furthermore, they observed that the most important environmental factor affecting grain protein in their experiments was temperature. At high temperature (27^{0} C) during the day, grain protein increased and grain yield decreased. They concluded that protein synthesis is more enhanced than starch synthesis at high temperatures. Bhullar and Jenner (1985) observed that high temperatures during grain filling reduce starch accumulation, while N content is not usually affected. During the grain filling period, the proportion of protein relative to starch increased as temperatures rose from 15 to 30^0 C (Spiertz, 1977). Sofield et al. (1977) observed that the N content and dry weight of the grain increased linearly during the grain growth period. The percentage of grain N, however, fell sharply during the first few days after anthesis, but rose progressively thereafter. They also observed that the higher the temperature, the higher the percentage of N in the grain of the four cultivars studied. They concluded that the increase in protein percentage with higher temperatures was the result of the reduction in starch content of the grain, rather than a change in the quantity of N.

Grain yield vs. protein percentage

High grain yields usually mean lower grain protein, as yield is often negatively associated with protein percentage (McNeal et al., 1982; Loffler et al., 1985).

Bioenergetic considerations show that the synthesis of protein and carbohydrates are opposed to each other (Bhatia and Rabson, 1976). Penning de Vries et al. (1974) concluded that in plants under aerobic conditions, one gram of glucose can be used to produce 0.83 g of carbohydrates, or alternatively 0.40 g of proteins (assuming nitrate to be the N source).

Some successes in breaking this negative relation have been obtained, as shown by the release of the cultivar "Lancota" which was derived from the high protein cultivar Atlas 66. Lancota out-yielded the check cultivar "Centurk", and contained about 15% more protein (Schimdt et al., 1979).

Influence of harvest index on grain protein

The inverse association between yield and protein in modern wheat cultivars could be explained by increased grain yield with no change in total aboveground biomass as noted by Austin et al., 1980. They observed that newer cultivars of winter wheat out-yielded the older cultivars by 40% when grown in similar conditions. The yield increase in modern cultivars was associated with a greater harvest index, as total dry matter production was similar. They predicted that breeding for a still higher harvest index could prove difficult, and emphasized the need to detect and exploit genetic variability for total biomass. It was further noted that the newer semi-dwarf cultivars out-yielded the older tall ones. In their experiment, lodging, especially for the tall cultivars, was prevented by the use of nets. The older cultivars had higher grain protein, although the total grain N amount per plant was greater in modern cultivars. They suggested that N uptake is not keeping up with the larger amount of carbohydrates in the grain of modern cultivars resulting in lower grain protein percentage.

A significant negative correlation of 0.54 between grain protein and harvest index in randomly derived lines from crosses of spring wheat was reported by Loffler and Busch (1982). A non significant correlation between grain protein and biological yield was observed. McNeal et al. (1972) also observed a moderately large association between grain protein percentage and harvest index among F4 lines, ranging from -0.64 to -0.71.

Three isogenic lines of "Centana", representing tall, intermediate, and short plant heights were compared by McNeal et al. (1971). The short isoline had lower biological yield, higher harvest index and less protein translocated to the grain. Protein decreased as harvest index increased. They suggested that the amount of above-ground growth is important for the final protein content of the grain.

Modern semi-dwarf wheat cultivars have a larger sink than old cultivars (Waddington et al., 1986; Pepe and Heiner, 1975). McNeal and Davis (1966) noted that the later kernels formed from the top third of the spike had lower protein than those from the middle and bottom part of the spike. Thus, N may become limiting in maintaining the protein content of the later formed kernels in modern cultivars. The negative association between harvest index and grain protein could be the result of a larger sink in modern cultivars (Bhatia, 1975). He suggested that when the nitrogenous materials from the leaves are translocated to a small sink (low harvest index plant), high protein can be achieved. When the sink is large (high harvest index plant), protein percentage will be low.

Height and grain protein, however, were not associated in randomly derived F5 lines from a cross of hard red spring wheat (Pepe and Heiner, 1975). Stuber et al. (1962), found that there were no associations of grain protein with plant height, tiller number, flowering date and grain yield in a winter wheat cross involving Atlas 66.

Loffler et al. (1985), examined the association among traits using stepwise regression. The final regression model for predicting grain protein included harvest index, biological yield, N harvest index and total N at maturity. These variables accounted for virtually all of the variation among genotypes. Both N harvest index and total N at maturity had positive coefficients, while both harvest index and biological yield had negative coefficients in the regression equation.

Mechanisms for higher grain protein

Dalling (1985) suggested that there are three ways to improve grain protein: a) increase N accumulation during vegetative growth, b) higher N uptake after anthesis, and c) increase efficiency of redistribution of N present in the plant.

Vegetative growth before heading is apparently the most important source of grain protein. Austin et al. (1977), tested 47 wheat genotypes and reported that at anthesis, plants contained 83% of the total N present at maturity. Also that the grain at maturity had 68% of the total N in the plant. They found a strong positive correlation between dry matter accumulation and plant N content. Differences in plant metabolism which caused variation in plant weight, appeared to cause changes in N uptake. They concluded that this occurred because both carbon assimilation and nitrate reduction depend on energy made available from chloroplasts. Assimilate is also required to sustain the growth of roots, which is necessary for continued N uptake. Klepper

(1974) also postulated that high yielding, high protein wheats required enough photosynthetic capacity to provide energy to reduce CO2 and NO3. Cox et al. (1985) observed that 82% of the total N found at maturity was already present at anthesis. Although they did not detect an association between N assimilation prior to anthesis with protein content in randomly derived F5 lines of spring wheat. Van Sanford and MacKown (1987) observed that approximately 83% of the N at maturity was already present in the plant at anthesis in soft red winter wheat cultivars. Only 17% of the grain protein was provided by N uptake after anthesis.

Uptake of N during grain filling can be considered as a function of available soil N at this growth stage and the capacity of the roots to absorb and translocate to the shoot (Dalling, 1985). There seems to be considerable variation for N uptake during grain filling period. Austin et al. (1977) detected large genotypic differences under non limiting conditions of soil N, while McNeal et al. (1966) compared N accumulation in five spring wheat cultivars and observed only a limited uptake of N during grain filling period. This reduced N uptake could result from low soil fertility (Dalling, 1985). In environments where post-anthesis supply of N was low, the redistribution of N from vegetative parts contributed more than 80% of the grain N.

Redistribution of N from the vegetative organs accounts for at least 50% of grain protein, even under high post-anthesis N level (Ellen and Spiertz, 1978). Dalling et al. (1976) observed different translocation efficiencies from the different organs of the plant. Roots redistributed between 21 to 29% of the N while in the leaves nearly 80 %

of the N present at anthesis was removed at maturity. The translocation efficiency of the stems was 65%. They further noted that the roots offer potential for improvement. Apparently, applications of kinetin (cytokinin) during grain filling may increase N remobilization from the roots thus improving grain protein content (Dalling, 1985).

Bhatia et al. (1978) postulated that the "high grain protein" character is a complex trait affected by several factors. Nitrogen uptake and N harvest index were found to be the components of the high protein character.

The N economy of wheat has not been clearly elucidated as shown by reported N losses. Boatwright and Haas (1961) and also Daigger et al. (1976) reported losses of N and dry matter from anthesis to maturity. Smith et al. (1983) did not find N losses, but suggested that they may have occurred and been compensated by N uptake after anthesis. Kinsley et al. (1957) and Goatley and Lewis (1966) observed significant quantities of N present in the guttation fluids of wheat. Hooker et al. (1980) noted that volatilization of NH3 from plant tissue could partially account for the deficits in total N accumulation observed in plant tissue following flowering.

Inheritance of grain protein

Middleton et al. (1954) reported that cultivars which had "Fronteira" or "Frondoso" from Brazil in their parentage such as "Atlas 66" usually had high grain protein percentages. Chromosome 5D of Atlas 66 carries a major gene for grain protein and chromosome 5A carries a gene or genes with a lesser effect on grain protein (Morris et al.

1978). Law et al. (1978) showed that the genetic control of grain protein in Atlas 66 was governed by two genes: "Prol" and "Pro2", which were postulated to act independently of carbohydrate production. "Prol" was located on the long arm of chromosome 5D. While "Pro2" was not closely linked to "Prol" and was thought to be located on the short arm of 5D.

The presence of major genes controlling grain protein with minor genes affecting the intensity of expression was reported by Halloran (1975). Presence of minor genes controlling grain protein was also found by Klepper (1975), as high protein lines were obtained from crosses between parents with intermediate protein percentage.

The USA wheat collection was screened at the University of Nebraska (Johnson and Mattern, 1979), and genetic differences of at least five percentage points were found. They identified the cultivar "Nap Hal" as a source of high protein. Lines derived from Nap Hal have shown yields similar to the check cultivars but with higher protein percentage. This indicated that it is possible to raise grain protein content without reducing grain yield (Rodriguez, 1984).

The cultivar "Plainsman V" is another source of high grain protein (Johnson et al., 1979). Its high protein genes have been successfully transferred from Aegilops ovata (goatgrass), according to Johnson et al. (1979). Recently, Stein et al. (1988) suggested that the high protein genes of Plainsman V were located on chromosomes 1A, 1B and 7A chromosomes.

Genes for high protein apparently influence wheat N nutrition (Day et al., 1985). Differences in N harvest index (ratio of grain N to total plant N) were responsible for the high grain protein percentage of the cultivars "Lancota" and Plainsman V. Efficient N translocation was highly correlated with grain protein percentage and was independent of plant stature. Other studies, however, have revealed no association between N harvest index and grain protein content (Cox et al., 1986).

Heritability estimates of grain protein percentage are usually low or intermediate when means of early generations (F3 to F5) are used. Davis et al. (1961) found intermediate broad sense heritability estimates ranging between 54 to 69% in four populations of winter wheat derived from Atlas 66. Sampson et al. (1983) reported estimates of heritability in standard units of 0.25 to 0.50 in crosses of spring wheat. In winter wheat, Lofgren et al. (1968), and Corpuz et al. (1983) reported similar values of heritability in standard units ranging from 0.16 to as high as 0.73.

When single plant data from F2 were regressed on F3 means, Sunderman et al. (1965) observed broad sense heritability estimates ranging from as low as 0.16 to 0.25 in winter wheat. Haunold et al. (1962), working with different populations, observed intermediate values for single plants of winter wheat ranging between 0.42 to 0.58.

Narrow sense heritability estimates of grain protein have ranged from low (Haunold et al., 1962) to high (Stuber et al.,1962; Schumaker,1980).

Additive gene action has been postulated for grain protein by many authors in spring wheat (Chapman and McNeal, 1970; Halloran, 1981; Sampson et al., 1983) and also in winter wheat (Corpuz et al., 1983).

Partial dominance for low protein has also been observed in spring wheat (Chapman and McNeal, 1970; Halloran, 1981).

Transgressive segregation in the F2 populations has been observed many times in winter wheat (Corpuz et al., 1983; Johnson et al., 1973; Stuber et al., 1962) and in a spring by winter wheat cross (Schumaker, 1980).

Association of grain protein content with seed characters

A positive association between grain protein content and kernel hardness has been postulated (Sampson et al., 1983). However, genetic studies have shown no association between these traits (Davis et al., 1961; Trupp, 1976; Sampson et al., 1983; Lorenzo, 1985). A slight environmental influence was reported by Trupp (1976). He observed that when protein increased, kernel texture became harder.

A single gene was detected in the variety "Cheyenne" by Mattern et al. (1973) determining grain hardness. It was designated "Ha" and located in the short arm of the chromosome 5D (Law et al., 1978). Baker (1977) stated that one or two major genes were acting to determine kernel hardness in spring wheat, depending on the parents crossed. The presence of a polypeptide of approximate molecular weight of 15,000 in the endosperm appears to play an important role in determining endosperm softness (Greenwell and Schonfield, 1986). Sulfur deficiency usually increases kernel hardness and reduces the level of this low molecular weight polypeptide (Castle and Randall, 1987). Estimates of broad sense heritability of grain hardness are usually high, Sampson et al. (1983) observed values ranging between 0.55 to 0.92. Schumaker (1980) found a high narrow sense heritability (0.90) in a cross between a soft and a hard wheat.

No association between grain protein percentage and kernel color was detected by Corpuz et al. (1983) in a cross between the high protein hard red winter wheat Plainsman V with a hard white winter line (KS75216). This is not surprising as the kernel color genes are located on chromosomes 3A, 3B, and 3D while the high protein genes of Plainsman V have been located on 1A, 1B and 7A (Stein et al., 1988).

Selection schemes

Some researchers have suggested using protein yield (protein percentage multiplied by grain yield) as selection criterion instead of protein percentage to increase grain yield and stabilize grain protein. McNeal et al. (1982) compared lines selected for protein percentage with a different group of lines selected for protein yield. The lines selected by protein percentage had protein yields similar to the parents, but lower grain yields. Lines selected for protein yield were high yielding and had intermediate protein percentages. They suggested that protein yield would be a better selection criterion than protein percentage to obtain high yielding lines with acceptable protein percentage levels. Loffler and Busch (1982), also compared these selection criteria in spring wheat. Selection for protein percentage decreased grain yield. Selection for protein yield increased grain yield but in some populations it decreased grain protein percentage. Nitrogen harvest index was the best selection criteria to improve both grain yield and protein percentage.

MATERIALS AND METHODS

Experimental procedures

Four selections and a cultivar representing Hard Red Winter Wheat were used as parental material. These included: ORCR 8601, ORCR 8313, P5221, and Centura. This material was selected based on their morphological differences for the traits of interest. Selection P5221 was the common parent crossed with the other three genotypes. Pedigrees and descriptions of the cultivar and selections are shown in Appendix Table 1.

Parents, F1, F2, and F3 generations of the three crosses were spaced-planted in the field at the Crop Science Field Laboratory on October 10, 1986. Reciprocal backcross generations were also obtained for the cross P5221/ORCR 8601. The experiment was planted as a split-plot, randomized complete block design with three replications. Crosses were the main plots and generations the subplots. Each cross was analyzed separately as a randomized block. Individual sub-plots of the parents, F1's and F3's consisted of a one meter row with 10 seeds planted per row. The F2 seed was planted in 10 rows with 10 seeds planted per row. Three rows with 10 seeds per row were used for the backcross populations. The planting distance was 10 cm between plants and 30 cm between rows. Barley was planted as a border to reduce competition effects.

The soil type at the experimental site is a fine, silty mixed mesic Aquultic Argixeroll. Prior to planting, 40 kg ha^{-1} of N and 6 kg ha^{-1} of sulfur were applied. A total of 150 kg N ha^{-1} and 30 kg S ha^{-1} was later applied in the form of 30-0-0-6 fertilizer in three split applications made at the following growth stages: tillering (stage 4), jointing (stage 8), and heading (stage 10.3). The Feekes growth stage is shown in parenthesis.

Weeds were controlled with a fall application of 1.68 kg a.i. ha^{-1} of Diuron. Plants were protected from foliar diseases by four applications of the fungicide Propiconazole used at the rate of 0.23 kg a.i. ha^{-1}.

The following measurements were collected from individual plants:

a) Heading date: Number of days from January 1 to the date when approximately 50% of the spikes had emerged.

b) Maturity date: Number of days from January 1 to the date when approximately 50% of the glumes had turned yellow.

c) Grain filling period: Number of days between heading date and maturity.

d) Number of fertile tillers: spikes per plant were counted at maturity.

e) Plant height: distance (cm) from the base of the culm to the tip of the spike (awns excluded) of the tallest tiller.

f) Biological yield: weight (g) of the whole mature plant, excluding the roots.

h) Grain yield: weight (g) of all the kernels from a plant. Plants which yielded less than 10 grams of grain were discarded.

i) Harvest index: Grain yield divided by biological yield and multiplied by 100.

g) Kernel weight: weight (g) of individual kernels, determined from a sample of 200 kernels from an individual plant.

j) Grain protein content and grain hardness: determined by near infrared reflectance spectroscopy with a Technicon Infralyser 400 from approximately 10 g of whole-meal flour obtained from a Udy flour mill with a 0.5 mm mesh sieve. Grain protein content was expressed on a dry weight basis.

Analytical procedures

a) Analysis of variance of generation means for each trait was used to analyze the data. Fisher's protected LSD Test was used to detect significant differences among mean values.

b) Broad sense heritability estimates for plant and seed traits were calculated for each cross, using the variance of the parents and the F1 as a measure of environmental variance, and the F2 variance as a measure of both environmental and genetic variance (Allard, 1960).

c) Narrow sense heritability estimates were also calculated for the same traits in the cross P5221/ORCR 8601, using the variance of the F2 and the backcross generations to calculate the additive genetic component of variance (Warner, 1952).

d) Expected gain from selection (G.S.) was calculated for the P5221/ORCR 8601 cross following the method proposed by Allard (1960), using k=2.06 (most desirable 5% of the F2 plants).

e) Phenotypic correlations were used to estimate associations among traits for each cross, utilizing F2 individual plant data. Confidence intervals for the phenotypic correlations (Snedecor and Cochran, 1980) were determined for the association between grain protein content and harvest index. Also the hypothesis that this correlation was -0.50 was tested using the method described by Snedecor and Cochran (1980).

f) Path coefficient analyses using phenotypic correlations (Li, 1956) and the procedure regression from the SAS statistical program, were utilized to determine the direct and indirect effects of plant traits on grain protein content for each cross. The selection of variables was done with the stepwise procedure, and the traits that were significant at the 15% probability level were included in the analysis.

RESULTS

The results presented in this section will focus on the following selected traits: a) biological yield, b) grain yield, c) harvest index, d) grain hardness, e) grain protein content, and f) protein yield. These traits were measured on an individual plant basis for the parents, F1, F2, and F3 generations of three crosses involving Selection P5221 when crossed to three other Hard Red Winter Wheat parental lines. In the cross P5221/ORCR 8601, the backcross generations were also evaluated.

Analysis of variance

Analyses of variance were conducted to test for differences among generations for the traits measured in each cross.

Differences were observed among generations for cross P5221/ORCR 8601 for all six traits (Table 1). The coefficients of variation ranged from intermediate for biological yield (9.81%), grain yield (8.43%) and protein yield (8.36%) to low for grain hardness (4.30%), harvest index (2.96%) and grain protein content (1.68%).

For cross P5221/Centura, differences were observed among generations for all six traits (Table 2). Intermediate coefficients of variation were noted for protein yield (10.81%), grain yield (9.87%), biological yield (8.79%), and harvest index (6.16%). These were low for hardness (4.46%) and protein content (2.31%).

From Table 3, differences can be noted among generations for all selected traits with the exception of protein yield for the cross

Table 1. Observed mean squares for six agronomic traits involving parents, F1, F2, F3, and reciprocal backcross generations from the cross P5221 / ORCR 8601, grown at the Crop Science Field Laboratory, 1987.

Source of variation	d.f.	Biological yield (g)	Grain yield (g)	Harvest index (%)	Grain hardness	Protein content (gkg^{-1})	Protein yield (g)
Generations	6	453.16**	293.98**	40.30**	200.36**	0.22*	575.78**
Replications	2	380.33	84.06	61.47	2506.21	0.27	214.55
Error	12	50.78	31.85	0.75	23.01	0.06	69.52
Total	20						
C.V.		9.81	8.43	2.96	4.30	1.68	8.36

* and ** indicate 5% and 1% significance levels, respectively.

Table 2. Observed mean squares for six traits involving parents, F1, F2, and F3 generations from the cross P5221 / Centura, grown at the Crop Science Field Laboratory, 1987.

Source of variation	d.f.	Biological yield (g)	Grain yield (g)	Harvest index (%)	Grain hardness	Protein content (gkg^{-1})	Protein yield (g)
Generations	4	377.83**	392.61**	30.43**	373.15**	10.22**	1148.15**
Replications	2	102.20	77.42	39.27	3404.43	38.09	674.25
Error	8	36.78	45.54	3.68	23.48	1.24	127.86
Total	14						
C.V.		8.79	9.87	6.16	4.46	2.31	10.81

* and ** indicate 5% and 1% significance levels, respectively.

Table 3. Observed mean squares for six agronomic traits involving parents, F1, F2, and F3 generations from the cross P5221 / ORCR 8313, grown at Crop Science Field Laboratory, 1987.

Source of variation	d.f.	Biological yield (g)	Grain yield (g)	Harvest index (%)	Grain hardness	Protein content (gkg^{-1})	Protein yield (g)
Generations	4	144.93*	177.33*	43.43**	318.20**	1.20**	286.63
Replications	2	286.07	287.45	0.80	2509.88	0.45	870.52
Error	8	32.48	45.11	4.13	7.99	0.15	89.50
Total	14						
C.V.		8.83	9.99	6.20	2.83	2.56	9.38

* and ** indicate 5% and 1% significance levels, respectively.

P5221/ ORCR 8313. Coefficients of variation were intermediate for grain yield (9.99%), protein yield (9.38%), biological yield (8.83%) and harvest index (6.20%). Values were low for grain hardness (2.83%) and protein content (2.56%).

When the selected traits are considered among crosses, differences among generations were noted for all selected traits, with the only exception of protein yield in the cross P5221/ORCR 8313. Coefficients of variation were intermediate to low. Protein yield, biological yield and grain yield usually had the highest coefficients, while harvest index had intermediate to low coefficients. Grain protein content and grain hardness had the lowest coefficient of variation values.

Observed mean squares for the additional traits measured from the crosses P5221/ORCR 8601; P5221/Centura; and P5221/ORCR 8313 are presented in Appendix Table 2, 3, and 4, respectively.

Separation of means

Mean values within crosses were analyzed using the Fisher's protected LSD test (FPLSD) to determine if differences existed for the traits measured among generations.

Generation means of the selected traits for the cross P5221/ORCR 8601 are shown in Table 4. In Table 5 the generation means for the cross P5221/Centura are found. Generation means for the cross P5221/ORCR 8313 are presented in Table 6. The FPLSD test was not carried out for protein yield in cross P5221/ORCR 8313, as there were no differences for this trait.

Table 4. Mean values for parents and five resulting generations for six agronomic traits for the cross P5221 / ORCR 8601 using Fisher's protected LSD (FPLSD).

Generation	Biological yield (g)	Grain yield (g)	Harvest index (%)	Grain hardness	Protein content (gkg^{-1})	Protein yield (g)
P5221	50.0c	16.9c	33.8a	106.1bcd	148.2bc	2.5d
ORCR 8601	85.3a	19.6bc	23.0c	127.2a	148.4bc	2.9cd
F1	81.0a	27.1a	33.5a	105.9cd	144.3c	3.9a
F2	80.0a	22.3b	27.9b	114.6b	153.3a	3.4b
F3	74.0ab	21.1b	28.5b	112.0bc	148.8ab	3.1bc
BC/P5221	62.7bc	20.2b	32.2a	102.4d	149.8ab	3.0bc
BC/ORCR 8601	75.3ab	21.1b	28.0b	112.8bc	150.3ab	3.2bc

Generation means displaying the same letter on the same column are not significantly different at the 5% probability level.

Table 5. Mean values for parents and three resulting generations for six agronomic traits for the cross P5221 / Centura using Fisher's protected LSD (FPLSD).

Generation	Biological yield (g)	Grain yield (g)	Harvest index (%)	Grain hardness	Protein content (gkg^{-1})	Protein yield (g)
P5221	57.7c	21.1ab	36.0a	94.4c	148.2b	3.1b
Centura	69.7b	19.3b	27.3c	124.6a	159.2a	3.1b
F1	87.3a	27.8a	31.7b	112.8b	157.9a	4.4a
F2	67.3bc	21.2b	31.0b	106.7b	146.1b	3.1b
F3	63.0bc	18.8b	29.7bc	104.2b	150.9b	2.8b

Generation means displaying the same letter on the same column are not significantly different at the 5% probability level.

Table 6. Mean values for parents and three resulting generations for six agronomic traits of the cross P5221 / ORCR 8313 using Fisher's protected LSD (FPLSD).

Generation	Biological yield (g)	Grain yield (g)	Harvest index (%)	Grain hardness	Protein content (gkg^{-1})	Protein yield[1] (g)
P5221	52.7b	19.9b	37.3a	90.8c	142.9b	2.8
ORCR 8313	68.0a	19.1b	28.0ab	116.6a	157.4b	3.0
F1	70.7a	25.2a	35.7ab	102.3b	144.1b	3.6
F2	66.0a	21.8ab	32.7bc	95.1c	152.0b	3.3
F3	65.3a	20.3b	30.3cd	94.2c	153.9a	3.1

Generation means displaying the same letter on the same column are not significantly different at the 5% probability level.

(1) indicates that FPLSD was not conducted, as means were not statistically different.

Biological yield of P5221 was lower than for the other parents in the three crosses. The F1, F2, and F3 values were similar to the highest parent in the crosses P5221/ORCR 8601 and P5221/ORCR 8313. However, in the cross P5221/Centura, the F1 value was higher than the highest parent and the resulting generations. It can also be noted that the mean values for biological yield of the backcrosses were skewed towards the value of the recurrent parent.

When grain yield is considered, the F1 mean values were greater than that of either parent and of the segregating generations, with the exception of the F2 of the cross P5221/ORCR 8313 which was similar to the F1 value.

P5221 had a higher harvest index than the other parents in each of the crosses. The F1 values were similar to those of P5221, except for the cross P5221/Centura, in which the F1 approached the mid-parental value.

When grain hardness is considered, P5221 had a softer kernel texture than the other parental genotypes. The F1 values were close to the mid-parental value, except for the F1 value of the cross P5221/ORCR 8601 which was similar to the softer parent's value. The backcrosses tended to approach the value of their recurrent parent.

Mean values of grain protein content for the different generations did not show a consistent pattern among crosses. In the cross P5221/ORCR 8601, the parents were similar, while the F1 was below the mid-parental value. A difference was noted for the F2 mean of this cross which was higher than that of the F1 and both parents. The mean of the F1 generation was as low as the lower parent (P5221) in the cross

P5221/ORCR 8313. The F2 mean value for this cross was as high as that of the high parent. An opposite situation was observed for the cross P5221/Centura, as the mean of the F1 was as high as the mean of the high parent, but the F2 mean was similar to the mean of the lower parent.

Differences of protein yield mean values among generations mainly followed changes in grain yield. Values were higher for the F1 than for both parents in the crosses P5221/ORCR 8601 and P5221/Centura. The F1 mean was also higher than that of the parents in the cross P5221/ORCR 8313, although differences were not statistically significant.

Appendix Tables 5, 6, and 7 show the separation of means for the other traits measured.

Means, and standard deviations for the crosses P5221/ORCR 8601, P5221/Centura, and P5221/ORCR 8313 are presented in Appendix Tables 8, 9, and 10, respectively.

The standard deviations for grain protein content of the three crosses were similar. The standard deviations of the uniform generations (parental and F1) were relatively smaller only for the cross P5221/ORCR 8601. In the other two crosses, the standard deviation of the uniform generations were closer to the value of the F2. The F1 P5221/Centura even showed a larger standard deviation than the F2 for this trait.

Frequency distribution of grain protein content

Frequency distributions and standard deviations of grain protein values for the parental, F1, backcrosses (only for cross P5221/ORCR 8601), and F2 generations are presented for each cross in Tables 7, 8,

Table 7. Frequency distribution and standard deviations (S.D.) of grain protein content for the parental, F1, F2, and backcross generations of the cross P5221 / ORCR 8601.

	Grain Protein* (gKg^{-1})											
	105	115	125	135	145	155	165	175	185	195	205	215	S.D.
Generation	Number of plants per class												
P5221				2	11	6	1						6.2
ORCR 8601				2	8	9							7.7
F1				5	17	2							5.0
F2		1	10	38	53	78	38	17	9	1			14.3
BC/P5221				13	24	16	7	5					11.7
BC/ORCR 8601			3	5	23	12	2	3			1		12.6

*: Mid class values.

Table 8. Frequency distribution and standard deviations (S.D.) of grain protein content for the parental, F1, and F2 generations of the cross P5221 / Centura.

	Grain Protein* (gKg^{-1})											
	105	115	125	135	145	155	165	175	185	195	205	215	S.D.
Generation	Number of plants per class												
P5221				6	7	5	2						9.3
Centura				1	3	8	6	5	1				12.0
F1			1	1	2	3	6			1			16.3
F2	1	6	31	70	79	54	31	5	7		1	1	15.3

*: Mid class values.

and 9. Normal distributions were observed in the F2 generations of the three crosses. Transgressive segregation was also noted in the F2 for both low and high protein content. The cross P5221/Centura exhibited more transgressive segregants than the other two crosses.

Broad sense heritability

Broad sense heritability estimates for the six selected traits of the three crosses are presented in Table 10.

Heritability estimates for biological yield ranged from a low of 41% for cross P5221/Centura to moderate in the cross P5221/ORCR 8601 (59%) and P5221/ORCR 8313 (61%). Grain yield heritability estimates showed the same pattern among crosses as it was low for cross P5221/Centura, and moderate for the other two crosses. Heritability estimates for harvest index were moderate, with the exception of the low value (30%) for cross P5221/Centura. Grain hardness heritability estimates ranged from low (44%) in the cross P5221/ORCR 8601 to very low (13%) in the cross P5221/Centura. Grain protein content heritability estimates ranged from the moderate value of 56% in the cross P5221/ORCR 8601 to moderately low in the other two crosses. Protein yield heritability estimates were low (34%) for cross P5221/Centura, and moderate (59%) in the other two crosses.

When crosses are compared, it was noted that the broad sense estimates were consistently higher for crosses P5221/ORCR 8601 and P5221/ORCR 8313, in contrast with the consistently low estimates for the cross P5221/Centura.

Table 9. Frequency distribution and standard deviations (S.D.) of grain protein content for the parental, F1, and F2 generations of the cross P5221 / ORCR 8313.

	Grain Protein* (gKg^{-1})												
	105	115	125	135	145	155	165	175	185	195	205	215	S.D.
Generation	Number of plants per class												
P5221			1	4	9	4							7.7
ORCR 8313			1	1	4	5	5	3	1				13.9
F1		2		3	5	6							12.7
F2		3	19	41	67	55	46	22	5	5			15.6

*: Mid class values.

Table 10. Broad sense heritability estimates for six selected traits from the parental, F1 and F2 generations of the three crosses.

	Broad sense heritability (%)		
	Cross		
Traits	P5221 / ORCR 8601	P5221 / Centura	P5221 / ORCR 8313
Biological yield	59	41	61
Grain yield	57	39	56
Harvest index	56	30	46
Grain Hardness	44	13	31
Protein content	56	29	43
Protein yield	59	34	59

Broad sense heritability estimates for the rest of the measured traits are presented in Appendix Table 11.

Narrow sense heritability

Narrow sense heritability estimates and expected genetic advance for the cross P5221/ORCR 8601 are displayed in Table 11.

These heritability estimates were moderate to low for all traits, with the lowest estimate observed for harvest index which was only 5%.

The highest narrow sense heritability estimate were observed for biological yield (66%), grain hardness (65%), and protein yield (65%). Narrow sense heritability estimates for these traits were larger than the broad sense heritability estimates.

Narrow sense estimates for the other measured traits are displayed in Appendix Table 12.

Genetic advance

Estimates of the expected gain from selection for the six selected traits are also presented in Table 11.

The largest genetic gain were predicted for biological yield (41.87%), and grain hardness (34.41%), while the lowest predicted genetic gains were for protein yield (1.87%) and harvest index (0.61%). Predicted gain for grain yield was low. Even though the narrow sense heritability estimate for grain protein content was low (28%), predicted genetic gain for this trait showed a moderate 8.25%. Protein yield, in contrast, had a higher narrow sense heritability estimate (39%), but a much lower predicted gain (1.87%).

Table 11. Narrow sense heritability (Hns) estimates and expected genetic advance for six traits from the F2 and the two backcross generations for the cross P5221 / ORCR 8601.

Traits	Hns (%)	G.S.* (%)
Biological yield	66	41.87
Grain yield	29	5.30
Harvest index	5	0.61
Grain hardness	65	34.41
Protein content	28	8.25
Protein yield	65	1.87

* Genetic advance (G.S.) represents the expected percent increase in the F3 above the F2 mean when the best 5% of the F2 plants are selected.

Appendix Table 12 also shows the estimates of genetic advance for the rest of the measured traits.

Association between grain protein content and selected traits

The phenotypic correlation coefficients between grain protein content and six traits in the F2 generation were low for all variables with the exception of the moderate negative value with harvest index (Table 12). The negative association with harvest index was very similar among crosses, as the coefficients ranged from -0.39 in the cross P5221/Centura to -0.46 in the cross P5221/ORCR 8601. The positive correlation with biological yield was significant but of low magnitude in the crosses P5221/Centura and P5221/ORCR 8313, and non significant for the cross P5221/ORCR 8601. Coefficients with grain yield among crosses were all very low and not significantly different from zero. Correlations with grain hardness ranged from the low negative value (-0.31) of the cross P5221/ORCR 8313 to a low positive value (0.25) for the cross P5221/Centura. The correlations with protein yield and also with grain filling period followed a similar pattern as with biological yield: they were significant, but low for the crosses P5221/Centura and P5221/ORCR 8313, while not being significantly different from zero in the cross P5221/ORCR 8601.

Confidence intervals were calculated for the correlation coefficients between grain protein content and harvest index, and are presented in Table 13. Also in Table 13, the normal deviates for the test that ρ was not significantly different from -0.50 are shown.

Table 12. Phenotypic correlation coefficients between grain protein content and five traits measured in the F2 progeny of three crosses.

	Cross		
	P5221 / ORCR 8601	P5221 / Centura	P5221 / ORCR 8313
Protein content and			
Biological yield	0.12	0.20**	0.18**
Grain yield	-0.13	0.03	0.01
Harvest index	-0.46**	-0.39**	-0.42**
Grain Hardness	0.13	0.25**	-0.31**
Protein yield	0.09	0.27**	0.23**
Number of plants	245	286	263

**: Indicates significantly different from zero at the 1% probability level.

Table 13. Confidence limits of the value of rho (ρ), between grain protein content and harvest index obtained from the r values in each cross, and normal deviates resulting from testing ρ to be -0.50.

Cross	Observed correlation coefficient	Confidence limits[1] of ρ	Normal deviate
P5221/ORCR8601	-0.46	$-0.32 \leq \rho \leq -0.58$	0.81
P5521/Centura	-0.39	$-0.25 \leq \rho \leq -0.51$	2.32*
P5221/ORCR8313	-0.42	$-0.28 \leq \rho \leq -0.54$	1.62

[1] 99% confidence interval.

*: significantly different at the 5 % probability level.

This test suggests that for crosses P5221/ORCR 8601 and P5221/ORCR 8313, the correlations are not significantly different from -0.50. For the cross P5221/Centura, with an observed r value of -0.39, ρ was found to be significantly different from -0.50 at the five percent probability level.

Appendix Table 13 shows the phenotypic correlation coefficients between grain protein content and the rest of the traits measured. Phenotypic correlation coefficients among all measured traits for each cross are displayed in Appendix Tables 14, 15, and 16.

Path coefficient analyses showing the direct and indirect effects of selected traits on grain protein content were performed for the three crosses. Results of the path coefficient analyses for the crosses P5221/ORCR 8601, P5221/Centura, and P5221/ORCR 8313 are presented in Tables 14, 15, and 16, respectively. In the three crosses, the association between grain protein content and harvest index was almost completely determined by the direct effect of harvest index. In the cross P5221/ORCR 8313, a large direct effect of biological yield on grain protein content was observed, while tiller number and harvest index had moderate direct effects on protein content. The r value between grain protein content and biological yield appeared to be affected by the negative indirect effect of tiller number. The association between tiller number and grain protein content was also apparently reduced by the indirect effect of biological yield.

The R^2 values of the path coefficient analyses were very low for the crosses P5221/ORCR 8601 and P5221/Centura. The R^2 was larger for the cross P5221/ORCR 8313, although it only explained 39% of the

Table 14. Path coefficient analyses of the direct and indirect effects of harvest index, plant height and kernel weight on grain protein percentage (GPC) for the cross P5221 / ORCR 8601.

			Indirect effects via		
Relations of GPC and	r with GPC	Direct effect	Harvest index	Plant height	Kernel weight
Harvest index	-0.46	-0.53		0.03	0.04
Plant height	0.02	-0.14	0.13		0.03
Kernel weight	0.02	0.16	-0.13	0.03	

$R^2 = 0.245$

Residual = 0.755

N = 245

Table 15. Path coefficient analyses of the direct and indirect effects of harvest index, physiological maturity and biological yield on grain protein percentage (GPC) for the cross P5221 / Centura.

			Indirect effects via		
Relations of GPC and	r with GPC	Direct effect	Harvest index	Phys. Maturity	Bio. Yield
Harvest index	-0.39	-0.37		0.01	0.01
Maturity	0.22	0.23	0.02		-0.03
Biolog. yield	0.20	0.20	0.03	-0.03	

$R^2 = 0.255$

Residual = 0.745

N = 245

Table 16. Path coefficient analyses of the direct and indirect effects of harvest index, plant height and kernel weight on grain protein percentage (GPC) for the cross P5221/ ORCR 8313.

			Indirect effects via					
Relations of GPC and	r with GPC	Direct effect	Biolog. yield	Plant height	Tillers	Grain fill	Harvest index	Kernel weight
Bio. yield	0.18	0.64		-0.10	-0.38	0.03	0.03	-0.04
Height	0.13	-0.24	0.27		-0.06	-0.01	0.19	-0.02
Tillers	0.05	-0.46	0.53	-0.03		0.04	-0.01	-0.02
G. filling	-0.02	0.30	0.07	0.00	-0.07		-0.05	-0.01
Harvest index	-0.42	-0.44	-0.05	0.10	-0.01	0.04		-0.05
Kernel weight	-0.18	-0.15	0.23	-0.04	0.07	0.02	-0.17	

$R^2 = 0.39$

Residual = 0.61

N = 263

variability in grain protein content.

DISCUSSION

The development of high yielding Hard Red Winter Wheat cultivars with acceptable grain protein content is one of the major efforts of the Oregon State University wheat breeding and genetics program.

The objective of this investigation was to study possible associations between grain protein content and selected plant traits. Such information is important in selecting for a higher grain protein content while enhancing high yields of Hard Red Winter Wheat when grown in Oregon.

Parents, F1, F2, and F3 generations of three crosses and reciprocal backcrosses of one cross, were space planted to evaluate these associations. Differences among generations were observed for the selected traits. The coefficients of variation were low for most traits, indicating that experimental precision was high. However, it should be pointed out that these coefficients were calculated using plot means, not on the individual plant values.

Parent P5221, the source of high grain protein content used in this study, failed to express a high grain protein content in the growing conditions prevalent during the 1986/1987 season at the Oregon State University Crop Science field laboratory. This failure may be because this selection was developed for the Great Plains, where grain yields are lower than in Oregon.

Contrasting conclusions have been reported regarding the genetic nature of grain protein content. Partial dominance for low protein was noted by Halloran (1981), and Sampson et al. (1983). While Mandloi et al. (1974), Cowley and Wells (1980) and Corpuz et al. (1983) observed dominance for high grain protein content. In the present study, the mean grain protein content of the F1 population was as low as that of the lower parent in the cross P5221/ORCR 8313, indicating dominance for low protein. On the other hand, the F2 mean value for this cross was not significantly different from that of the high grain protein content parent. In the cross P5221/Centura the opposite was found: the mean of the F1 was as high as the high grain protein content parent, suggesting dominance for high grain protein content, while the mean was similar to that of the low parent in the F2. The apparent shifts in the genetic nature of grain protein content could be interpreted as resulting from the relative small number of parental and F1 plants evaluated and the large influence of the environment on the expression of this trait. Inferences of gene action were not drawn from the cross P5221/ORCR 8601, as no significant differences were detected between the parents.

The F2 progenies of the three crosses showed continuous variation in grain protein content with no breaks in the distribution to suggest a simple Mendelian explanation for the inheritance pattern. Differences in grain protein content may also be caused by genes whose effects are masked by the large influence of environmental factors. As shown by the frequency distributions, transgressive segregation of grain protein content was observed in the F2 populations of the three crosses. This indicates that effective selection for high and low protein could be made within each cross. It also suggests that genes for high protein may exist in P5221 which differ from the other selections and Centura. Transgressive segregation for grain protein content was also observed by

Stuber et al. (1962), Johnson et al. (1973), Schumaker (1980) and Corpuz et al. (1983).

Broad sense heritability estimates of grain protein content ranged from low (29%) to moderate (56%) among crosses, agreeing with the values reported by Lofgren et al. (1968) and Corpuz et al. (1983). The magnitude and variability of the broad sense heritability estimates suggests that the environment exerts a large influence on the expression of grain protein content.

The narrow sense heritability estimate of grain protein content obtained from the P5221/ORCR 8601 cross was only 28%, indicating that only half of the genetic variance for grain protein content was of additive nature. This result agrees with Haunold et al. (1962). It contrasts with those observed by Stuber et al. (1962) and Schumaker (1980) who observed mainly additive gene action. Narrow sense heritability is of particular importance for breeding of self-pollinating species, as it a measure of the additive genetic variance which can be fixed by selection.

Grain hardness showed low broad sense heritability estimates. This is in contrast to the high estimates found by Sampson et al. (1983). These low heritability estimates of grain hardness can be explained by the small differences present in grain texture in the parental material, as the four genotypes used to derive the segregating populations are classified as hard wheats. Narrow sense heritability estimates were larger than the broad sense estimates, suggesting that the environment affected differently the various generations.

Grain protein content was not associated with grain hardness in the three crosses evaluated. A positive correlation has been postulated (Sampson et al., 1983), although genetic studies have shown no association between these traits (Davis et al., 1961; Lorenzo, 1985). The results obtained in the present study, does not provide evidence to elucidate this association as the four parental lines have hard kernel texture. Thus, the gene for "softness" (Greenwell and Schonfield, 1986) would not be present in the segregating populations.

Grain yield is usually negatively associated with grain protein content (Loffler et al., 1985; Cox et al., 1985). Therefore, direct selection for grain protein content will tend to reduce grain yield. Indirect selection could be used in these situations by selecting for a related trait of high heritability associated with grain protein and grain yield (Falconer, 1960). However, in this study, none of the examined traits showed a large enough association to justify the use of indirect selection in the populations developed from these crosses. In the three crosses evaluated, grain yield was not associated with grain protein content as measured by the phenotypic correlation coefficients which were all low and non significant. Thus, simultaneous selection for high grain protein content and high grain yield should be possible in these populations. Halloran (1981), also found that grain protein content and grain yield were not associated in randomly derived F4 lines.

Protein yield was shown to be of relative use in selecting for high yield and grain protein content. As it was largely affected by variation in grain yield. Correlation coefficients between protein yield and grain yield were high (0.97) in the three crosses.

The largest phenotypic correlation coefficient between grain protein content and a selected plant trait was with harvest index. McNeal (1972), and Loffler et al. (1985), also observed a significant association between these traits. In the present study, the r values were only low to moderate in magnitude, ranging from -0.39 to -0.46, depending on the cross. These observed values were close to those found by Loffler and Busch (1982). In the crosses P5221/ORCR 8601 and P5221/ORCR 8313, these same correlation coefficients were not significantly different from -0.50, confirming the moderate nature of this association. While in the cross P5221/Centura, the correlation observed was significantly different from -0.50 at the 5 % probability level. The confidence intervals of these three correlation coefficients were all small. The negative association between grain protein content and harvest index is of particular importance because the grain yield advantage of modern semi-dwarf cultivars seem to be the result of an increased harvest index (Austin et al., 1980). The ratio of above-ground biomass to grain biomass seems to play a role in determining the grain protein content. Austin et al. (1977) suggested that the source of N to the grain has been relatively reduced in modern cultivars by increasing grain yield without a corresponding increase in biological yield. If most of the grain N is already present at anthesis, as shown by Van Sanford and MacKown (1987) and Cox et al. (1985), redistribution from vegetative tissue becomes the largest factor in determining a high grain protein content. As a result, grain protein content will be affected by the relative proportion of straw and grain.

To investigate if there was a direct effect of harvest index on grain protein content, path coefficient analyses for each cross were performed using grain protein content as dependent variable. The phenotypic correlation coefficients of grain protein content with selected plant traits were partitioned into direct and indirect effects. Path analyses suggested that the association between grain protein content and harvest index was mostly through a direct effect of harvest index, with little indirect influence from other plant traits for the three crosses. Assuming that the causal relationships expressed in the path coefficient analyses are correct, the correlation between grain protein content and harvest index is the result of a true cause and effect relation and not a spurious association through indirect pathways via the other traits. Other plant traits exhibited little direct or indirect influence on protein content, except for biological yield and tiller number in the cross P5221/ORCR 8313. The direct effect of biological yield on grain protein content in this cross was moderately large (0.64). The correlation coefficient between biological yield and grain protein content was only 0.18 as there was a negative indirect effect via number of tillers. Tiller number had a moderate direct effect on grain protein content of -0.46. This negative effect was offset by the positive indirect effect via biological yield, resulting in a phenotypic correlation of only 0.05.

The residual mean square was large for the three crosses, indicating that most of the variation in grain protein content was not explained by the variables included in these analyses. The influence of other variables such as the total plant N uptake and N harvest index could explain the low magnitude of the observed R^2. Loffler et al. (1985), using stepwise regression to examine the associations among traits, observed that harvest index alone accounted for 0.62 of the grain protein content variation in a sample of spring wheat cultivars. They observed a small residual variation when N harvest index, biological yield and total N at maturity were included in the model.

The possible association between harvest index and grain protein content, suggests that if selection for high yields is based on further increases of harvest index, grain protein will decrease. By breeding for higher harvest indices, the source of photosynthates is reduced in proportion to the grain (sink). To increase both grain yield and protein, breeders should focus on increasing plant photosynthesis. This can be achieved by a larger biomass or by higher rates of photosynthate production.

To increase grain yield without increasing harvest index, cultivars with higher biological yield should be developed. Increases in biological yield are possible as shown by the results of this study. Crosses between a genotype with low biomass and genotypes with higher values resulted in progenies with means as high as the highest parent. The narrow sense heritability for this trait was moderate, and the predicted gain from selection was the largest of the selected traits.

SUMMARY AND CONCLUSIONS

Parents, F1 generations and segregating populations of three crosses involving the common parental Selection P5221 were grown in a space planted experiment. The objective was to evaluate possible associations between grain protein content and harvest index and other plant traits in Hard Red Winter Wheat segregating populations grown in Oregon.

Plant traits measured on an individual plant basis were: heading date, days to maturity, grain filling period, plant height, biological yield, number of fertile tillers, grain yield, harvest index, kernel weight, grain hardness, grain protein content, and protein yield.

Analyses of variance of generation means were conducted for all traits. Broad sense and narrow sense heritability (only for the cross P5221/ORCR 8601) estimates were also determined. Associations among traits were evaluated by phenotypic correlations. A path coefficient analysis using grain protein content as dependent variable was conducted for each cross.

The following conclusions were made from the results of this study:

1. Selection P5221 failed to express a high grain protein content under the growing conditions at the Crop Science Field Laboratory in the 1986/1987 season. This was probably caused by the lack of adaptation of P5221 or to a large genotype by environment interaction in this particular year.

2. The F2 progenies of the three crosses showed continuous variation in grain protein content, suggesting that the differences may be caused by genes whose effects are affected by the environment.
3. Broad sense heritability estimates for grain protein content ranged from low to moderate, suggesting that the environment exerts a large influence in grain protein content expression.
4. The narrow sense heritability estimate of grain protein content from the cross P5221/ORCR 8601 was low, indicating that at least half of the genetic variance for grain protein content was of additive nature.
5. Transgressive segregation for grain protein content was detected in the F2 of the three crosses, indicating that different genes for high grain protein content may exist in P5221 than in the other parental genotypes.
6. Grain yield and grain protein were not associated in the three crosses as measured by the phenotypic correlations, which were all low or close to zero, suggesting that simultaneous increases in grain protein content and grain yield should be possible in these populations.
7. Protein yield followed closely variation in grain yield. Thus it was of little use to increase both grain yield and protein content.
8. Grain protein content was not associated with grain hardness. This result has only relative value as the four parental lines have hard kernel texture.
9. None of the evaluated traits was closely associated with grain protein content to justify the use of indirect selection.
10. Harvest index was found to be negatively correlated with grain protein content. Although the correlation values were only low to

moderate. This could suggest that wheat breeders should not base further increases of grain yield on increases of harvest index because grain protein content will tend to decrease.

11. Path coefficient analyses revealed that harvest index had a direct effect on grain protein content with little indirect effect from the other plant traits in the three crosses.

12. In the cross P5221/ORCR 8313, biological yield had an important direct effect on grain protein content, but the correlation was reduced by the indirect effect of tiller number.

13. From the results of this study, it can be concluded that breeding for higher yields through a differential partitioning of biomass without increasing the source of photosynthates, can cause lower protein in the grain.

BIBLIOGRAPHY

Allard, R.W. 1960. Principles of plant breeding. John Wiley and sons (ed.) New York.

Austin, R.B., J. Bingham, R.D. Blackwell, L.T. Evans, M.A. Ford, C.L. Morgan, and M. Taylor. 1980. Genetic improvements in winter wheat yields since 1900 and associated physiological changes. J. Agric. Sci. 94:675-689.

Austin, R.B., M.A. Ford, J.A. Edrich, and R.D. Blackwell. 1977. The nitrogen economy of winter wheat. J. Agric. Sci. 88:159-167.

Baker, R.J. 1977. Inheritance of kernel hardness in spring wheat. Crop Sci. 17:960-962.

Bhatia, C.R., 1975. Criteria for early generation selection in wheat breeding programs for improving protein productivity. Euphytica 24:789-794.

Bhatia, C.R., R. Mitra, S.G. Bhagwat, and R.M. Desai. 1978. Genetic variation in the components of the "high protein" character in wheat. Proc. 5th Int. Wheat Symposium, New Delhi.

Bhatia, C.R., and R. Rabson. 1976. Bioenergetic considerations in cereal breeding for protein improvement. Science (Washington, D.C.) 194:1418-1421.

Bhullar, S.S., and C.F. Jenner. 1985. Differential responses to high temperatures of starch and nitrogen accumulation in the grain of four cultivar of wheat. Aust. J. Plant Physiol. 12:363-375.

Boatwright, G.O., and H.J. Haas. 1961. Development and composition of spring wheat as influenced by nitrogen and phosphorus fertilization. Agron. J. 53:33-36.

Campbell, C.A., and H.R. Davidson. 1979. Effect of temperature, nitrogen fertilization and moisture stress on yield, yield components, protein content and moisture use efficiency of Manitou spring wheat. Can. J. Plant Sci. 59:963-974.

Castle, S.L., and P.J. Randall. 1987. Effects of sulfur deficiency on the synthesis and accumulation of proteins in the developing wheat seed. Aust. J. Plant Physiol. 14:503-516.

Chapman, S.R., and F.H. McNeal. 1970. Gene effects for grain protein in five spring wheat crosses. Crop Sci. 10:45-46.

Corpuz, L.M., G.M. Paulsen, and E.G. Heyne. Relationship between color and protein content in hard red x hard white winter wheat progeny. 1983. Euphytica 32:617-624.

Cowley, C.R., and D.G. Wells. 1980. Inheritance of seed protein in crosses involving "Hand": a hard red winter wheat. Crop Sci. 20:55-58.

Cox, M.C., C.O. Qualset, and W. Rains. 1985. Genetic variation for nitrogen assimilation and translocation in wheat. I. Dry matter and nitrogen accumulation. Crop Sci. 25:430-435.

Cox, M.C., C.O. Qualset, and W. Rains. 1986. Genetic variation for nitrogen assimilation and translocation in wheat. III. Nitrogen translocation in relation to grain yield and protein. Crop Sci. 26:737-740.

Daigger, L.A., D.H. Sander, and G.A. Peterson. 1976. Nitrogen content of winter wheat during growth and maturation. Agron. J. 68:815-818.

Dalling, M.J., G. Boland, and J.H. Wilson. 1976. Relation between acid proteinase activity and redistribution of nitrogen during grain development in wheat. Aust. J. Plant Physiol. 3:721-730.

Dalling, M.J. 1985. The physiological basis of nitrogen redistribution during grain filling in cereals. In Exploitation of physiological and genetic variability to enhance crop productivity. Harper, J.E., L.E. Schrader and R.W. Howell Eds. American Society of Plant Physiologists.

Davis, W.H., G.K. Middleton, and T.T. Herbert. 1961. Inheritance of protein, texture, and yield in wheat. Crop Sci. 1:235-238.

Day, G.E., G.M. Paulsen, and R.G. Sears. 1985. Nitrogen relations in winter wheat cultivars differing in grain protein percentage and stature. Journal of Plant Nutrition 8(7):555-566.

Falconer, D.S. 1960. Introduction to Quantitative Genetics. 2nd edition. Reprinted with amendments 1983. Longman Inc., New York.

Finney, K.F., W.T. Yamazaki, V.L. Youngs, and G.L. Rubenthaler. 1987. Quality of hard, soft, and durum wheats. pp. 677-748. In Wheat and wheat improvement. Agronomy Monograph no. 13. 2nd edition.

Forde, J., and B.J. Mifflin. 1983. Isolation and identification of mRNA for the high molecular weight storage proteins of wheat endosperm. Planta 157:567-576.

Goatley, J.L., and R.W. Lewis. 1966. Composition of guttation fluid from rye, wheat and barley seedlings. Plant Physiology 41:373-375.

Greenwell, P., and Schofield, J.D. 1986. A starch granule protein associated with endosperm softness in wheat. Cereal Chem. 63:379-380.

Halloran, G.M. 1981. Grain yield and protein relationships in a wheat cross. Crop Sci. 21:699-701.

Halloran, G.M. 1975. Genetic analysis of grain protein percentage in wheat. Theor. Appl. Genet. 46:79-86.

Haunold, A., V.A. Johnson, and J.W. Schimdt. 1962. Genetic measurements of protein in the grain of Triticum aestivum L. Agron. J. 54:203-206.

Hooker, M.L., D.H. Sander, and G.A. Peterson. 1980. Gaseous nitrogen losses from winter wheat. Agron. J. 72:789-792.

Johnson, V.A., P.J. Mattern, J.W. Smith, and J.E. Stroike. 1973. Genetic advances in wheat protein quantity and composition. Proc. 4th Int. Wheat Genetics Symposium. pp. 547-556. Missouri Agr. Exp. Stn., Columbia, Missouri.

Johnson, V.A., P.J. Mattern, and S.L. Kuhr. 1979. Genetic improvement of wheat protein. Seed Improvement in cereals and legumes. Vol II. In Proc. of a Symposium of IAEA-FAO, Neuherberg. 1978. IAEA, Vienna, pp. 165-181.

Kingsley, A.F., C.O. Clagett, H.J. Klosterman, and T.E. Stoa. 1957. Loss of minerals from mature wheat and flax by simulated rain. Agron. J. 49:37-39.

Klepper, L.A. 1975. Nitrate assimilation enzymes and seed protein in wheat. Proc Int. 2nd Winter Wheat Conf. 1975. pp. 334-340.

Klepper, L.A. 1974. Nitrate reductase and its role in the accumulation of protein in the grain of wheat. Latin American Wheat Conference. Porto Alegre, Brazil. pp.337-343.

Kramer, T. 1979. Environmental and genetic variation for protein content in winter wheat (Triticum aestivum L.). Euphytica 28:209-218.

Law, C.N., C.F. Young, J.W.S. Brown, J.W. Snape, and A.J. Worland. 1978. The study of grain protein control in wheat using whole chromosome substitution lines. In Seed protein improvement by nuclear techniques. Proc. of two research co-ordination meetings. Baden, 28 March-1 April 1977, and Vienna, 26-30 September 1977. IAEA, pp. 483-502.

Li, C.C. 1956. The concept of path coefficient and its impact on population genetics. Biometrics 12:190-210.

Loffler, C.M., and R.H. Busch. 1982. Selection for grain protein, grain yield, and nitrogen partitioning efficiency in hard red spring wheat. Crop Sci. 22:591-595.

Loffler, C.M., T.L. Rauch, and R.H. Busch. 1985. Grain and plant protein relationships in hard red spring wheat. Crop Sci. 25:521-524.

Lofgren, J.R., K.F. Finney, E.G. Heyne, L.C. Bolte, R.C. Hoseney, and M.D. Shogren. 1968. Heritability estimates of protein content and certain quality and agronomic properties of bread wheats (Triticum aestivum L.). Crop Sci. 8:563-567.

Lorenzo, A. 1985. Feasibility of developing bread wheat cultivars with acceptable protein content for non-traditional areas. PhD thesis. Oregon State University, Corvallis, Oregon.

Mandloi, K.C., M.V. Rao and A. Austin. 1974. Protein inheritance in common wheat. Indian J. Genet. Plant Breed. 34:642-645.

Mattern, P.J., R. Morris, J.W. Schimdt, and V.A. Johnson. 1973. Location of genes for kernel properties in the wheat variety "Cheyenne" using chromosome substitution lines. Proc. 4th Int. Wheat Genet. Symposium. Columbia, Missouri. pp. 703-708.

McNeal, F.H., and D.J. Davis. 1966. Protein content of wheat kernels from different parts of the spike. Agron. J. 58:635-636.

McNeal, F.H., C.F. McGuire, and D.L. Klindworth. 1982. Agronomic and quality characteristics of spring wheat lines selected for protein content and protein yield. Euphytica 31:377-381.

McNeal, F.H., M.A. Berg, and C. A. Watson. 1966. Nitrogen and dry matter in five spring wheat varieties at successive stages of development. Agron. J. 58:605-608.

McNeal, F.H., M.A. Berg, C.F. McGuire, V.R. Stewart, and D.E. Baldridge. 1972. Grain and plant nitrogen relationships in eight spring wheat crosses, Triticum aestivum L. Crop Sci. 12:599-601.

McNeal, F.H., M.A. Berg, P.L. Brown, and C.F. McGuire. 1971. Productivity and quality response of five spring wheat genotypes, Triticum aestivum L. to nitrogen fertilizer. Agron. J. 63:908-910.

Middleton, G.K., C.E. Bode, and B.B. Bayles. 1954. A comparison of the quantity and quality of protein in certain varieties of soft wheat. Agron. J. 46:500-502.

Mifflin, B.J., J.M. Field, and P.R. Shewry. 1983. Cereal storage proteins and their effect on technological properties. pp. 255-

319. In Seed proteins. Annual proceedings of the Phytochemical society of Europe, no. 20. Ed. J. Daussant, J. Mosse, J. Vaughan.

Morris, C.F., and G.M. Paulsen. 1985. Development of hard winter wheat after anthesis as affected by nitrogen nutrition. Crop Sci. 25:1007-1010.

Morris, R., P.J. Mattern, J.W. Schimdt, and V.A. Johnson. 1978. Studies on protein, lysine and leaf rust reactions in the cultivar Atlas 66 using chromosome substitutions. pp. 567-568. In Seed protein improvement by nuclear techniques. IAEA, Vienna.

Olson, R.A., A.F. Dreier, C. Thompson, K. Frank, and P.H. Grabouski. 1964. Using fertilizer effectively on grain crops. Nebraska Agr. Exp. Sta. Bull. S.B. No. 479.

Olson, R.A., and H.F. Rhoades. 1953. Commercial fertilizers for winter wheat in relation to the properties of Nebraska soils. Nebr. Agr. Exp. Sta. Res. Bull. 172.

Penning de Vries, F.W.T., A.H.M. Brunsting, and H.H. Van Laar. 1974. Products, requirements and efficiency of biosynthesis: A quantitative approach. J. Theor. Biol. 45:339-377.

Pepe, J.F. and R.E. Heiner. 1975. Plant height, protein percentage and yield relationships in spring wheat. Crop Sci. 15:793-797.

Rodriguez, R. 1984. Germplasm development. pp. 66-75. In CIMMYT Report on wheat improvement 1984.

Salisbury F.B. and C.W. Ross. 1985. Plant Physiology. 3rd edition. Wadsworth Inc., California.

Sampson, D.R., D.W. Flynn, and P.Y. Jui. 1983. Inheritance of kernel protein in five spring wheat crosses. Canad. J. Genet. Cytol. 25:398-402.

Sampson, D.R., D.W. Flynn, and P.Y. Jui. 1983. Genetic studies on kernel hardness in wheat using grinding time and near infrared reflectance spectroscopy. Can. J. Plant Sci. 63:825-832.

Schimdt, J.W., V.A. Johnson, P.J. Mattern, A.F. Dreier, and D.V. McVey. 1979. Registration of Lancota wheat. Crop Sci. 19:749.

Schumaker, K.S. 1980. Evaluation of four quality factors in a selected winter x spring cross (Triticum aestivum Vill., Host). MS Thesis. Oregon State University. Corvallis, Oregon.

Smith, T.L., G.A. Peterson, and D.H. Sander. 1983. Nitrogen distribution in roots and tops of winter wheat. Agron. J. 75:1031-1036.

Snedecor, G.W., and W.G. Cochran. 1980. Statistical Methods. 7th edition. The Iowa State University Press, Iowa.

Sofield, I., L.T. Evans, M.G. Cook, and I.F. Wardlaw. 1977. Factors influencing the rate and duration of grain filling in wheat. Aust. J. Plant Physiol. 4:785-797.

Spiertz, J.H.J., and J. Ellen. 1978. Effects of nitrogen on crop development and grain growth of winter wheat in relation to assimilation and utilization of assimilates and nutrients. Neth. J. Agric. Sci. 26:210-231.

Spiertz, J.H.J. 1977. The influence of temperature and light intensity on grain growth in relation to carbohydrate and nitrogen economy of the wheat plant. Neth. J. Agric. Sci. 25:182-197.

Stein, I.S., R.G. Sears, B.S. Gill, D.L. Wetzel, C.R. Hoseney, and T.S. Cox. 1988. Chromosomal location of high protein genes in "Plainsman V". Agronomy Abstracts. 80th Annual Meeting, Anaheim, California, 27 November-2 December, 1988. p. 97. American Society of Agronomy, Wisconsin.

Stuber, C.W., V.A. Johnson, and J.W. Schimdt. 1962. Grain protein content and its relationship to other plant and seed characters in the parents and progeny of a cross of _T_. _aestivum_ L. Crop Sci. 2:506-508.

Sunderman, D.W., M. Wise, and E.M. Sneed. 1965. Interrelationships of wheat protein content, flour sedimentation value, farinograph peak time and dough mixing and baking characteristics in the F2 and F3 generations of winter wheat, _T_. _aestivum_ L. Crop Sci. 5:537-540.

Terman G.L., R.E. Ramig, A.F. Dreier and R.A. Olson. 1969. Yield protein relationships in wheat grain, as affected by nitrogen and water. Agron. J. 61:755-759.

Trupp, C.R. 1976. Particle size index -Breeding behavior and association with protein percentage in wheat. Crop Sci. 16:618-620.

Van Sanford, D.A., and C.T. MacKown. 1987. Cultivar differences in nitrogen remobilization during grain fill in soft red winter wheat. Crop Sci. 27:295-300.

Waddington, S.R., J.K. Ransom, M. Osmanzai, and D.A. Saunders. 1986. Improvement in the yield potential of bread wheat adapted to Northwest Mexico. Crop Sci. 26:698-703.

Warner, J.N. 1952. A method for estimating heritability. Agron J. 44:427-430.

APPENDIX

Appendix Table 1. Pedigrees and description of the Hard Red Winter Wheat selections and cultivar used in the study.

Protein 5221: Privately developed semi-dwarf selection from the Great Plains of the U.S.A.

Centura: (Warrior*5 / Agent // NE 68457 /3/ Centurk 78). Tall cultivar released by the University of Nebraska.

ORCR 8601: (Pumafen // Ciano "S" / Gallo). Semi-dwarf selection from the Oregon State University Spring x Winter breeding program.

ORCR 8313: (Probstorfer Extrem / Tobari 66). Semi-dwarf selection from the Oregon State University Spring x Winter breeding program.

Appendix Table 2. Observed mean squares for six agronomic traits involving parents, F1, F2, F3, and reciprocal backcross generations resulting from the cross P5221/ORCR 8601, grown at the Crop Science Field Laboratory, 1987.

Source of variation	d.f.	Days to heading	Plant Height (cm)	Tiller number	Phys. maturity (days)	Kernel weight gx1000	Grain filling (days)
Generations	6	15.16**	90.41**	1.94	4.97**	185.99**	3.87
Replications	2	4.42	26.33	26.33	3.19	29.67	15.05
Error	12	0.87	13.72	9.80	0.30	8.18	1.32
Total	20						
C.V.		9.81	0.74	3.53	7.16	0.31	8.43

* and ** indicate 5% and 1% significance levels, respectively.

Appendix Table 3. Observed mean squares for six traits involving parents, F1, F2, and F3 generations resulting from the cross P5221/Centura, grown at the Crop Science Field Laboratory, 1987.

Source of variation	d.f.	Days to heading	Plant Height (cm)	Tiller number	Phys. maturity (days)	Kernel weight (g)	Grain filling (days)
Generations	4	10.27**	593.83**	2.73	1.33	236.42**	14.60**
Replications	2	2.07	39.47	1.87	0.20	21.89	1.27
Error	8	0.57	8.63	1.53	0.53	9.63	1.60
Total	14						
C.V.		0.60	2.56	8.68	0.42	2.68	2.60

* and ** indicate 5% and 1% significance levels, respectively.

Appendix Table 4. Observed mean squares for six agronomic traits involving parents, F1, F2, and F3 generations from the cross P5221/ORCR 8313, grown at Crop Science Field Laboratory, 1987.

Source	d.f.	Days to heading	Plant height (cm)	Tiller number	Physiological maturity (days)	Kernel weight gx1000	Grain filling (days)
Generations	4	16.93**	105.83**	3.00	4.43	127.37**	6.67
Replications	2	2.60	25.87	2.07	2.40	11.65	6.20
Error	8	1.43	13.28	1.15	1.23	9.94	2.12
Total	14						
C.V.		0.95	3.58	9.46	0.63	2.60	2.97

* and ** indicate 5% and 1% significance levels, respectively.

Appendix Table 5. Mean values for parents and five resulting generations for six agronomic traits for the cross P5221/ORCR 8601 using Fisher's protected LSD (FPLSD).

Generation	Days to heading	Plant height (cm)	Tiller number[1]	Physiological maturity (days)	Grain filling (days)	Kernel weight gx1000
P5221	123.7d	93.3b	12.3	175.0c	51.3	37.9c
ORCR 8601	129.7a	106.3a	13.7	177.7a	48.0	37.8c
F1	123.7d	106.0a	13.3	174.0d	50.3	44.9a
F2	125.0cd	110.3a	13.0	174.7cd	49.7	40.4b
F3	126.0c	104.7a	12.7	175.3bc	49.3	38.0c
BC/P5221	124.3d	105.0a	12.0	174.0d	49.7	39.8b
BC/ORCR8601	127.7b	108.7a	11.3	176.0b	48.3	40.0b

Generation means displaying the same letter on the same column are not significantly different at the 5% probability level.

(1) indicates that FPLSD was not conducted, as differences among means were not statistically significant.

Appendix Table 6. Mean values for parents and three resulting generations for six agronomic characters for the cross P5221/Centura using Fisher's protected LSD (FPLSD).

Generation	Days to heading (days)	Plant height (cm)	Tiller number[1]	Physiological maturity (days)	Grain filling (days)	Kernel weight gx1000
P5221	125.3 b	92.0 c	13.0	174.3	50.3a	38.5 ab
Centura	128.7 a	128.0 a	14.0	173.7	45.0b	33.1 c
F1	124.7 b	124.3 b	15.7	175.0	50.3a	40.1 a
F2	125.3 b	116.3 b	14.3	173.3	48.0a	36.7 b
F3	124.7 b	112.7 b	14.3	173.7	49.0a	34.6 c

Generation means displaying the same letter on the same column are not significantly different at the 5% probability level.

(1) indicates that FPLSD was not conducted, as differences among means were not statistically significant.

Appendix Table 7. Mean values for parents and three resulting generations for six agronomic characters of the cross P5221/ORCR 8313 using Fisher's protected LSD (FPLSD).

Generation	Days to heading (days)	Height (cm)	Tiller number[1]	Physiological maturity[1] (days)	Grain filling[1] (days)	Kernel weight gx1000
P5221	122.7 c	91.7 b	12.3	173.7	51.0	37.8 bc
ORCR 8313	129.3 a	102.0 a	9.7	176.7	47.3	36.5 c
F1	125.3 b	106.3 a	11.7	175.3	50.0	41.5 a
F2	126.0 b	102.3 a	11.3	174.3	48.0	39.0 b
F3	125.7 b	106.0 a	11.7	174.0	48.7	36.6 c

Generation means displaying the same letter on the same column are not significantly different at the 5% probability level.

(1) indicates that FPLSD was not conducted, as differences among means were not statistically significant.

Appendix Table 8. Means and standard deviations of 12 agronomic traits from parents, F1, F2, and reciprocal backcross generations for the cross P5221/ORCR 8601.

	P5221		ORCR 8601		F1		F2		F3		BC1		BC2	
Trait	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.
Biol. yield(g)	50.1	14.4	88.1	26.4	81.9	15.8	80.2	30.8	73.7	26.3	63.3	22.2	74.6	27.9
Days to heading	123.5	1.1	129.7	1.4	123.6	2.0	125.3	5.4	126.1	5.7	124.4	2.9	127.9	4.6
Plant height(cm)	93.5	6.3	106.0	4.3	106.0	4.9	110.2	21.1	104.7	23.7	104.8	17.5	109.3	18.6
Tiller number	12.1	2.4	13.9	3.5	13.1	2.6	13.1	3.7	12.9	3.3	11.7	3.0	11.4	2.9
Phys. maturity(days)	175.2	1.3	177.8	1.4	174.3	1.6	174.5	3.8	175.2	3.7	174.2	3.2	176.1	3.0
Grain yield(g)	17.0	5.6	20.1	6.5	27.1	5.9	22.3	9.2	21.1	7.9	20.2	7.4	21.1	8.1
Kernel weight(gx100)	37.9	1.7	37.9	2.5	45.1	2.6	40.3	4.7	37.9	4.6	39.8	3.8	40.0	4.1
Grain filling(days)	51.6	1.8	48.0	1.9	50.7	2.8	49.3	3.6	49.1	4.0	49.8	3.3	48.2	3.5
Harvest index(%)	33.4	3.4	22.8	4.7	32.6	3.6	27.9	5.9	28.6	5.5	31.9	5.5	28.4	6.0
Grain hardness	105.9	21.6	128.9	19.1	107.5	16.5	114.6	25.7	111.0	24.8	103.9	17.4	110.8	24.3
Protein cont.(gKg^{-1})	148.1	6.2	148.3	7.7	144.4	5.0	153.2	14.3	148.8	14.7	149.9	11.7	149.9	12.6
Protein yield(g)	2.5	0.9	2.9	0.9	3.9	0.9	3.4	1.4	3.1	1.2	3.0	1.0	3.1	1.2

Appendix Table 9. Means and standard deviations of 12 traits from parents, F1, F2, and F3 generations for the cross P5221/Centura.

	P5221		Centura		F1		F2		F3	
Trait	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.
Biol. yield(g)	57.2	11.9	70.3	20.3	87.9	20.8	67.6	23.7	62.8	19.9
Days to heading	123.8	1.4	128.6	1.1	124.5	2.0	125.2	3.4	124.7	3.2
Plant height(cm)	92.7	6.6	128.1	6.7	124.3	5.1	116.4	15.1	112.9	15.2
Tiller number	13.0	2.7	14.3	3.9	15.8	2.9	14.2	4.2	14.3	4.2
Phys. maturity(days)	174.2	1.7	173.7	1.7	174.8	1.8	173.2	3.2	173.6	3.2
Grain yield(g)	20.5	5.7	19.4	6.2	27.8	7.2	21.2	8.2	18.7	7.0
Kernel weight(gx1000)	38.6	1.9	33.0	2.6	40.0	2.2	36.7	3.4	34.6	3.4
Grain filling (days)	50.4	1.6	45.0	2.0	50.3	3.2	48.0	3.2	48.9	2.8
Harvest index(%)	35.3	4.7	27.2	3.7	31.1	3.3	31.0	4.7	29.5	6.0
Grain hardness	93.8	20.6	127.0	25.1	111.2	26.0	107.9	25.7	104.7	26.0
Protein cont.(gKg^{-1})	147.0	9.3	159.9	12.0	156.9	16.3	146.2	15.3	151.1	16.0
Protein yield(g)	3.0	0.9	3.1	1.0	4.4	1.3	3.1	1.3	2.8	1.0

Appendix Table 10. Means and standard deviations for 12 traits from parents, F1, F2, and F3 generations for the cross P5221/ORCR 8313.

	P5221		ORCR 8313		F1		F2		F3	
Trait	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.
Biol. yield(g)	56.9	18.5	67.7	14.0	70.6	14.2	66.2	25.2	65.1	23.6
Days to heading	122.3	1.6	129.2	1.0	124.9	2.0	126.1	4.3	126.0	4.9
Plant height(cm)	91.1	3.2	102.0	3.4	105.3	5.2	106.1	27.0	112.9	15.2
Tiller number	13.1	3.2	9.3	1.7	11.7	2.1	11.6	3.4	11.6	3.2
Phys. maturity(days)	173.5	1.6	176.7	0.6	174.9	2.1	174.0	3.3	174.0	3.7
Grain yield(g)	21.6	7.4	19.2	4.5	24.9	5.6	21.9	9.0	20.2	8.2
Kernel weight(gx1000)	38.0	2.1	36.6	5.1	41.4	1.9	39.0	4.2	36.6	3.9
Grain filling(days)	51.2	1.9	47.4	1.1	50.0	3.2	47.9	3.2	48.0	3.6
Harvest index(%)	37.1	2.3	28.2	5.7	34.9	3.6	32.8	5.6	30.9	6.1
Grain hardness	91.5	19.5	116.1	18.3	98.8	20.1	95.9	23.2	94.3	23.4
Protein cont.(gKg^{-1})	143.6	7.7	157.4	13.9	144.0	12.7	151.9	15.6	153.7	16.1
Protein yield(g)	3.1	1.1	3.0	0.7	3.6	0.9	3.3	1.4	3.1	1.3

Appendix Table 11. Broad sense heritability estimates for six traits from the parental, F1 and F2 generations of the three crosses.

	Cross		
	P5221 / ORCR 8601	P5221 / Centura	P5221 / ORCR 8313
Traits	Broad sense heritability (%)		
Days to heading	91	79	86
Phys. maturity	85	72	78
Grain filling	63	45	51
Tiller number	39	42	49
Plant height	94	83	96

Appendix Table 12. Narrow sense heritability (Hns) estimates and expected genetic advance for six traits from the F2 and the two backcross generations for the cross P5221/ORCR 8601.

Traits	Hns (%)	G.S.* (%)
Days to heading	38	4.20
Physiological maturity	33	2.57
Grain filling period	14	1.05
Tiller number	33	3.86
Plant height	42	18.26
Kernel weight	29	16.93

* Genetic advance (G.S.) represents the expected percent increase in the F3 above the F2 mean when the best 5% of the F2 plants are selected.

Appendix Table 13. Phenotypic correlation coefficients between grain protein content and six traits measured in the progeny of three crosses.

	Cross		
	P5221 / ORCR 8601	P5221 / Centura	P5221 / ORCR 8313
Protein content and			
Days to heading	0.11	0.04	-0.15
Days to maturity	0.11	0.22**	0.05
Grain filling period	-0.05	0.17**	0.25**
Plant height	0.02	0.24**	0.13
Tiller number	-0.06	0.04	0.05
Kernel weight	0.02	-0.03	-0.18**
Number of plants	245	286	263

**: indicates significantly different from zero at the 1% probability level.

Appendix Table 14. Matrix of phenotypic correlations among 11 traits in the F2 of the cross P5221/ORCR 8601.

Trait	2)	3)	4)	5)	6)
1)B. yield	-0.05	-0.38**	-0.67**	-0.08	0.82**
2)Heading		-0.14*	-0.16*	0.73**	-0.27**
3)P. height			0.03	-0.25**	0.21**
4)Tillers				0.22**	0.72**
5)Maturity					-0.26**

	7)	8)	9)	10)	11)
1)B. yield	0.22*	-0.01	-0.24**	0.15*	0.85**
2)Heading	-0.33**	-0.71**	-0.37**	0.07	0.25**
3)P. height	0.16*	-0.05	-0.25**	0.04	0.22**
4)Tillers	0.09	0.05	0.08	0.06	0.70**
5)Maturity	-0.20**	-0.04	-0.27**	0.02	-0.23**
6)G. yield	0.35**	0.13*	0.31**	0.06	0.97**
7)K. weight		0.28**	0.24**	0.00	0.35**
8)G. filling			0.27**	-0.13*	0.13*
9)H. index				-0.16*	0.22**
10)G. hardness					0.09
11)P. yield					

Number of plants = 245.

* and ** indicate significantly different from zero at the 5% and 1% probability level, respectively.

Appendix Table 15. Matrix of phenotypic correlations among 11 traits in the F2 of the cross P5221/Centura.

Trait	2)	3)	4)	5)	6)	7)	8)	9)	10)	11)
1)B. yield	-0.26	-0.36**	-0.79**	-0.14*	0.91**	0.18**	-0.12*	-0.07	0.07	0.92**
2)Heading		-0.13*	-0.22**	0.53**	-0.29**	-0.18**	-0.51**	-0.09	0.01	-0.27**
3)P. height			0.02	-0.19**	0.16**	0.35**	-0.05	-0.47**	0.02	0.21**
4)Tillers				0.12*	0.82**	0.12*	0.10	0.17**	0.02	0.79**
5)Maturity					-0.15**	-0.17**	-0.45**	-0.04	0.09	-0.09
6)G. yield						0.22**	0.15**	0.31**	0.04	0.97**
7)K. weight							0.01	0.16**	-0.06	0.20**
8)G. filling								0.05	0.07	0.19**
9)H. index									-0.05	0.21**
10)G. hardness										0.10
11)P. yield										

Number of plants = 286.

* and ** indicate significantly different from zero at the 5% and 1% probability level, respectively.

Appendix Table 16. Matrix of phenotypic correlations among 11 traits in the F2 of the cross P5221/ORCR 8313.

Trait	2)	3)	4)	5)	6)
1)B. yield	-0.26	-0.42**	-0.82**	-0.22**	0.91**
2)Heading		-0.22**	-0.24**	0.66**	-0.29**
3)P. height			0.13*	-0.30**	0.21**
4)Tillers				0.17*	0.80**
5)Maturity					-0.20**

	7)	8)	9)	10)	11)
1)B. yield	0.36**	-0.12*	-0.08	0.00	0.93**
2)Heading	-0.24**	-0.64**	-0.07	0.05	-0.32**
3)P. height	0.19**	-0.03	-0.44**	0.02	0.25**
4)Tillers	0.15*	0.14*	0.03	-0.04	0.79**
5)Maturity	-0.23**	-0.15*	-0.03	0.05	-0.19**
6)G. yield	0.22**	0.15*	0.31**	0.04	0.97**
7)K. weight		0.08	0.40**	-0.25**	0.43**
8)G. filling			0.13*	-0.02	0.23**
9)H. index				0.27**	0.20**
10)G. hardness					0.02
11)P. yield					

Number of plants = 263.

* and ** indicate significantly different from zero at the 5% and 1% probability level, respectively.

Appendix Table 17. Summary of climatic data on a per month basis for the Crop Science Field Laboratory, during the 1986-87 growing season.

Month	Precipitation (mm)	Temperature (^{0}C) Ave. Max.	Temperature (^{0}C) Ave. Min.	Temperature (^{0}C) Mean
October	71.1	18.5	7.2	12.9
November	218.9	12.2	4.4	8.3
December	88.9	7.8	0.3	4.0
January	208.8	7.9	0.6	4.2
February	114.3	10.9	2.6	6.7
March	94.0	13.4	3.7	8.6
April	39.6	18.5	4.6	11.6
May	35.6	21.2	7.8	14.5
June	7.4	25.4	9.6	17.5
July	56.6	25.3	11.5	18.4
Total	935.2			