AN ABSTRACT OF THE THESIS OF

Jose Maria Costa for the degree of Doctor of Philosophy in Crop Science presented on November 29, 1990.

Title: Possible Association of Grain Protein Content, Harvest Index and Biological Yield in Winter Wheat Populations

Abstract approved: Redacted for Privacy

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A negative relation between grain protein content and grain yield is frequently observed in wheat (Triticum aestivum L. em Thell) i.e. as grain yield increases, grain protein decreases. It has been suggested that the inverse relation between grain yield and protein is in part the result of developing high yielding semi-dwarf wheat cultivars with an increased harvest index. This investigation was undertaken to determine the nature of the possible association of grain yield and protein content as influenced by harvest index, biological yield, plant height and kernel weight in winter wheat populations grown in Oregon.

Progenies derived from three crosses of winter wheat were solid-planted in two environments during two seasons. Phenotypic correlations showed a moderate negative association of grain protein content with both grain yield and harvest index. The magnitude of the genetic

correlations suggested the presence of genetic relationships among these traits. Selection for harvest index among these crosses could cause a correlated reduction of grain protein content.

To investigate if the relationships between grain protein content and selected plant growth traits were similar when grown under space-planted and solid seeded stands, progenies of two winter wheat crosses were evaluated during two seasons. Performance for grain yield and grain protein content was different under contrasting sowing densities as values were not correlated between sowing densities. This indicates the need to evaluate these traits in solid-seeded stands. Harvest index, as well as plant height and heading date, could be effectively selected under space-planted or solid seeded conditions. Associations among traits were reliably estimated in space-planted stands.

To evaluate the effect on grain protein content when grain yield and harvest index are modified, the plant growth regulator Paclobutrazol was applied to selected winter wheat genotypes under field and greenhouse conditions. Paclobutrazol increased grain yield and harvest index values of all genotypes in the greenhouse, while only some genotypes improved these traits under field conditions. Grain protein content, however, remained unchanged. Higher grain yields were obtained in both greenhouse and field experiments.

Possible Association of Grain Protein Content, Harvest Index and Biological Yield in Winter Wheat Populations

By

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A THESIS

submitted to

Oregon State University

In partial fulfillment of
the requirements for the
degree of

Doctor of Philosophy

Completed November 29, 1990

Commencement June 1991

APPROVED:

Redacted for Privacy

Professor of Crop and Soil Science in charge of major

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Date thesis is presented: November 29, 1990

Typed by researcher for Jose Maria Costa

Dedicated to

my wife,

Gillian

my children,

Emilia and Daniel

my father,

Jose Maria

and in memory of my mother,

Luisa

ACKNOWLEDGEMENT

I wish to state my sincere gratitude to Dr. Warren E. Kronstad, for his advice, example, encouragement, critical review of this thesis and for providing me with this opportunity to further my education.

Appreciation is extended to Drs. Patrick Hayes, Neil Christensen, David Thomas, and James Baggett for serving in my graduate committee.

A sincere thanks is also extended to my fellow graduate students: Miguel Camacho, Modan Das, Apichart Vanavichit, Shi-Ping Wang, Andres Encinas, Mou Bei-Quan, Karim Ammar, Salah Rezgui, Mourad Abdennadher and staff of the cereal project: Randy Knight, Mike Moore, Connie Love, Mary Verhoeven, Debbie Kelly, Sonnia Rowe and Nan Scott for their friendship and help in the long hours of field work. A special acknowledgement for Ann Corey for her help and friendship.

I am very grateful to my wife, Gillian, for her patience, understanding, and encouragement. A very special thanks to my father, Jose Maria and my sister, Luisa for their moral and financial support.

I am most grateful to the Oregon State University Crop and Soil Science Department for providing financial support throughout the course of this study.

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INTRODUCTION

The influence of the environment on the expression of grain yield and grain protein content in wheat and the causes of a possible negative relationship between these traits has not been fully explored. It has been suggested that when grain yields increase, grain protein content will decrease. In the Pacific Northwest, grain yield of wheat is high and grain protein is low, usually less than ten percent. Such protein levels favor the production of soft white pastry wheats. To diversify wheat production in terms of end product uses, it would be desirable to achieve higher grain protein content levels without sacrificing grain yield.

It has been suggested that a possible cause for the negative relation between grain yield and grain protein content is the indirect result of using harvest index (ratio of grain yield to total biomass) to improve yield. Semi-dwarf cultivars have higher grain yield through improvements of harvest index (Austin et al., 1980). Furthermore, wheat breeders have traditionally considered that a certain plant phenotype is associated with high protein content. Thus, the selection of certain plant types may be precluding the development of high yielding cultivars with acceptable

protein content, when grown in the Pacific Northwest.

Trait associations can be estimated using three approaches: 1) isolines differing for genes controlling the characters of interest, 2) evaluation of random progenies from segregating populations, and 3) or creation of variability within a cultivar through artificial manipulation (Fehr, 1987).

The second approach was used to determine if possible associations exist between grain protein content and selected agronomic traits in Hard Red Winter wheat populations. To provide such information, randomly derived progenies were grown in two environmentally diverse locations in Oregon (Chapter 1).

Wheat breeders commonly evaluate plants under spaced planted conditions although commercial wheat production is performed using solid stands. Grain protein content is a quantitatively inherited trait, and single plant selection for other quantitative characters such as yield is usually not effective in wheat, although some researchers have reported progress by selecting for yield among single F2 plants. With the availability of fast and efficient protein determination techniques, it would be desirable to evaluate grain protein content among spaced plants in early segregating generations. Certain plant growth traits such as total dry matter, harvest index and protein yield can

have an effect on grain protein content, according to previous investigations. It was of interest to evaluate grain protein content and plant growth traits under different sowing densities to determine if early evaluation of these traits could be indirectly used to improve grain protein content (Chapter 2).

The third approach to study trait associations was the application of a plant growth regulator (Paclobutrazol) to artificially manipulate plant traits within genotypes. Paclobutrazol has been shown to change harvest index in cool-season grasses (Albeke et al., 1983). To evaluate the effect of harvest index on grain protein content, Paclobutrazol was applied on wheat genotypes to manipulate harvest index and observe changes on grain protein content (Chapter 3).

REVIEW OF LITERATURE

Influence of the environment on grain protein content

Environmental factors usually cause the largest variation in grain protein (Kramer, 1979; McNeal et al., 1982). Kibite and Evans (1984) stated that grain protein content was more influenced by environmental factors than by genetic effects. Major environmental factors influencing protein content are: a) soil fertility, b) water availability, and c) temperature (Campbell and Davidson, 1979).

Both high grain yield and high protein content can be obtained with high nutrient availability as shown by Morris and Paulsen (1985) and Spiertz and Ellen (1978). Kramer (1979) observed that at very low fertility levels, grain yields increase linearly with added N while protein remains unchanged. With added nitrogen (N), grain yields level off, but a higher grain protein percentage is achieved. Campbell and Davidson (1979), noted that N 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.

Terman et al. (1969) observed that N applied with adequate moisture increased grain yield, but when water was limited the main effect of N was to increase protein

content. They also noted that in dry-land experiments, both yield and protein increased in response to applied N. When no grain yield response occurred, added N increased protein content. Campbell and Davidson (1979) noted that 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) 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 at high temperatures, protein synthesis is more enhanced than starch synthesis. 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 N quantity.

Grain yield vs. protein percentage

Higher grain yields usually means lower grain protein, as yield is often negatively associated with protein percentage (McNeal et al., 1982; Loffler et al., 1985). 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 approximately 15% more protein (Schimdt et al., 1979). Bio-energetic 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 grown 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).

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 (Austin et al., 1980). In their study, newer cultivars of winter wheat released in the U.K. out-yielded 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. 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. Cox et al. (1989), however, did not detect significant differences in grain protein content between old and modern Hard Red Winter Wheat cultivars released in the U.S.A in the last seventy years.

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 spring wheat lines, ranging from -0.64 to -0.71.

Three spring wheat 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.

Semi-dwarf wheat cultivars have a larger sink than taller 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 semi-dwarf cultivars. According to Bhatia (1975) the negative association between harvest index and grain protein could be the result of a larger sink in semi-dwarf cultivars. 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.

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) increase 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. A strong positive correlation between dry matter accumulation and plant N content was detected. 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 (Spiertz and Ellen, 1978). Dalling et al. (1976) observed different translocation efficiencies from the different organs of the plant. Nearly 80 % of the N present in the leaves at anthesis was removed at maturity. The translocation efficiency of the stems was 65%. Roots redistributed between 21 to 29% of their N. They noted that the roots offer a potential for improvement in N translocation. 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 (ratio of grain N to total plant N) 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. Morgan and Parton (1989) observed that ammonia volatilization is highest during wheat grain filling.

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: "Pro1" and "Pro2", which were postulated to act independently of carbohydrate production. "Pro1" was located on the long arm of chromosome 5D. "Pro2" was not closely linked to "Pro1" 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 United States Department of Agriculture 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 winter wheat 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). Stein et al. (1988) have suggested that the high protein genes of Plainsman V are located on chromosomes 1A, 1B and 7A.

Genes for high protein apparently influence wheat N nutrition (Day et al., 1985). Differences in N harvest index of grain N to total plant N) were responsible for the high grain protein percentage of the winter wheat 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 0.54 to 0.69 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 low broad sense heritability estimates ranging from 0.16 to 0.25 in winter wheat. Haunold et al. (1962), working with different crosses, 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 values (Haunold et al., 1962) to high values (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 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 and plant traits

A positive association between grain protein content and kernel hardness has been postulated (Sampson et al., 1983). Genetic studies, however, have shown no association between these traits (Davis et al., 1961; Trupp, 1976; Sampson et al., 1983; Lorenzo, 1985). Trupp (1976) observed that when protein increased, kernel texture became harder. However, Pomeranz et al. (1985) observed that grain protein content was not correlated with hardness in a test of fifteen cultivars across eleven locations, although some cultivars showed significant relationships between protein content and hardness.

Baker (1977) stated that one or two major genes were acting to determine kernel hardness in spring wheat, their expression depended on the parents crossed. A single gene was detected in the cultivar "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).

The presence of a polypeptide of approximate molecular weight of 15,000 Daltons in the endosperm appears to play an important role in determining endosperm softness (Greenwell and Schonfield, 1986). Sulphur 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).

Plant height and grain protein 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. Nitrogen harvest index and total N at maturity had positive coefficients, while both harvest index and biological yield had negative coefficients in the regression equation.

Protein yield

Several researchers (McNeal et al., 1982; Loffler and Busch, 1982; McKendry et al., 1988) 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 higher yielding and had intermediate protein percentages. 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.

CHAPTER 1

POSSIBLE ASSOCIATIONS BETWEEN GRAIN PROTEIN CONTENT AND SELECTED TRAITS IN WINTER WHEAT POPULATIONS

Abstract

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 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, to enhance grain yield. Parents, F4, and F5 generations of three crosses were solid-planted in two environments in Oregon during two years to study the association of grain protein content with grain and biological yields, harvest index and related traits. Correlation coefficients showed moderate negative associations between grain protein and grain yield, and also between grain protein content and harvest index. Genetic correlations were larger than phenotypic correlations, while environmental correlations were low, suggesting the presence of negative genetic relationships between grain protein content with grain yield and with harvest index. Grain yield and harvest index were the most important traits affecting grain protein content as estimated by path coefficient analyses. These results suggest that selection for high yield should not be based on further increases of harvest index because grain protein will decrease.

Introduction

Grain yield and grain protein content in wheat have been reported to be inversely associated (Loffler and Busch, 1982; Cox et al., 1985). Under the environment observed in the Pacific Northwest, grain yield of wheat is high and grain protein content is usually low. As a consequence, this region is known for the production of low protein soft white winter wheat. One objective of the Oregon State University breeding program is to provide options for the growers through the development of Hard Winter Wheat cultivars with enhanced grain protein content. By elucidating the factors contributing to a possible negative association between grain yield and protein content, breeders may be able to select a plant type which combines high grain yield with acceptable protein levels.

The inverse association of grain yield and protein could result from the use of harvest index to improve grain yield. Austin et al. (1980) observed that the higher grain yield in semi-dwarf cultivars results from increasing harvest index. They suggested that N uptake is not keeping up with the larger amount of carbohydrates in the grain of semi-dwarf 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). McNeal et al. (1972) found negative associations, ranging from -0.64 to -0.71, between grain protein percentage and harvest index among F4 lines. Negative associations between harvest index and grain protein could be the result of a larger sink in modern semi-dwarf cultivars (Bhatia, 1975). 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 nitrogen translocated to the grain. Protein decreased as harvest index increased.

Austin et al. (1980) reported that at anthesis, plants contained 83% of the total N present at maturity, and the grain had 68% of the total N in the mature plant. A strong positive correlation between dry matter accumulation and plant N content was detected. Austin et al. (1977) suggested that plant biomass could be used as a selection criterion to improve nitrogen uptake. Loffler and Busch (1982), however, observed no association between grain protein content and biological yield. Lorenzo (1985) reported that the nature of the associations between grain protein content and biological yield were different for spring and winter wheat. He suggested that biomass yield could be used as a selection criteria in winter wheat to improve grain yield and grain protein content simultaneously. In spring wheat he observed a negative

association between grain protein content and biological yield.

Several researchers (McNeal et al., 1982; Loffler and Busch, 1982; McKendry et al., 1988) 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. Mc Neal et al. (1982) were able to obtain lines with high yield and intermediate protein content by selecting for protein yield. While Loffler and Busch (1982) observed that selection for protein yield increased grain yield and decreased grain protein content.

Three populations developed from crosses of Hard Red Winter Wheat were evaluated in two environmentally diverse locations in the Pacific Northwest. The objective was to evaluate the importance of associations between grain protein content and morphological traits and also examine the inheritance of grain protein content, biological yield, harvest index and protein yield.

Materials and methods

Experimental materials

Three selections and a cultivar representing Hard Red Winter Wheat germplasm were used as parental material. These included:

1) Protein 5221: A semi-dwarf high protein selection developed by a private company for the Great Plains of the U.S.A.
2) CR8601: (Pumafen // Ciano "S" / Gallo)
3) CR8313 (Probstorfer Extrem / Tobari 66). Semi-dwarf selections resulting from the CIMMYT/Oregon State University International Spring x Winter germplasm enhancement program.
4) Centura: (Warrior*5 / Agent // NE 68457 /3/ Centurk 78). Standard height cultivar released by the University of Nebraska.

Experimental sites

Experiments were conducted in the 1987/1988 season at Chambers farm, near Corvallis, Oregon; and at Rugg farm near Pendleton, Oregon. In the 1988/1989 season, experiments were conducted at the Crop Science Field laboratory near Corvallis; and at Rugg farm near Pendleton.

Soil type information: At the Chambers farm in Corvallis is a Chehalis Silty Clay Loam (fine-silty, mixed,

mesic Cumulic Ultic Haploxeroll). At the Crop Science Field laboratory in Corvallis is a fine, silty mixed mesic Aquultic Argixeroll. The soil type at Pendleton is a coarse silty typic Haploxeroll.

At Chambers in the 1987/88 season, a total of 170 kg N ha^{-1} were applied at Feekes scale 4. At the Crop Science Field laboratory in the 1988/89 season, a total of 120 kg N ha^{-1} and 24 kg S ha^{-1} were applied in the form of 30-0-0-6 fertilizer in two evenly split applications made at the following growth stages: tillering (Feekes stage 4) and jointing Feekes (stage 8). Prior to planting, 40 kg N ha^{-1} and 6 kg S ha^{-1} as ammonium sulphate were applied in the 1988/1989 season. Weeds were controlled with a fall application of 1.68 kg a.i. ha^{-1} of Diuron each year. Plants were protected from foliar diseases each year by four applications of the fungicide Propiconazole used at the rate of 0.23 kg a.i. ha^{-1}.

At Pendleton, nitrogen (anhydrous ammonia) at the rate of 100 kg N ha^{-1} and sulphur at the rate of 20 kg S ha^{-1} were applied at the time of planting each year. Bromoxynil was applied each year in the spring at a rate of 1.4 l ha^{-1}. A summary of climatological data for both sites is presented in Appendix Tables 1 and 2.

Experimental procedures

Selection P5221 was the common parent used to develop

three populations: P5221/CR8601; P5221/CR8313; and P5221/Centura. The F1 plants were grown in the greenhouse in 1985 and harvested on 20 January 1986. F2 seeds were space-planted on 19 February 1986 in the field at East Farm, near Corvallis, Oregon. One-hundred F2 plants chosen at random from each of the three crosses were harvested on 15 August 1986. The resulting F3 progenies from individual F2 plants were planted at a seeding rate of approximately 200 seeds m^{-2}, as two row plots at Corvallis on 14 October 1986 and harvested on 27 July 1987. Parents, 100 F2-derived F4 progenies of the crosses P5221/CR8313 and P5221/Centura were solid-planted on 10 October 1987 in Pendleton. Parents, 100 F_2-derived F4 progenies of the crosses P5221/ CR8313 and P5221/CR8601 were planted in the field at Corvallis on 17 October 1987. Plots at both sites consisted of three 1.5 m rows. Seeding rate was approximately 220 seeds m^{-2}. A randomized complete block with three replications was used at both sites.

In the 1988/1989 season two experiments at each of the two locations were planted at a seeding rate of approximately 220 seeds m^{-2} on 8 October 1988 at Pendleton and 16 October 1988 at Corvallis. These experiments included 51 randomly selected F2-derived F5 progenies from the P5221/CR8313 and P5221/CR8601 crosses. The cross P5221/Centura was not planted in 1988/1989 because of lack of seed due to lodging problems in 1987/1988. Harvest dates

were 23 July 1989 at Pendleton and 31 July 1989 at Corvallis. The experimental design used a replications-in-blocks design (Comstock and Robinson, 1952), with three replications and three blocks. Degrees of freedom and expectation of mean squares for experiments with F4 and F5 progenies are presented in Appendix Table 3.

Data collection

The following measurements were collected on a per plot basis for both growing seasons:

a) Heading date: Number of days from January 1 to the date when approximately 50% of the spikes had emerged (determined in both years at Corvallis and in 1988/1989 at Pendleton).

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

c) Grain filling period: Number of days between heading date and maturity (determined at Corvallis only).

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

e) Biological yield: weight (Mg ha^{-1}) of two 0.5 m row sections of plants at maturity, excluding the roots.

f) Grain yield: weight (Mg ha^{-1}) of all the kernels from a two 0.5 m row sections of plants at maturity for the F3, and F4 trials. In the F5 trials, whole plots were harvested with a combine.

g) Harvest index (%) : Grain yield divided by biological yield and multiplied by 100.

h) Non-grain biomass (Leaf + culm + chaff): weight (Mg ha^{-1}) obtained by difference between biological yield and grain yield.

i) Kernel weight: weight (g) of individual kernels, determined from a sample of 100 kernels.

j) Grain protein content (g kg^{-1}): determined by near infrared reflectance spectroscopy with a Technicon Infralyser 400 from approximately 20 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 140 g kg^{-1} moisture basis.

Analytical procedures

a) Analysis of variance was conducted for each trait using plot values. A random effects linear model was assumed.

b) Estimates of heritability (H) were determined from the components of variance (Knapp et al., 1987). Exact confidence intervals (1- α = 90%) of heritability estimates were also calculated (Knapp et al., 1985).

Estimates of heritability in standard units were computed using parent-offspring correlation (Fehr, 1987).

c) Phenotypic correlations were estimated as $r_p = M_{ij}[(\sigma^2_{ii})(\sigma^2_{jj})]^{-0.5}$, where rp is the phenotypic correlation coefficient , M_{ij} is the mean cross product for

progenies, and σ^2_{ii} and σ^2_{jj} are phenotypic variances for traits i and j, respectively. Confidence intervals (99%) for the phenotypic correlations were determined for those correlations that were significantly different from zero (Snedecor and Cochran, 1980).

d) Environmental correlation coefficients were estimated as $r_e = \sigma^2_{eij} \; [(\sigma^2_{eii})(\sigma^2_{ejj})]^{-0.5}$, where r_e is the environmental correlation coefficient, σ^2_{eij} is the error covariance and σ^2_{eii} and σ^2_{ejj} are the error variances for traits i and j, respectively.

e) Genetic correlations were calculated as $r_g = \sigma^2_{pij}[(\sigma^2_{ii})(\sigma^2_{jj})]^{-0.5}$, where r_g is the genetic correlation coefficient, σ^2_{pij} is the genetic covariance of traits i and j, σ^2_{ii}, σ^2_{jj} are the genetic variances for trait i and j, respectively.

f) Path coefficient analyses using phenotypic correlations (Li, 1956) and the procedure regression from SAS (SAS, 1985) were used to determine direct and indirect effects of different traits on grain protein content for each cross. Selection of variables was carried out using the stepwise method, and only traits significant at the 15% probability level were included.

g) Predicted correlated responses for grain protein content by selecting for harvest index were estimated using the equation proposed by Falconer (1981).

Results

Mean values for seven traits of interest of the parents of the three crosses grown at Pendleton are presented in Table 1.1. In the 1987/1988 season, there were no significant differences between parents for any of these traits. In the 1988/1989 season, CR8313 had higher biological yield, non-grain biomass (leaves + culms + chaff), grain yield, and lower grain protein content than P5221. No differences were detected for these parents for harvest index, plant height and protein yield. At Pendleton in the 1988/1989 season (Table 1.1), CR8601 was taller, had higher biological yield and non-grain biomass than P5221. There were no significant differences between these selections for grain yield, harvest index, grain protein content and protein yield.

Table 1.2 shows mean values of the seven main traits of interest for the parental selections P5221 and CR8601 grown at Corvallis during two seasons. CR8601 was taller and had higher biological yield and non-grain biomass than P5221 in both seasons. CR8601 had higher grain protein content than P5221 in 1987/1988, but no significant differences were observed for this trait in 1988/1989. In the 1987/1988 season, grain yield was similar for both parents, while CR8601 had higher yield than P5221 in 1988/1989. No significant differences between these parents were detected

for harvest index and protein yield in either season.

Mean squares for seven traits of the progenies of the three crosses is presented in Table 1.3. Differences were detected among progenies within populations for most traits in each cross. There were no significant differences for biological yield, grain yield and protein yield in the F4 progenies of the P5221/8313 and P5221/Centura crosses. Differences among progenies were observed for grain protein content in all progenies, except among F4 progenies of the P5221/Centura cross.

Components of variance heritability estimates are presented in Table 1.4. Heritability estimates for biological yield, non-grain biomass and harvest index were all moderate to low. Grain yield had high to low values, and it was not different from zero in the F4 of the crosses P5221/CR8313 and P5221/Centura. Estimates for harvest index, grain protein content and protein yield ranged from high to low in the three crosses. In the P5221/Centura cross, a negative value in the lower limit of the confidence interval was observed for grain protein content. Plant height had moderate to high values of heritability.

When heritability was estimated with the parent-offspring correlation (Table 1.5), the values for grain yield, biological yield, non-grain biomass and protein yield, ranged from low to values not significantly different from zero. Heritability estimates for harvest index were

low to moderate, while plant height had consistently high values. Grain protein content estimates ranged from moderate to not different from zero.

Phenotypic correlations revealed no associations between grain protein content with biological yield, non-grain biomass, plant height, and protein yield (Table 1.6). Moderate to low negative associations between grain yield and grain protein content were detected. The phenotypic correlations between grain protein content and harvest index were also negative and moderate to low in magnitude. The range of the confidence intervals of the significant phenotypic correlations was moderate to large.

No significant phenotypic associations were detected between protein yield and grain protein content. Protein yield was highly correlated with grain yield, as measured by the magnitude of the phenotypic associations between these traits ranging from 0.81 to 0.92 (data not shown).

Genetic correlations were generally larger in magnitude than the phenotypic correlations (Table 1.7). Environmental correlations were generally non-significant (Table 1.8). The environment was important in the correlation between grain protein content and grain yield in the F5 of the P5221/CR8313 cross and in the F4 of the P5221/CR8601 cross. The environmental correlation between grain protein content and harvest index was also significant in the F4 of the P5221/CR8601 cross.

Path coefficient analyses showed that the most important traits affecting grain protein content were grain yield and harvest index (Table 1.9). The direct effect of harvest index and grain yield was only moderate and not significant in some cases. The effect of other plant traits was small and in most cases not significant. R^2 values were low in magnitude, indicating a large residual variation.

Selection for harvest index in these crosses, would have a moderate effect on grain protein content as shown by the predicted correlated response in Table 1.10. The indirect effect on grain protein by selecting for harvest index ranged from -1.02 to -8.99 g kg^{-1}, representing a reduction ranging between 1 to 7% in grain protein content in the selected progenies.

Discussion

High protein wheats are usually grown in areas with continental climate where grain yields are usually moderate. In areas with oceanic climate like the Pacific Northwest, wheat grain yields are high but grain protein is usually low.

The objective of this investigation was to suggest breeding strategies for the development of Hard Red Winter Wheat cultivars with enhanced grain protein content levels in the Pacific Northwest's high yielding environment.

Populations of Hard Red Winter Wheat were developed from crosses with the wheat Selection P5221, a source of high grain protein from the Great Plains. P5221 generally failed to express a higher protein level than the other wheat parents used in this study. Grain yield of P5221 was generally similar to the other parental selections under the conditions prevalent during two seasons at two testing locations in Oregon. A possible explanation is that this selection was developed for the Great Plains where grain yields are usually lower than in the Pacific Northwest. Nevertheless, F4 and F5 progenies derived from the crosses involving P5221 showed significant variability for grain protein content, suggesting that this Selection could be used for the improvement of grain protein content.

Components of variance heritability estimates of grain

protein content ranged from low to high in the three crosses, agreeing with results reported by Lofgren et al. (1968) and Corpuz et al. (1983). In the P5221/Centura cross, the negative value observed for the lower limit of the confidence interval indicated absence of genetic variability for grain protein content among the progenies of this particular cross. Heritability of grain protein content estimated by parent-offspring correlations were mostly not significantly different from zero. Sampson et al. (1983) reported similar values for this trait. These results suggest that selection for grain protein content in early segregating generations would be of little use. However, if a trait with high heritability were associated with grain protein content, indirect selection for grain protein content could be applied by selecting for the related trait (Falconer, 1981). In this study, none of the examined traits was highly associated with grain protein content. Thus, direct selection for grain protein content in late generations would be more effective than indirect selection in these crosses.

Parent-offspring heritability estimates for harvest index were low to moderate but were consistently significant, indicating that harvest index could be selected in early generations.

Grain yield and grain protein content are usually inversely associated in wheat (Cox et al., 1985; Loffler et

al., 1985). In this study, phenotypic correlations between grain protein content and grain yield were moderate to low in the three crosses evaluated. These results agree with those reported by Cox et al. (1985) who evaluated random progenies of a wheat cross. While contrasting with the high values observed by Loffler et al. (1985) who used fixed cultivars and selections in his experiment. Genotypic correlations were similar in sign but larger in magnitude than phenotypic correlations. Genetic differences were apparently responsible for the magnitude of the phenotypic correlations, as the environmental correlations were generally not significantly different from zero. In contrast with the results reported by Kibite and Evans (1984), these results suggest a genetic relationship between grain protein content and grain yield. The usually negative relation between grain protein content and grain yield is generally considered to be due to genetic causes (Stuber et al., 1962; McNeal et al., 1972). Genetic correlations between two traits are caused by either linkage or pleiotropy. Simultaneous improvements of grain yield and grain protein content have been obtained in some wheat cultivars (Middleton et al., 1954; Schmidt et al., 1979), indicating that pleiotropy does not play a role in controlling these traits. Simultaneous progress in these traits observed by Loffler et al. (1983) through the use of recurrent selection suggest that this negative relationship

is caused by linkage. Kibite and Evans (1987), however, failed to break this negative relation using recurrent selection, although this failure could be attributed to the use of only one cycle of intermating.

The association between grain protein content and harvest index among F4 and F5 progenies were also negative and moderate to low in magnitude as measured by phenotypic and genotypic correlations, which agrees with the results of Loffler and Busch (1982). The environment did not generally influence this relationship as environmental correlations were not significantly different from zero in most cases.

Grain yield and harvest index were the most important traits directly affecting grain protein content as determined by path coefficient analyses, although their direct effect was not significant in some cases. The magnitude of the R^2 values was low, indicating that only part of the variability observed in grain protein content could be explained by these traits.

The association between grain protein content and harvest index indicates that grain protein will be reduced by continued selection for higher yields through harvest index. Selection for harvest index in these crosses, would have a moderate effect ranging between 1 to 7% on grain protein content as shown by the predicted correlated responses.

Increases in grain yield have been made by breeders in

the last seventy years while maintaining grain protein content levels (Cox et al., 1989). The yield advantage of semi-dwarf cultivars is apparently due to an increased harvest index (Austin et al., 1980). To achieve further improvement of grain yield and protein content, biomass yield should be increased. Higher biomass yields would increase the amount nitrogen to be redistributed at maturity.

The most important source of nitrogen for the grain is nitrogen redistributed from the non-grain biomass into the grain. Van Sanford and McKown (1987) have reported that approximately 80% of the nitrogen in the grain was already present at anthesis suggesting that the amount of vegetative growth is important in determining the final protein content of the grain. Biological yield has been used as a measure of vegetative growth but it also tends to reflect variation in grain yield, as grain yield is included in biological yield. In this study, the yield of non-grain biomass (leaves + culm + chaff) was reported with the aim of finding a plant growth variable independent of grain yield which could be related to grain protein content. Dalling (1985) indicated that one factor affecting grain nitrogen is total plant nitrogen uptake which is redistributed at maturity. By increasing biomass yield, total plant nitrogen uptake would be enhanced and more nitrogen would be available for redistribution into the grain. However, in these crosses

and environments, there was generally no association between grain protein content with either biological yield or non-grain biomass. In contrast with the results reported by Lorenzo (1985) who detected positive associations between grain protein content and biological yield among cultivars and selections of winter wheat.

Protein yield was not phenotypically associated with grain protein content. Protein yield was largely affected by variation in grain yield, as phenotypic correlations between grain yield and protein yield were high (ranging from 0.81 to 0.92). These results agree with those of Loffler and Busch (1982). In these populations and environments selection for protein yield would favor high grain yield but not higher grain protein content.

Based on the results of this study, a successful breeding strategy for increased grain protein content and high yield for the Pacific Northwest should include parents with high yield but also high biological yield, resulting in a low harvest index. Higher biomass yields would increase the amount of nitrogen to be redistributed at maturity contributing to a higher grain protein content, although plant height would be increased. Selection for grain yield, biological yield and grain protein content should be delayed until late generations because of their moderate to low heritability.

Table 1.1. Mean values for seven traits involving parental selections evaluated at Pendleton (Oregon) in 1987/1988 and 1988/1989.

Parent or progeny	Biological yield	Non-grain biomass	Grain yield	Harvest index	Plant height	Grain protein	Protein yield
	Mg ha^{-1}	Mg ha^{-1}	Mg ha^{-1}	%	cm	g kg^{-1}	kg ha^{-1}
1987/1988							
P5221	17.7	11.6	5.8	34.7	108.9	111.0	682.1
CR8313	17.3	10.9	5.9	37.2	109.2	113.0	720.5
$LSD_{0.05}$	3.2	2.0	1.3	3.3	8.1	18.3	164.7
P5221	14.4	9.5	4.9	34.0	110.9	134.7	657.6
Centura	15.0	10.2	4.8	32.0	119.4	132.6	635.9
$LSD_{0.05}$	2.9	2.0	1.1	3.7	8.9	17.5	167.1
1988/1989							
P5221	15.4b	10.4b	5.1b	33.5	110.6	123.8a	631.5
CR8313	18.4a	13.2a	6.0a	32.9	116.7	112.6b	675.2
$LSD_{0.05}$	2.5	2.0	0.6	3.2	7.4	10.9	75.4
P5221	19.4b	14.3b	5.1	26.6	119.4b	108.0	552.9
CR8601	22.3a	16.7a	5.6	25.3	128.3a	117.6	663.0
$LSD_{0.05}$	2.7	2.3	0.5	2.0	6.4	14.2	111.3

Mean values displaying different letters on the same column within year and between parents are significantly different at the 5% probability level.
$LSD_{0.05}$ indicates significant differences at the 5% probability level between parental means.

Table 1.2. Mean values for seven traits of selections P5221 and CR8601 evaluated during two seasons at Corvallis (Oregon).

Parent or progeny	Biological yield	Non-grain biomass	Grain yield	Harvest index	Plant height	Grain protein	Protein yield
	Mg ha^{-1}	Mg ha^{-1}	Mg ha^{-1}	%	cm	g kg^{-1}	kg ha^{-1}
1987/1988							
P5221	17.7b	14.0b	3.7	19.8	114.6b	137.9b	499.8
CR8601	24.2a	20.5a	3.7	15.3	127.9a	154.2a	554.7
$LSD_{0.05}$	5.3	4.5	1.5	5.3	3.8	7.9	108.3
1988/1989							
P5221	11.5b	7.4b	4.1b	35.6	116.7b	111.7	500.8
CR8601	16.7a	11.8a	5.0a	31.2	130.0a	105.4	538.8
$LSD_{0.05}$	3.6	3.4	0.6	5.8	2.8	8.3	79.0

Mean values displaying different letters on the same column within year are significantly different at the 5% probability level.
LSD indicates significant differences between parental means at the 5% probability level.

Table 1.3. Observed mean squares of F4 and F5 progenies for seven traits involving three crosses of winter wheat grown at two locations in 1987/88 and 1988/89.

Cross	Biolog. yield	Non-grain biomass	Grain yield	Harvest index	Plant height	Grain protein content	Protein yield
P5221/8313							
F4	10.4	6.79**	1.1	32.4**	835.4**	284.6 *	182.8
C.V. (%)	17.7	18.6	16.5	12.9	8.5	12.0	23.5
F5	14.7**	12.21**	1.3**	42.6**	546.2**	304.7 **	130.7**
C.V. (%)	15.0	17.6	12.8	10.0	7.2	9.4	13.1
P5221/8601							
F4	49.0**	36.0**	3.5**	35.6**	558.9**	285.3 **	529.9*
C.V. (%)	22.4	19.9	20.1	17.1	7.9	6.0	34.0
F5 Corvallis	27.1**	19.7**	1.3**	56.1**	478.0**	265.4 **	130.4**
C.V. (%)	26.3	34.0	14.4	17.1	4.4	9.6	16.0
F5 Pendleton	18.2**	13.4**	1.9**	66.2**	450.2**	528.2 **	178.8**
C.V. (%)	15.9	19.8	11.0	14.1	7.9	13.1	15.6
P5221/Centura							
F4	9.5	5.2*	1.3	25.2**	222.4**	275.6	221.9
C.V. (%)	19.5	19.6	18.1	11.1	8.2	11.6	26.5

* ,** F test significant at the 0.05 and 0.01 levels of probability, respectively.

Table 1.4. Estimates of components of variance heritability with 90% exact confidence intervals (in parentheses) for seven traits involving three winter wheat crosses grown at two locations in 1987/88 and 1988/89.

Cross	Biological yield	Non-grain biomass	Grain yield	Harvest index	Plant height	Grain protein content	Protein yield
	%						
P5221/8313							
F4	40(16,57)	54(36,67)	20(-11,43)	67(53,76)	88(83,91)	32(6,52)	15(-16,38)
F5	63(44,76)	67(50,78)	75(63,84)	76(65,85)	85(78,90)	54(32,70)	61(42,75)
P5221/8601							
F4	50(30,54)	55(38,58)	35(10,54)	42(19,58)	89(84,92)	75(66,82)	27(-2,48)
F5 Corv.	62(44,75)	56(34,71)	80(70,87)	52(29,69)	92(88,95)	55(33,71)	70(55,80)
F5 Pend.	62(44,76)	56(34,71)	89(83,93)	80(70,87)	74(61,83)	57(35,72)	69(54,80)
P5221/Centura							
F4	16(-17,40)	30(3,50)	4(-34,31)	42(19,58)	56(38,58)	21(-10,43)	1(-20,22)

Table 1.5. Estimates of heritability (parent-offspring correlation[†]) for six traits of three crosses of winter wheat grown at two locations in 1987/88 and 1988/89.

Cross	Biolog. yield	Non-grain biomass	Grain yield	Harvest index	Plant height	Grain protein content	Protein yield
P5221/8313							
F3-F4	0.28*	0.40**	0.13	0.40**	0.87**	0.01	0.11
F3-F5	0.20	0.38**	0.00	0.56**	0.93**	0.06	0.01
F4-F5	0.15	0.25	0.19	0.56**	0.95**	0.18	0.15
P5221/8601							
F3-F4	0.41**	0.44**	0.24	0.39*	0.88**	0.46**	0.25
F3-F5 Corv.	0.34*	0.38*	0.21	0.34*	0.89**	0.05	0.19
F3-F5 Pend.	0.07	0.18	0.26	0.56**	0.90**	0.21	0.27
F4-F5 Corv.	0.22	0.24	0.42**	0.35*	0.92**	0.55**	0.43**
F4-F5 Pend.	0.16	0.20	0.32*	0.39*	0.93**	0.38**	0.34*
P5221/Centura							
F3-F4	0.04	0.26*	0.12	0.36*	0.86**	0.36**	0.09

*, ** Significantly different from zero at the 0.05 and 0.01 levels of probability, respectively.

[†]F3-F4 correlations, n = 100; F3-F5 and F4-F5 correlations, n = 51.

Table 1.6. Phenotypic correlation coefficients[†] with 99% confidence intervals (in parentheses) of grain protein content and six plant traits in three crosses of winter wheat grown at two locations in 1987/88 and 1988/89.

Cross	Grain protein content vs.					
	Bio. yield	Non-grain biomass	Grain yield	Harvest index	Plant height	Prot. yield
P5221/8313						
F4	0.03	0.16	-0.32*(-0.07,-0.53)	-0.42**(-0.18,-0.61)	0.24	0.28
F5	-0.18	0.00	-0.61**(-0.32,-0.79)	-0.48**(-0.15,-0.71)	0.19	0.11
P5221/8601						
F4 Corv.	-0.07	0.08	-0.50**(-0.28,-0.67)	-0.57**(-0.36,-0.72)	0.27	-0.24
F5 Corv.	-0.29	-0.22	-0.46**(-0.12,-0.70)	-0.59**(-0.30,-0.76)	0.31	-0.02
F5 Pend.	-0.25	-0.09	-0.53**(-0.21,-0.74)	-0.41**(-0.06,-0.67)	0.00	0.05
P5221/Centura						
F4	0.13	0.29	-0.32*(-0.07,-0.53)	-0.55**(-0.34,-0.70)	0.08	0.28

*, ** Significantly different from zero at the 0.05 and 0.01 levels of probability, respectively.

[†]F4 correlations, n = 300; F5 correlations, n = 153.

Table 1.7. Genotypic correlation coefficients[†] of grain protein content and six plant traits in three crosses of winter wheat grown at two locations in 1987/88 and 1988/89.

Cross	Grain protein content vs.					
	Biological yield	Non-grain biomass	Grain yield	Harvest index	Plant height	Protein yield
P5221/8313						
F4	0.62	0.79	-0.60	-0.93	0.65	0.47
F5	-0.15	0.10	-0.76	-0.68	0.35	0.01
P5221/8601						
F4 Corvallis	0.05	0.19	-0.60	-0.68	0.34	-0.23
F5 Corvallis	-0.48	-0.40	-0.66	-0.66	0.42	-0.33
F5 Pendleton	-0.21	-0.16	-0.67	-0.56	0.21	-0.29
P5221/Centura						
F4	0.61	0.65	-0.36	-0.70	0.29	0.39

[†]F4 correlations, n = 300; F5 correlations, n = 153.

Table 1.8. Environmental correlation coefficients[†] of grain protein content and six plant traits in three crosses of winter wheat grown at two locations in 1987/88 and 1988/89.

Cross	Grain protein content vs.					
	Biological yield	Non-grain biomass	Grain yield	Harvest index	Plant height	Protein yield
P5221/8313						
F4	-0.30*	-0.31*	-0.22	0.03	-0.35*	0.26
F5	-0.21	-0.15	-0.72**	-0.13	-0.18	0.28
P5221/8601						
F4 Corvallis	-0.26	-0.14	-0.48**	-0.50**	-0.02	-0.33*
F5 Corvallis	-0.06	-0.01	-0.08	-0.01	-0.09	0.48**
F5 Pendleton	-0.30	-0.01	-0.25	-0.11	-0.12	0.63**
P5221/Centura						
F4	0.11	0.16	-0.01	-0.18	-0.02	0.42**

*, ** Significantly different from zero at the 0.05 and 0.01 levels of probability, respectively.

[†]F4 correlations, n = 300; F5 correlations, n = 153.

Table 1.9. Direct effects of various plant traits on grain protein content from path coefficient analyses of three crosses of winter wheat grown at two locations in 1987/88 and 1988/89.

Cross	Direct effect							R^2
	Grain yield	Harv. index	Bio. yield	Kernel weight	Head. date	Matur. date	Height	
P5221/8313								
F4	-0.06	-0.35	NS	NS	-	-	NS	0.43
F5	-0.48	NS	NS	NS	NS	NS	NS	0.32
P5221/8601								
F4	NS	-0.57	NS	NS	NS	NS	NS	0.34
F5 Corv.	-0.48	NS	0.37	NS	NS	-0.38	0.30	0.42
F5 Pend.	-0.52	NS	NS	NS	-0.30	-	NS	0.40
P5221/ Centura								
F4	NS	-0.53	NS	-0.26	-	-	NS	0.38

NS indicates not significant at the 0.15 probability level. "-" indicates not measured.

[†]F4 path analyses, n = 100; F5 path analyses, n = 51.

Table 1.10. Predicted correlated responses for grain protein content (g kg^{-1}) by selecting for harvest index at two selection intensities in three crosses of winter wheat.

	Cross					
	P5221/8313		P5221/8601			P5221/ Centura
Selection intensity	F4	F5	F4	F5 Pend.	F5 Corv.	F4
%						
5	-8.59	-7.70	-4.86	-8.99	-1.16	-2.58
10	-7.50	-6.72	-4.24	-7.84	-1.02	-2.26

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CHAPTER 2

EVALUATION OF GRAIN PROTEIN CONTENT AND PLANT GROWTH TRAITS IN SOLID AND SPACE-PLANTED WHEAT

Abstract

The objective of this study was to investigate if grain protein content, grain yield, harvest index and biological yield performance in wheat are related when plants are grown under different sowing densities. Randomly derived F4 and F5 progenies from two crosses of Hard Red Winter Wheat were planted during the 1987/1988 and 1988/1989 season at Corvallis (Oregon). Values for grain protein content and selected agronomic traits obtained from individually spaced plants were correlated with solid-seeded plot means using simple and Spearman's rank correlations. Plant height and heading date were highly correlated between solid and space-planted conditions. Harvest index had a moderate correlation between the two planting densities, while grain protein content and grain yield were generally not associated. Phenotypic correlations between grain protein content and selected agronomic traits were also compared for the two planting arrangements with no significant differences detected. These results suggest that harvest index could be evaluated under space-planted conditions while grain protein content and grain yield would require solid seeded plantings.

Introduction

Wheat breeders commonly evaluate early generation progenies under space-planted environments although wheat is commercially produced using solid stands. Space-planting is suitable for qualitatively inherited traits, where there is little interaction with the environment. Single plant selection for quantitative characters such as yield is usually not effective in wheat (McGinnis and Shebeski, 1968) or barley (Hanson et al., 1979). Although Mitchell et al. (1982) observed a significant response for yield by selecting single F2 plants.

Grain protein content is a quantitatively inherited trait (Stuber et al., 1962; Chapman and McNeal, 1970; Halloran, 1981). Sunderman et al. (1965) observed low heritability values when F2 single plant data was regressed on F3 means. Haunold et al. (1962) and Sampson et al. (1983), however, reported intermediate values of heritability of grain protein content for space-planted segregating populations. Different planting densities favored different genotypes with respect to grain protein content in trials conducted by Kibite and Evans (1984). "Glenlea" had a higher grain protein content than "Sinton" (the high protein parent) when grown under space-planted conditions, but not in solid-seeded conditions. Phenotypic correlation coefficients between grain protein content and

other traits among progenies, however, were apparently similar in both planting arrangements although no statistical tests were performed. Several studies have shown that certain plant growth traits, such as protein yield (Loffler and Busch, 1982; Cox et al., 1985), total dry matter (Austin et al., 1980), and harvest index (McNeal et al., 1972) could have an effect on grain protein content. It was of interest to estimate if these traits could be evaluated under different densities, allowing breeders to select for these traits in early generations to indirectly improve grain protein content.

To investigate if the performance of individually spaced plants can be related to solid seeded stands for grain protein content and plant growth traits, progenies of two crosses were evaluated as individual plants and in solid stands during the 87/88 and 88/89 growing seasons at the Crop Science Field Laboratory near Corvallis, Oregon.

Materials and methods

Experimental materials

Three selections representing Hard Red Winter Wheat germplasm were used as parental material. These included:

1) Selection P5221: A semi-dwarf high protein selection developed by a private company for the Great Plains of the U.S.A.
2) CR8601: (Pumafen // Ciano "S" / Gallo)
3) CR8313 (Probstorfer Extrem / Tobari 66).

Both CR8601 and CR8313 are semi-dwarf selections resulting from the CIMMYT/Oregon State University International Spring x Winter germplasm enhancement program.

Experimental procedures

Selection P5221 was the common parent used to develop two populations: P5221/CR8601 and P5221/CR8313. Crosses were made in 1985 and the resulting F1 plants were grown in the greenhouse and harvested on 20 January 1986. F2 seed were space-planted on 19 February 1986 in the field at East Farm, near Corvallis, Oregon. F2 plants chosen at random from each of the two crosses were harvested on 15 August 1986. The resulting F3 progenies from individual F2 plants were planted at a seeding rate of approximately 200 seed m^{-2}, as two row plots at the Crop Science Field Laboratory

near Corvallis on 14 October 1986 and harvested on 27 July 1987. Parents and 30 F2-derived F4 progenies of the two populations were solid-planted and also space-planted in the field at Corvallis on 16 October 1987 and harvested on 2 August 1988. Parents and 30 F2-derived F5 progenies of the two crosses were solid and space-planted in the field at Corvallis on 20 October 1988 and harvested on 1 August 1989. Solid-seeded plots consisted of three 1.5 m rows in 1987/1988 and six 5 m rows in 1988/1989. The seeding rate was approximately 220 seeds m^{-2} for solid plantings. For spaced plants, the planting distance was 10 cm between plants and 30 cm between rows. Each row consisted of ten plants. Barley was planted around the experimental area as a border to reduce competition effects. A randomized complete block with three replications was used in both years.

The soil type at the experimental site is a fine, silty mixed mesic Aquultic Argixeroll. Prior to planting, 40 kg N ha^{-1} and 6 kg S ha^{-1} were applied. A total of 120 kg N ha^{-1} and 24 kg S ha^{-1} was later applied in the form of 30-0-0-6 fertilizer in two evenly split applications made at the following growth stages: tillering (Feekes stage 4), and jointing (Feekes stage 8). 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}.

Data collection

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

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

c) Biological yield: weight (g) of the whole mature plant, excluding the roots. For solid-seeded plantings: weight (Mg ha^{-1}) of two 0.5 m row sections of plants at maturity, excluding the roots.

d) Grain yield: weight (g) of all the kernels from a plant. Plants which yielded less than 10 grams of grain were discarded. For the solid-seeded plantings: weight (Mg ha^{-1}) of all the kernels from a two 0.5 m row sections of plants at maturity for the F4 trials. In the F5 solid-seeded trials, the whole plots were harvested with a combine at maturity.

e) Non-grain biomass (Leaf + culm + chaff): weight (Mg ha^{-1}) obtained by difference between biological yield and grain yield.

f) 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 100 kernels from an individual plant.

h) Grain protein content: 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 14% moisture basis.
A summary of climatological data for both growing seasons is presented in Appendix Tables 1 and 2.

Analytical procedures

a) Analysis of variance of row means for each trait was used to analyze the data from individual plants. Plot values were used for the solid-seeded experiments.

b) Simple correlations and Spearman's rank correlations estimated from progeny means were used to compare the relative performance of progenies in space and solid-seeded conditions.

c) Phenotypic correlations among progenies were estimated as $r_p = M_{ij}[(\sigma^2_{ii})(\sigma^2_{jj})]^{-0.5}$, where rp is the phenotypic correlation coefficient , M_{ij} is the mean cross product for progenies, and σ^2_{ii} and σ^2_{jj} are phenotypic variances for traits i and j, respectively. Significant coefficients were compared for both planting environments using the test proposed by Snedecor and Cochran (1980).

Results

Mean values of the F4 and F5 progenies of the two crosses grown under two planting densities are presented in Appendix Tables 4 and 5.

Mean squares for nine traits of the F4 and F5 progenies of the two crosses grown under two planting environments are presented in Table 2.1. Significant differences among progenies within populations were detected for most traits of each cross. Only for protein yield were differences not observed among space-planted F4 progenies in both crosses.

Performance of progenies for plant height and heading date were highly correlated between planting densities (Table 2.2). These correlations were moderate but highly significant for harvest index, and moderate and significant at the 5% level for kernel weight. There were no significant associations between values of individual plants and solid-seeded plots for grain protein content and grain yield except in the F5 of the P5221/CR8313 cross, where there were moderate associations between planting densities for these traits.

Differential response of genotypes for biological yield, non-grain biomass, grain yield, grain protein content and protein yield in the two planting densities was further confirmed by the low and non-significant ($P > 0.05$) coefficients of rank correlations for these traits (Table

2.3). Plant height, heading date and harvest index had moderate and highly significant rank correlation coefficients between planting environments. Kernel weight showed significant but low rank correlations with one exception: the F4 of the cross P5221/CR8313 in which the rank correlation was not significant.

Phenotypic correlations coefficients between grain protein content and eight traits measured among F4 and F5 progenies of the two crosses in both planting situations are presented in Table 2.4. Grain yield and harvest index were negatively associated with grain protein content. These correlations were significant in most cases except among F5 progenies of the P5221/CR8601 cross. There were two exceptions for a complete coincidence of the magnitude of phenotypic correlations between planting densities. These were detected in the F4 of the P5221/CR8601 cross: 1) plant height was highly correlated (0.69) with grain protein content among space-planted rows while it was very low among solid plots, and 2) kernel weight was moderately correlated (0.50) with grain protein content only among solid-seeded plots (Table 2.4).

The hypothesis that the phenotypic correlation values obtained from individually spaced plants and solid-seeded plots were estimates of the same rho (population correlation coefficient) was tested for the associations between grain protein content both with grain yield and harvest index.

Differences between phenotypic correlations in different planting densities were not significant for the relationship between grain protein content and grain yield, as detected by the lack of significance of the normal deviates (Table 2.5). These were also not significant for the relation between grain protein content and harvest index.

Discussion

Several studies of inheritance of grain protein content and plant growth traits, i.e. harvest index and biological yield have been carried out under space-planted conditions (Austin et al., 1977; McKendry et al., 1988). These investigations have assumed that responses would be similar to solid-seeded conditions. Wheat breeders, who use the pedigree system, commonly select among space-planted individual plants in early generations although wheat is commercially grown in solid stands.

Kibite and Evans (1984) reported that an observed negative association between grain protein content and grain yield was similar for space-planted and solid-seeded wheat. Although the parental cultivars used showed a different performance under the contrasting growing conditions.

The objective of the present investigation was to evaluate the validity of the information obtained from space-planted individuals by comparing with results obtained from solid-seeded stands. To address the question if the associations between grain protein content and plant growth traits are similar for individual plants and solid-seeded stands, wheat progenies were evaluated during two growing seasons.

Random F4 and F5 progenies derived from crosses with the source of high protein (Selection P5221) showed

significant variability for grain protein content and most plant growth traits in both seasons of evaluation. Performance of genotypes with respect to grain protein content, grain yield, biological yield and protein yield differed under the contrasting planting densities as shown by simple and rank correlation coefficients which were generally low and non-significant. This suggest that selection for grain protein content and grain yield should be delayed in a breeding program until genotypes can be grown under replicated solid-seeded stands.

Plant height and heading date were reliably evaluated in the space-planted situation as simple and rank correlations between space-planted and solid stands were moderate to high. Indicating that these two traits could be effectively evaluated among space-planted individuals. This was expected as these traits are qualitatively inherited (Gale and Youssefian, 1985).

Harvest index also showed a consistent performance between space-planted and solid stands as measured by simple and rank correlations. This indicates that harvest index could be reliably selected among individual plants in early generations. In the past, wheat breeders have been successful in increasing grain yield by selecting genotypes with a higher harvest index, as it is positively associated with grain yield (Sharma and Smith, 1986). Although by selecting for a higher harvest index, breeders may have

indirectly selected against grain protein content as harvest index is usually negatively associated with grain protein content, as detected in this study.

Phenotypic correlations between grain protein content and plant growth traits were generally similar under space and solid stands. Grain yield was negatively associated with grain protein content under both sowing densities, agreeing with results from Kibite and Evans (1984). Harvest index was negatively associated with grain protein content, in agreement with the results of McNeal et al. (1972) and Loffler et al. (1985) under both growing conditions. Statistical tests performed to evaluate differences between phenotypic correlation coefficients for the grain protein content relationships with grain yield and harvest index were not significant. These results suggest that studies of correlations among individual plants for these traits can be extrapolated to solid stands, although evaluation of grain protein content, grain yield, biological yield, and protein yield is not reliable in a space-planted environment.

Table 2.1. Observed mean squares of F4 and F5 progenies for nine traits involving two crosses of winter wheat grown under space-planted and solid-seeded conditions at the Crop Science Field Laboratory during the 1987/88 and 1988/89 seasons.

Cross	Biolog. yield	Non grain biomass	Grain yield	Harvest index	Plant height	Grain protein content	Protein yield	Heading date	Kernel weight
P5221 /8313									
F4 solid	29.3**	18.7**	5.9**	112.6**	1397.6**	236.2**	638.7**	92.3**	17.2**
F4 ind.	521.2*	237.1*	97.3*	54.2**	1120.3**	2.4**	1.1	79.2**	16.1**
F5 solid	11.9*	8.6*	1.6**	41.5**	596.9**	382.6*	1688.3**	76.9**	19.1**
F5 ind.	879.1**	472.6**	129.3**	65.7**	1302.1**	2.3**	1.6*	81.4**	15.0**
P5221 /8601									
F4 solid	31.4**	12.3**	4.3**	98.7**	791.8**	281.4**	832.1**	86.9**	16.3**
F4 ind.	633.5**	364.1**	112.7**	66.3**	672.2**	3.2**	1.3	81.3**	18.6**
F5 solid	16.8*	11.6**	2.4**	61.4**	933.4**	293.1*	1120.5**	86.4**	17.3**
F5 ind.	798.7**	274.2**	110.1**	57.1**	841.1**	2.2*	1.4*	75.3**	14.1**

*, ** indicate F test significant at the 0.05 and 0.01 levels of probability, respectively.

Table 2.2. Simple correlations[†] between traits for F4 and F5 progenies from two crosses of winter wheat grown under space-planted and solid-seeded conditions at the Crop Science Field Laboratory during the 1987/88 and 1988/89 seasons.

Cross	Bio. yield	Non grain biom.	Grain yield	Harv. index	Plant height	Grain prot. cont.	Prot. yield	Head. date	Kern. weight
P5221 /8313									
F4	0.08	0.14	0.32	0.67**	0.93**	0.26	0.15	0.89**	0.46*
F5	0.15	0.21	0.52*	0.65**	0.92**	0.45*	0.29	0.83**	0.47*
P5221 /8601									
F4	0.11	0.14	0.28	0.63**	0.86**	0.28	0.05	0.81**	0.49*
F5	0.01	0.06	0.25	0.60**	0.80**	0.39	0.02	0.71**	0.51*

*,** indicate significantly different from zero at the 0.05 and 0.01 levels of probability, respectively.

[†]n = 30.

Table 2.3. Spearman's rank correlations[†] between traits for F4 and F5 progenies from two crosses of winter wheat grown under space-planted and solid-seeded conditions at the Crop Science Field Laboratory during the 1987/88 and 1988/89 seasons.

Cross	Bio. yield	Non grain biom.	Grain yield	Harv. index	Plant height	Grain prot. cont.	Prot. yield	Head. date	Kern. weight
P5221 /8313									
F4	0.04	0.29	0.26	0.51**	0.70**	0.25	0.14	0.65**	0.24
F5	0.11	0.08	0.19	0.50**	0.65**	0.18	0.07	0.59**	0.30*
P5221 /8601									
F4	0.06	0.16	0.16	0.48**	0.63**	0.12	0.06	0.61**	0.35*
F5	0.08	0.09	0.12	0.48**	0.58**	0.16	0.08	0.54**	0.37*

*,** indicate significantly different from zero at the 0.05 and 0.01 levels of probability, respectively.

[†]n = 30.

Table 2.4. Phenotypic correlation coefficients[†] of grain protein content and eight plant traits among F4 and F5 progenies from two crosses of winter wheat grown under space-planted and solid-seeded conditions at the Crop Science Field Laboratory during the 1987/88 and 1988/89 seasons.

	Grain protein content vs.							
Cross	Bio. yield	Non grain biom.	Grain yield	Harv. index	Plant height	Prot. yield	Head. date	Kern. weight
P5221 /8313								
F4 ind.	-0.16	0.03	-0.52*	-0.52*	0.16	-0.26	-0.17	0.03
F4 solid	-0.02	0.00	-0.45*	-0.51*	0.12	0.12	-0.18	0.09
F5 ind.	-0.29	0.03	-0.56*	-0.44*	0.35	-0.28	-0.23	-0.14
F5 solid	0.04	0.30	-0.55*	-0.55*	0.14	-0.11	-0.14	0.11
P5221 /8601								
F4 ind.	0.28	0.32	-0.56*	-0.71**	0.69**	0.03	-0.30	0.08
F4 solid	0.00	0.07	-0.50*	-0.67**	0.15	0.30	-0.20	-0.50*
F5 ind.	-0.22	-0.11	-0.38	-0.38	0.10	0.07	-0.32	-0.26
F5 solid	-0.05	0.08	-0.30	-0.32	0.09	0.18	0.07	0.08

*,** indicate significantly different from zero at the 0.05 and 0.01 levels of probability, respectively.

[†]n = 90.

Table 2.5. Normal deviates between phenotypic correlations measured on individual plants and solid-seeded plots among F4 and F5 progenies of two crosses of winter wheat for the associations between grain protein content with grain yield and harvest index.

	Grain protein content vs.	
Cross	Grain yield	Harvest index
P5221/CR8313		
F4	0.26 NS	0.04 NS
F5	0.04 NS	0.54 NS
P5221/CR8601		
F4	0.22 NS	0.15 NS
F5	0.27 NS	0.22 NS

NS indicate normal deviates not statistically significant at the 0.05 probability level.

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CHAPTER 3

INFLUENCE OF HARVEST INDEX ON GRAIN PROTEIN CONTENT IN WHEAT: MANIPULATION OF HARVEST INDEX THROUGH THE USE OF A PLANT GROWTH REGULATOR (PACLOBUTRAZOL)

Abstract

Grain yield and grain protein are often negatively associated in wheat i.e. when yield increases, grain protein decreases. This effect adversely affects bread-making quality and other end product uses requiring elevated protein levels. A plant growth regulator (Paclobutrazol) was applied to winter wheat to study how biological yield and harvest index influence grain protein quantity. The grain flour was analyzed by NIR spectroscopy to detect differences in protein. Selections and cultivars of winter wheat were planted in the field and in the greenhouse and treated at the rate of 0.03 g/m^2 of Paclobutrazol. In the greenhouse, plants treated with Paclobutrazol had reduced plant height but had higher grain yield and harvest index. Paclobutrazol reduced plant height, increased grain yield and harvest index of some genotypes under field conditions. However, no difference in grain protein was observed between treated and control plants under either greenhouse or field conditions, even when higher grain yield and harvest index were detected.

Introduction

As the world population continues to grow, increased yields of wheat are needed. Higher grain yields, usually mean lower grain protein because yield is often negatively associated with protein content (Halloran, 1981; McNeal et al., 1982; Loffler et al., 1985). In bread wheat, a decrease in grain protein adversely affects the baking quality of the flour.

Biological yield (total biomass) is the most important source of grain protein. Austin et al. (1977) and Cox et al. (1985) reported that 83% of the grain nitrogen is already present in the plant at anthesis. The inverse association between yield and protein in semi-dwarf wheat cultivars can be explained by increased grain yield with no change in biological yield, resulting in a higher harvest index (Austin et al., 1980). In semi-dwarf genotypes, the same amount of protein is distributed into a larger amount of grain resulting in lower protein per grain.

To investigate trait associations it may be possible to create variability within a cultivar using artificial rather than genetic manipulation (Fehr, 1987). Pendleton et al. (1968) mechanically manipulated leaf angle of a maize cultivar to investigate the relation between leaf angle and grain yield. In this study an attempt was made to chemically manipulate harvest index with the use of a plant

growth regulator (Paclobutrazol). This growth regulator has been shown to change harvest index in cool-season grasses (Albeke et al., 1983).

The plant growth regulator (2RS, 3RS)-1-(4-chlorophenyl)-4,4 dimethyl 1-2-1,1,2,3-triazol-1-y 1 (pentan-3-01) (Paclobutrazol) was applied to winter wheat in the field and in the greenhouse to investigate the influence of changes in grain yield, biological yield and harvest index have on grain protein content.

Materials and methods

Attempts to manipulate the relative proportion of grain and straw and observe the effect on grain protein were made by using a plant growth regulator (Paclobutrazol: "Parlay"). Responses were measured in the greenhouse (using four genotypes) and in the field (using six genotypes).

Greenhouse experiment

A winter wheat cultivar from Nebraska (Centura), a line from Montana (Selection P5221) and two lines from the Oregon State University Spring x Winter wheat program (CR8313 and CR 8601) were sown in vermiculite flats on 20 October 1986. The seedlings were vernalized in a growth chamber for 61 days at 8 C and 8 hours of light and watered with Hoagland solution (Hoagland and Arnon, 1950) as needed.

Paclobutrazol was sprayed at a rate of 0.03 g a.i./m^2 onto 15-cm diameter wide, 17-cm tall pots filled with a silt-loam soil (fine, silty mixed mesic Aquultic Argixeroll) amended with 11 g of lime, 3 g of 20-20-20 and 3 g of 30-0-0-6 fertilizers. The vernalized seedlings were transplanted immediately after treatment and moved into the greenhouse.

A factorial experimental design was used with the application of Paclobutrazol being one factor and genotype the second factor.

After transplanting, each pot was fertilized twice with 5 g of 20-20-20 (30 days after transplant and at anthesis). The greenhouse temperature was initially set at 21^0 C with 12 hours day-length. Thirty days after transplanting, the temperature was raised to 24^0 C and day-length increased to 18 hours.

Fertile tillers were counted at maturity. The plants were individually harvested. Biological yield was measured by weighing the whole mature plant, excluding the roots. Harvest index was determined by dividing grain yield by biological yield. Kernel weight was obtained from a sample of 100 kernels per plant.

Field experiment

The same wheat selections and cultivar used in the greenhouse experiment were planted at a seeding rate of 250 seeds m^{-2} at the Crop Science Field Laboratory on 14 October 1988. In addition, two other wheat cultivars were included. These were: 1) Norstar, a tall Hard Red Winter Wheat and 2) Stephens, a semi-dwarf Soft White Winter Wheat. The soil type is a fine, silty mixed mesic Aquultic Argixeroll. A total of 120 kg N ha^{-1} and 24 kg S ha^{-1} were applied in the form of 30-0-0-6 fertilizer in two evenly split applications made at the following growth stages: tillering (Feekes stage 4) and jointing Feekes (stage 8). Prior to planting, 40 kg N ha^{-1} and 6 kg S ha^{-1} were applied. 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 experimental design was a split-plot randomized complete block with four replications. The main plots were Paclobutrazol treated and untreated control. Subplots consisted of six winter wheat genotypes. Plots were six 5.0 m rows spaced 28 cm apart. Paclobutrazol was applied at a rate of 0.03 g a.i. m^{-2} when plants were at stage 5 of the Feekes scale (late tillering). Grain yield data was obtained by harvesting the whole plot with a combine on 25 July 1989. Harvest index was estimated from a sample of 30 tillers taken at random from each plot. Biological yield was estimated indirectly from harvest index and grain yield data. Non-grain biomass was obtained by the difference between biological yield and grain yield. Kernel weight was estimated from a sample of 100 kernels. Spikes per unit area were estimated indirectly from plot grain yield and grain yield of the 30-tiller sample. Kernels per spike were also indirectly estimated from spikes per unit area, plot grain yield and kernel weight.

Grain samples from both experiments were ground in a Udy flour mill, using a 0.5-mm mesh sieve. Grain protein content of the whole-meal flour was determined by near infrared reflectance spectroscopy using a Technicon Infralyser 400. Grain protein content was expressed on a

140 g kg^{-1} moisture basis.

A summary of climatological data for the 1988/1989 growing season is presented in Appendix Table 1.

Analytical procedures

Standard analysis of variance was used to analyze the data. Fisher's protected LSD test was used to test means for significant differences. Phenotypic correlations were estimated as $r_p = M_{ij}[(\sigma^2_{ii})(\sigma^2_{jj})]^{-0.5}$, where r_p is the phenotypic correlation coefficient , M_{ij} is the mean cross product for progenies, and σ^2_{ii} and σ^2_{jj} are phenotypic variances for traits i and j, respectively. Differences between correlation coefficient under greenhouse and field conditions were tested for significance using the test of Snedecor and Cochran (1980).

Results

In the field experiment, Paclobutrazol treatment significantly affected grain yield, harvest index and plant height (Table 3.1). Its effect was different across genotypes, as shown by the significance of the treatment by genotype interaction for these three traits. Application of Paclobutrazol did not significantly affect biological yield, non-grain biomass, grain protein content or protein yield. Genotypic differences were detected for all measured traits.

Means of control and treated plots of six genotypes are presented in Table 3.2. Paclobutrazol treatment significantly increased grain yield and harvest index for most genotypes. The cultivar Centura had the largest increases in grain yield and harvest index, while grain yield and harvest index of Stephens remained unchanged. Table 3.2 shows that biological yield, non-grain biomass, grain protein content, and protein yield remained unchanged, while plant height was significantly reduced in treated plots for most genotypes.

Analysis of yield components showed that grain yield increased in treated plots through a combination of higher number of spikes per unit area (12% increase) and a higher number of seeds per spike (13%), with kernel weight remaining unchanged (Table 3.3).

The magnitude of associations among grain yield, harvest index and grain protein content were reduced in treated plots as measured by the phenotypic correlations in the field experiment (Table 3.4). Although differences were only significant for the association between grain yield and harvest index. Grain yield was not associated with grain protein content in treated plots.

In the greenhouse experiment, Paclobutrazol treatment affected all the measured traits except for grain protein content which remained unchanged (Table 3.5). Genotypic differences were detected for all traits except grain yield and protein yield. Paclobutrazol by genotype interaction was detected for plant height, indicating that the effect of Paclobutrazol treatment on plant height was different across genotypes.

Values for Paclobutrazol treated and control means in the greenhouse are presented in Table 3.6. Biological yield, grain yield, non-grain biomass, harvest index and protein yield increased in treated plants. Plant height was significantly lower in treated plants, while means for grain protein content were not significantly different between treated and control plants.

Mean values for yield components in the greenhouse are presented in Table 3.7. Grain yield increased in treated plants solely through an increase in spikes per plant (69%), seeds per spike and kernel weight were not different between

treated and control plants.

Associations in the greenhouse experiment among grain yield, harvest index and grain protein content were not significantly different from zero either in control or treated plants (Table 3.8).

Discussion

Paclobutrazol is a soil-active compound which acts by inhibiting gibberellic acid synthesis at the ent-kaurene oxidase reaction, thus reducing plant height (Hedden and Lenton, 1988). This effect has been previously reported in cool season grasses (Albeke et al., 1983). In this experiment, grain yield was reduced across treated genotypes under greenhouse conditions, but only for some genotypes in the field experiment.

Differences in the effect of Paclobutrazol were observed between greenhouse and field experiments. Paclobutrazol treatment drastically reduced plant height in the greenhouse. In the field, height reduction was less noticeable, and it was not different for some genotypes. Analysis of yield components show that Paclobutrazol uniformly increased grain yield through an increase of fertile tillers in the greenhouse. While under field conditions, grain yield increased only in some genotypes, such as Centura (tall and low harvest index genotype) through a combination of higher spike number per unit area and more kernels per spike. Stephens (semi-dwarf and high harvest index genotype) did not increase its grain yield in treated plots. Plants in the greenhouse were grown individually as single plants while in the field plants were spaced in a standard solid seeded density. These conditions

represent different competition environments among plants and among tillers in the same plant which could explain differences in response. Plants in the greenhouse are not as limited in space as plants growing in dense stands, allowing for a larger increase in spikes per plant.

Grain yield is usually negatively correlated with grain protein content, when grain yield increases grain protein content decreases (Cox et al., 1985; Loffler et al., 1985). In this study, some winter wheat genotypes treated with the plant growth regulator Paclobutrazol showed higher yield without a reduction in their grain protein content. This result suggests that these genotypes have a different genetic make-up for grain protein content than the standard cultivar Stephens which had high yield and low grain protein content in both treated and untreated situations. This was an unexpected result as these genotypes also showed an increased harvest index. This trait is usually negatively related with grain protein content, and it has been implicated as playing a role in the relation between grain yield and grain protein content (Austin et al., 1980; Loffler et al., 1985; McNeal et al., 1972). However, the association between harvest index and grain protein was not changed among treated and control plants.

Dalling (1985) suggested that plant growth regulators are involved in nitrogen redistribution at maturity. Inhibition of gibberellin synthesis by the application of

Paclobutrazol would change the relative proportion of growth regulators naturally occurring in the wheat plant. This change in plant hormones could affect nitrogen remobilization at maturity and thus indirectly affect grain protein content levels. Results of this study indicate that Paclobutrazol treatment can improve grain yield of some genotypes without affecting their grain protein content.

Table 3.1. Observed mean squares for seven traits involving six winter wheat genotypes in a field experiment conducted at the Crop Science Field Laboratory, 1988/1989.

Source	df	BY	NGB	GY	HI	PH	GPC	PY
Total	47							
Reps	3	3.4	1.8	0.34	4.14	26.9	75.2	23.3
PGR	1	50.2	8.4	17.30*	184.9**	1813.0**	21.3	1660.8
Error(A)	3	15.7	6.7	1.80	1.0	51.9	80.8	374.8
G	5	23.9**	17.8**	9.50**	211.5**	3179.3**	257.1**	659.9**
PGR x G	5	6.4	3.6	1.11**	19.0*	161.8**	26.8	103.3
Error (AB)	30	5.7	4.2	0.26	6.8	16.9	43.1	50.24
C.V. (%)		13.4	16.8	9.0	8.3	3.3	6.4	12.4

PGR = Plant growth regulator, G = Genotypes, BY = Biological yield, NGB = Non-grain biomass, GY = Grain yield, HI = Harvest index, PH = Plant height, GPC = Grain protein content, PY = Protein yield.

Table 3.2. Treated and control mean values for seven traits involving six genotypes of winter wheat in a field experiment conducted at the Crop Science Field Laboratory, 1988/1989.

Gen.	Biological yield Mg ha^{-1}		Non-grain biomass Mg ha^{-1}		Grain yield Mg ha^{-1}		Harvest index %		Plant height cm		Grain protein content g kg^{-1}		Protein yield kg ha^{-1}	
	C	T	C	T	C	T	C	T	C	T	C	T	C	T
5221	15.3	17.0	10.8	11.2	4.4	5.8	28.9	34.3	117	106	102	104	456	609
8313	17.7	18.3	11.9	11.8	5.8	6.5	33.0	36.0	124	116	102	101	598	661
8601	17.4	21.3	11.9	14.5	5.5	6.8	31.7	32.5	129	117	105	107	579	726
Cent.	14.3	16.8	10.2	10.4	4.1	6.3	28.9	38.0	139	109	101	98	424	624
Nors.	16.2	20.3	13.1	15.6	3.1	4.7	19.3	23.4	164	149	114	107	362	504
Step.	20.2	19.7	13.1	12.6	7.0	7.1	34.9	35.9	107	99	94	94	663	664
Mean	16.9	18.9	11.9	12.7	5.0b	6.2a	29.4b	33.4a	130a	116b	103	102	514	631

C = Control, T = Treated with Paclobutrazol.
Mean values displaying different letters on the same column between treatments are significantly different at the 5 % probability level.

Table 3.3. Treated and control mean values for three traits involving six genotypes of winter wheat in a field experiment conducted at the Crop Science Field Laboratory, 1988/1989.

	Spikes m^{-2}		Seeds $spike^{-1}$		Kernel weight mg	
	Control	Treated	Control	Treated	Control	Treated
P5221	485.1	511.3	23.6	29.2	38.5	39.2
CR8313	346.2	349.5	41.5	47.5	41.0	40.5
CR8601	354.4	391.3	38.9	43.4	41.2	41.7
Centura	417.4	545.9	26.1	30.5	38.5	38.2
Norstar	381.2	472.1	22.6	26.0	37.2	38.7
Stephens	435.6	449.1	35.3	35.9	46.0	44.5
Mean	403.3b	453.2a	31.3b	35.4a	40.4	40.5

Mean values displaying different letters on the same column between treatments are significantly different at the 5 % probability level.

Table 3.4. Phenotypic correlation coefficients[†] for seven traits involving genotypes of winter wheat control (above diagonal) and treated (below diagonal) with a plant growth regulator in the field.

	Grain yield	Harvest index	Grain protein content
Grain yield	_	0.82**	-0.34*
Harvest index	0.60**	_	-0.49*
Grain protein content	-0.23	-0.43*	_

*, ** indicate phenotypic correlation significantly different from zero at the 0.05 and 0.01 probability levels.

[†]n = 24.

Table 3.5. Observed mean squares for seven traits involving four winter wheat genotypes in a greenhouse experiment.

Source	df	BY†	NGB	GY	HI	PH	GPC	GPY
Total	31							
Reps	3	3.9	10.1	9.6	0.5	9.3	201.0	0.4
PGR†	1	106.9**	123.6**	465.9**	281.4**	8096.3**	205.0	21.0**
G	3	11.0*	124.3**	5.0	214.2**	32.7**	473.2*	0.5
PGR x G	3	1.9	7.4	3.5	7.7	91.6**	412.4	0.2
Error	21	3.1	7.2	9.4	3.3	3.6	122.6	0.4
CV (%)		14.5	12.9	17.7	4.0	2.6	5.5	17.4

†PGR = Plant growth regulator, G = Genotypes, BY = Biological yield, NGB = Non-grain biomass, GY = Grain yield, HI = Harvest index, PH = Plant height, GPC = Grain protein content, PY = Protein yield.

Table 3.6. Treated and control mean values involving four winter wheat genotypes in a greenhouse experiment.

Geno-type	Biological yield		Non-grain biomass		Grain yield		Harvest index		Plant height		Grain protein content		Protein yield	
	g		g		g		%		cm		g kg^{-1}		g	
	C	T	C	T	C	T	C	T	C	T	C	T	C	T
5221	28.5	40.0	14.5	19.1	13.9	20.9	49.0	52.2	93.0	54.0	192	213	2.7	4.5
8313	33.5	48.7	19.8	26.0	13.6	22.7	40.7	46.6	84.5	65.2	217	204	3.0	4.6
8601	37.7	45.5	24.5	26.1	13.2	19.3	34.9	42.4	87.7	65.0	199	196	2.6	3.8
Cent.	30.0	41.7	16.7	20.2	13.2	21.5	44.1	51.3	94.7	48.5	186	201	2.5	4.3
Mean	32.4b	44.0a	18.9b	22.9a	13.5b	21.1a	42.2b	48.1a	90.0a	58.2b	199	203	2.7b	4.3a

C = Control, T = Treated with Paclobutrazol.
Mean values displaying different letters on the same column between treatments are significantly different at the 5 % probability level.

Table 3.7. Treated and control mean values for three traits involving six genotypes of winter wheat in a greenhouse experiment.

	Spikes plant^{-1}		Seeds spike^{-1}		Kernel weight mg	
	Control	Treated	Control	Treated	Control	Treated
P5221	7.2	13.7	46.5	30.3	41.5	50.2
CR8313	6.5	10.2	51.1	63.9	41.5	35.5
CR8601	7.5	10.0	41.5	48.2	42.5	41.0
Centura	9.5	18.2	35.1	33.7	40.0	35.5
Mean	7.7b	13.0a	43.6	44.0	41.4	40.6

Mean values displaying different letters on the same column between treatments are significantly different at the 5 % probability level.

Table 3.8. Phenotypic correlation coefficients[†] for seven traits involving genotypes of winter wheat control (above diagonal) and treated (below diagonal) with a plant growth regulator in the greenhouse.

	Grain yield	Harvest index	Grain protein content
Grain yield	_	0.20	0.06
Harvest index	0.43	_	-0.33
Grain protein content	-0.30	0.23	_

[†]n = 16.

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CONCLUSIONS

Three studies were conducted to investigate the nature of inheritance of grain protein content and possible associations of grain protein content with plant growth traits in winter wheat. The following experiments were conducted: 1) F4 and F5 random progenies of three crosses of winter wheat genotypes were evaluated in the field at two locations in Oregon; 2) F4 and F5 progenies of two winter wheat genotypes were evaluated under solid-seeded and space-planted conditions; 3) A plant growth regulator (Paclobutrazol) was applied on winter wheat genotypes to evaluate the influence of changes in grain yield and harvest index on grain protein content. The following conclusions were drawn from these investigations:

1. Heritability estimates for grain protein content, grain yield, biological yield and protein yield were moderate to low, indicating that late generation selection would be appropriate for the improvement of these traits.
2. Grain protein content was negatively associated with grain yield and harvest index. These relationships were apparently due to genetic causes, as genetic correlations were large while environmental correlations were low.
3. Protein yield was not associated with grain protein content. Variation among progenies for protein yield closely followed the variation observed for grain yield,

resulting of little use to improve both grain yield and grain protein content.

4. Path coefficient analysis indicated that grain yield and harvest index were the most important traits affecting grain protein content in these crosses with small effects from the other traits evaluated in this study. Residual variation, however was relatively large.

5. Grain protein content, grain yield, biological yield and protein yield could not be effectively evaluated among spaced plants and their evaluation requires replicated solid-seeded planting environments.

6. Harvest index could be effectively selected under space-planted conditions as well as plant height and heading date.

7. Estimates of associations among different traits were reliably measured in spaced plants, although the performance of individual genotypes differed for most traits under contrasting seeding densities.

8. Attempts to manipulate the relative proportion of grain and straw by the application of a plant growth regulator were successful. Grain yield and harvest index were higher but grain protein content remained unchanged for all genotypes under greenhouse conditions. In the field experiment, some genotypes increased yield while maintaining the same grain protein content level.

9. Results of this investigation suggest that a possible breeding strategy to obtain high yield and high protein

should include selection for intermediate values of harvest index in early generations, delaying the evaluation of grain protein content and grain yield for later generations under replicated solid-seeded conditions.

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APPENDIX

Appendix Table 1. Summary of weather data on a per month basis for the Hyslop Crop Science Field Laboratory, 1987/1988 and 1988/1989 growing seasons.

Growing season	Month	Precipitation (mm)	Temperature ^{0}C		
			Average max.	Average Min.	Mean
1987/1988	October	6.9	23.0	5.3	14.1
	November	99.1	12.1	4.9	8.5
	December	290.1	6.5	1.4	3.9
	January	180.8	7.1	0.7	3.9
	February	43.2	11.2	1.6	6.4
	March	99.1	13.5	2.5	8.0
	April	84.6	16.1	5.6	10.8
	May	97.5	17.9	6.6	12.2
	June	46.5	22.0	9.2	15.6
	July	2.3	28.0	11.0	19.5
	Total	949.9			
1988/1989	October	3.6	20.1	8.1	14.1
	November	276.1	11.4	4.8	8.1
	December	100.8	7.7	1.2	4.5
	January	106.2	8.3	1.6	4.9
	February	81.5	5.8	-2.2	1.8
	March	172.7	11.7	3.4	7.6
	April	36.1	18.8	6.6	12.7
	May	37.1	19.3	6.7	13.0
	June	28.9	24.5	10.3	17.4
	July	8.4	24.8	10.9	17.8
	Total	851.4			

Appendix Table 2. Summary of weather data on a per month basis at the Pendleton Research Station, 1987/1988 and 1988/1989 growing seasons.

Growing season	Month	Precipitation (mm)	Temperature ^{0}C		
			Average max.	Average Min.	Mean
1987/1988	October	0.0	22.0	-1.4	10.3
	November	36.6	11.1	-0.2	5.5
	December	40.9	4.9	-3.9	0.5
	January	66.0	4.2	-4.2	0.0
	February	8.1	10.2	-3.4	3.4
	March	41.9	13.1	-0.6	6.2
	April	65.8	17.7	3.9	10.8
	May	45.5	20.7	5.6	13.1
	June	23.9	24.8	9.2	17.0
	July	0.0	32.0	10.5	21.2
	Total	328.7			
1988/1989	October	2.0	23.1	3.7	13.4
	November	92.7	11.1	1.8	6.4
	December	27.9	5.1	-3.1	1.0
	January	72.6	7.1	-1.9	2.6
	February	39.4	0.7	-9.6	-4.4
	March	74.9	11.1	1.0	6.1
	April	49.3	18.0	3.9	11.0
	May	55.6	20.5	5.4	12.9
	June	3.8	31.1	9.7	20.5
	July	30.2	28.2	11.0	19.6
	Total	456.8			

Appendix Table 3. Degrees of freedom and expectation of mean squares for experiments with F4 and F5 progenies of three crosses of winter wheat.

Source of variation	Degrees of freedom	Expected Mean square
F4 experiments[†]		
Replication	r - 1	$\sigma^2_e + p\sigma^2_r$
Progenies	p - 1	$\sigma^2_e + r\sigma^2_p$
Error	r (p - 1)	σ^2_e
F5 experiments[††]		
Block	b - 1	$\sigma^2_e + p\sigma^2_{r:b} + r\sigma^2_{p:b} + rp\sigma^2_b$
Replication:Block	b (r - 1)	$\sigma^2_e + p\sigma^2_{r:b}$
Progeny:block	b (p - 1)	$\sigma^2_e + r\sigma^2_{p:b}$
Error	b (r - 1)(p - 1)	σ^2_e

[†] randomized block design.

[††] replications-in-incomplete blocks design.

r is the number of replications, p is the number of progenies, b is the number of incomplete blocks.

σ^2_r is the block variance, σ^2_p is the progeny variance, σ^2_e is the error variance. σ^2_b is the incomplete block variance, $\sigma^2_{r:b}$ is the replication nested in incomplete block variance, $\sigma^2_{p:b}$ is the progeny nested in incomplete block variance.

Appendix Table 4. Mean values of F4 and F5 progenies for nine traits involving two crosses of winter wheat grown under space-planted conditions at the Crop Science Field Laboratory during the 1987/88 and 1988/89 seasons.

Cross	Biolog. yield	Non grain biomass	Grain yield	Harvest index	Plant height	Grain protein content	Protein yield	Heading date	Kernel weight
	g	g	g	%	cm	g kg^{-1}	g	days	mg
P5221/8313									
F4	92.3	62.0	30.3	32.8	125.3	131.1	4.0	134.2	40.1
F5	95.2	59.4	35.8	37.8	122.6	127.0	4.5	132.8	46.2
P5221/8601									
F4	105.3	71.1	34.2	32.5	133.7	135.3	4.6	136.6	48.2
F5	107.7	70.5	37.2	34.5	131.2	133.2	4.9	133.1	47.5

Appendix Table 5. Mean values of F4 and F5 progenies for nine traits involving two crosses of winter wheat grown under solid-planted conditions at the Crop Science Field Laboratory during the 1987/88 and 1988/89 seasons.

Cross	Biolog. yield	Non grain biomass	Grain yield	Harvest index	Plant height	Grain protein content	Protein yield	Heading date	Kernel weight
	Mg ha^{-1}	Mg ha^{-1}	Mg ha^{-1}	%	cm	g kg^{-1}	kg ha^{-1}	days	mg
P5221/8313									
F4	14.3	9.7	4.6	32.2	135.2	128.8	592.5	138.7	42.3
F5	11.8	7.5	4.3	36.5	129.3	119.7	514.7	136.5	39.5
P5221/8601									
F4	14.9	10.5	4.4	29.5	138.2	129.7	570.7	140.5	44.5
F5	13.5	8.8	4.7	34.8	135.7	121.3	570.1	138.8	43.1