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The objective of this investigation was to evaluate the possibility of developing high yielding wheat cultivars whose flour would result in acceptable loaf volumes for non-traditional bread wheat growing areas. Spring wheat germplasm employed included high protein hexaploid derivatives from Triticum dicoccoides, and selections from Argentina with good bread milling and baking properties. Winter wheat materials were from the Oregon State University International Winter x Spring Wheat Improvement Program.

Elevated protein content was found not to be a prerequisite in obtaining high loaf volumes. Electrophoretic analysis (SDS-PAGE) of the high molecular weight glutenin subunits, and the sodium dodecyl sulphate sedimentation (SDSS) test proved to be reliable indicators of protein quality. High molecular weight glutenin banding patterns were independent of environmental factors. Bands 5-10 contributed by the D genome, with either bands 1 or 2* from the A genome and bands 7-8 or 17-18 coded by the B genome, appeared to be the most critical

in influencing high loaf volume. For the experimental material used, SDSS values were found to be dependent upon variations in protein content. Five grams wholemeal flour samples with 2% SDS, 10 ml/l of 9.6% lactate solution and a reading time of 30 minutes provided the best combination to discriminate between lines with high or low loaf volume.

Grain yield was found to be negatively associated with grain protein content in the spring wheat material. In crosses with Argentine lines, high protein "dicoccoides" derivatives, did not contribute major genes for protein content. Grain hardness was found to be a qualitatively inherited trait, and not associated with grain protein content or loaf volume. No single criterion proved of value in improving protein content and grain yield simultaneously, other than delaying selection until later generations.

Strong negative associations between harvest index and grain protein content were observed for the winter wheat germplasm. Biological yield and kernel weight were the best selection criteria to improve grain protein without sacrificing grain yield. Early season applications of nitrate nitrogen resulted in a simultaneous increase in protein content and grain yield.

FEASIBILITY OF DEVELOPING BREAD WHEAT CULTIVARS WITH ACCEPTABLE PROTEIN CONTENT FOR NON-TRADITIONAL AREAS

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Typed by Ariel Lorenzo

DEDICATED TO:

my wife,

Maria de Lujan

my daughters,

Ana Rosa and Maria Martina

and my parents,

Andres Lorenzo and Cristina Garcia

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TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

LIST OF APPENDIX FIGURES

LIST OF APPENDIX TABLES

FEASIBILITY OF DEVELOPING BREAD WHEAT CULTIVARS WITH ACCEPTABLE PROTEIN CONTENT FOR NON-TRADITIONAL AREAS.

INTRODUCTION

Hard endosperm, high protein bread wheats are traditionally grown in the continental climates of North America, Australia and Argentina, where a short maturation period results in the desired grain quality. In the maritime climates of Western Europe and the Pacific Northwest, wheat yields are high, but grain protein content is low. Some concerns have been expressed that due to a negative association between grain yield and grain protein content, it has been difficult to develop agronomically superior cultivars with increased protein. Altering wheat quality by modifying the type of high molecular weight glutenin proteins has been suggested as an alternative, and within limits a superior protein quality can offset a mediocre grain protein content without sacrificing grain.

It was the objective of this investigation to evaluate the possibility of developing high yielding wheat cultivars with acceptable loaf volume for non-traditional hard red wheat growing areas. This breeding goal has become reasonable with the availability of new laboratory techniques and sources of germplasm. Techniques include 1) near-infrared reflectance spectroscopy, 2)sodium dodecyl sulphate sedimentation test (SDSS test), and 3) sodium dodecyl sulphate polyacrylamide gel electrophoresis (SDS-PAGE) of the high molecular weight (HMW) glutenin storage proteins.

Germplasm derived from Triticum dicoccoides with high protein potential, spring type selections from Argentina with good baking properties, and lines with winter growing habit from the Oregon State University Winter x Spring breeding program were evaluated as new sources of genetic variability for quality and quantity of protein and various agronomic traits.

In evaluating the potential of developing agronomically superior cultivars with acceptable quality and quantity of protein, the following approaches were undertaken. Laboratory techniques were tested for their reliability in identifying the desired protein quality factors. The inheritance of protein quantity and quality was studied using modifications of the laboratory techniques previously evaluated. Agronomic traits and management practices which could contribute to obtaining the desired grain yield with acceptable protein levels and baking properties were also investigated.

LITERATURE REVIEW

Wheat has received so much care and attention worldwide that it can rightly be regarded as the most important of all food crops. Of mankind basic nutrition, wheat contributes about 35 to 40 percent and about 60 percent of the total world protein supply (Milner, 1966). Grain yield has become the number one priority of many wheat breeding programs. However, wheat quality still remains an important breeding goal since wheat needs to be processed and prepared for human consumption. An understanding of the factors affecting wheat quality, as well as of the relationships between yield and quality is essential for progress.

Many end products are obtained from wheat based on various quality factors involving properties of the kernel.

Kernel Structure and Composition

The wheat kernel is botanically referred to as a caryopsis, a small, indehiscent, dry, one seeded fruit formed by the seed and the encasing pericarp. Different constituents of the wheat caryopsis are the following:

A. Pericarp or fruit coat (maternal tissue = 2n)
   - outer layer or epidermis
   - inner layer or endocarp

B. Seed
   - seed coat and pigment strand (2n maternal tissue)

- nucellar epidermis and nucellar projection (2n maternal tissue)
- endosperm (polar nuclei + pollen nucleus = 3n)
    - aleurone layer
    - starchy endosperm
- germ or embryo and scutellum (egg cell + pollen nucleus = 2n)

It is generally accepted that parts derived from the maternal tissue amount to about 8%, the embryo 7%, and the endosperm 85% of the total kernel weight (McMaster et al., 1971). Thus, it is the endosperm which contains the reserves from which the seedling draws its nourishment for germination and it is also the main constituent of white flour.

The texture of the endosperm is used as a criteria to classify wheats into hard or soft. Doughs formed by mixing flour of these two types with water have strong or weak mixing properties. In the milling of soft-textured wheats, fractures occur across the dehydrated protoplasm. Fine, irregular particles are formed which have poor flow properties. On milling a hard-textured wheat, the endosperm protoplasm resists fracturing due to the strong adhesion between protein and starch and thus cleavage occurs mainly along the lines of the cell walls to produce large, regular-shaped particles which flow easily. The starch granules are rigidly fixed in the protein matrix in hard red wheats, and are easily damaged during grinding (Kamara et al., 1982). This enables hard wheat flours to absorb twice as much water as soft milling flour, resulting in higher bread yields (Stenvert, 1974).

Protein content in the wheat kernel is presented in Appendix

Table 1 (Hinton, 1953). It can be observed that protein content of the endosperm is relatively low when expressed per 100 gr fraction, but it becomes more important when expressed per 100 gr of whole grain. Thus, when speaking of wheat flour protein, reference is made to the endosperm protein and to a lesser extent to aleurone protein. The difference between these fractions depends on the flour extraction percentage used during the milling process.

Kernel Proteins

Knowledge about the nature of various protein contained in the kernel is based essentially on the classification by solubility proposed by Osborne in 1907. According to his work, protein can be distinguished into four main fractions, albumins, globulins, gliadins and glutenins, depending on their differential solubility in water, saline solution, 70% aqueous ethanol and diluted alkali or acid solutions, respectively. This classification is still widely used although extraction made by more sophisticated techniques has already revealed the fact that the four originally described classes are mutually overlapping (Kasarda et al., 1976).

Albumins and globulins, called soluble or cytoplasmic proteins, are enzymes involved in metabolic activity, and are located mainly in the germ and aleurone layer. This amounts to about 20% of total protein content in the caryopsis. The higher the protein content, the lower the percentage of this fraction. These proteins are richer in essential amino acids (lysine) and their molecular weights (MW)

are between 12,000 and 16,000 for albumins and between 20,000 and 200,000 for globulins (Porceddu et al., 1982).

Gliadins and glutenins, referred to as storage proteins, are the main components of gluten, which is the product obtained by washing flour in water. Lipids and carbohydrates are also components of gluten and during the washing operation, these compounds react with the storage proteins producing complexes of high molecular weight. These complexes are less soluble than the glutenin fraction (Simmonds and Wrigley, 1972). Storage proteins are each composed of many different molecular species and it is from their structure and interaction that the viscoelastic properties of gluten are derived (Wall, 1978).

Gliadins occur as a complex mixture of single polypeptide chains stabilized by intrachain disulphide bonding (Bietz et al., 1977), with a particular amino acid composition that includes large amounts of glutamine (38-56% of all amino acid residues), proline (15-30%) and small amounts of lysine (Kasarda et al., 1974b). They have been classified into alpha, beta, delta, and omega gliadins, according to their relative mobility upon gel electrophoresis with aluminun lactate buffer (Woychik, 1961). The alpha, beta, and delta gliadins have about the same amino acid composition, a molecular weight ranging from 30,000 to 45,000 and similar N-terminal sequences. The omega gliadins have MW ranging from 65,000 to 80,000 and different amino acid composition (Charbonnier et al., 1980). Upon addition of reducing agents, the chemical structure of gliadin remains unchanged.

Under dissociating, but non-reducing conditions (Payne et al.,

1979a), glutenins occur as large heterogeneous aggregates (MW range by Gel Filtration Chromatography = 10^6 to 20-40 x 10^6). They are made up of numerous polypeptide subunits joined together by both covalent and hydrophobic interactions (Bietz and Huebner, 1980). They represent about 30 to 40% of total flour protein and are considered the most important contributors to the strength and viscoelastic properties of the wheat dough (Bietz et al., 1973). With the use of sodium dodecyl sulphate - polyacrylamide gel electrophoresis (SDS-PAGE), reduced glutenin components can be separated on the basis of their MW. It was recently discovered that much of the protein in the glutenin fraction is of high molecular weight (HMW) and made up of several subunits (Huebner and Wall, 1976) ranging from 31,500 to 140,000 (Payne et al., 1979b). The subunit composition varies according to the wheat cultivar. In general about 80% have MW by SDS-PAGE of 35,000 to 50,000, and are called low MW subunits (LMW) (Jackson, Holt, and Payne, 1983). The remaining subunits are larger, 90,000 to 145,000, and therefore are called HMW subunits (Payne et al., 1982).

Formation of the water soluble proteins begins at the same time as zygote development and a constant value is attained about 40 days after anthesis. Their synthesis occurs primarily in the cells of the aleurone and subaleurone layer which eventually will contain few protein bodies (cytological structures where protein is stored) and small starch granules (Barlow et al., 1974). Conversely, formation of insoluble storage proteins begins only during the third week after anthesis and their biosynthesis rises gradually until the 45th day,

being mostly located in protein bodies in the innermost portion of the endosperm. At the beginning of endosperm development, proteins accumulate in the vacuoles, later accumulation is more common on the distension of the endoplasmic reticulum (Campbell et al., 1974 and 1981).

Genetic Control of Bread-making Quality

Quality is appraised largely by subjecting the flour to physical tests which measure various rheological characteristics on flour-water doughs. These tests characterize the gluten portion of the protein by measuring such factors as extensibility and resistance to extension. Extensibility is the extent to which a properly developed gluten can be extended. Resistance to extension, sometimes referred to as peak elasticity, is the ability of that gluten to retain gas (Pratt, 1971). A strong wheat takes longer to reach peak elasticity with a high work input required. Weak wheats, by contrast, soon reach their peak and even at this stage, elasticity is low and extensibility high (Paredes-Lopez and Bushuk, 1983). Bread doughs must be highly elastic as well as somewhat extensible so that gases are retained during fermentation and a controlled expansion of the dough occurs.

The viscoelastic properties of wheat are principally governed by protein type and amount and it is these two variables which determine the mixing properties of the flour and the quality of the bread. Strong wheats are traditionally grown in continental climates where a

short maturation period results in moderate yields, but guarantees a high grain protein content. In the maritime climates wheat yields are high, but protein is low . The improvement of wheat quality by altering the kinds of protein may be an alternative even under the latter conditions (Flavell et al, 1984).

The genetic control of bread-making quality began to be recognized in 1964. In that year, Welsh and Hehn (1964) published a paper relating the presence of chromosome 1D to the flour quality of hexaploid wheat. To accomplish their research, they used a series of monosomic (2n-1) lines derived from the variety Kharkoff MC 22, a Hard Red Winter Wheat of poor bread-making quality, and Itana, known to have excellent quality. In 1968, Kaltsikes et al., reported a group of derived lines from Thatcher, Rescue and Prelude which were identical to their hexaploid counterpart except that they lack the D-genome. The derived tetraploids had even poorer bread-making quality than the standard durum wheats, except for "Tetraprelude" where a 1-D translocation had apparently occurred. The importance of Aegilops squarrosa as donor of the D-genome to the bread-making quality of hexaploid wheats was further verified by Kerber and Tipples (1969).

There has been much controversy over which of the storage proteins present in flour, gliadin or glutenin, are most important to bread-making quality. During the past few years, attempts have been made to correlate the presence or absence of specific gliadin or glutenin components to bread-making quality. The first step in the investigation of their genetics has been to develop gel-electrophoresis procedures which can give good separation of the

protein subunits so that hopefully each protein band or spot on the gel will consist of only one protein species and therefore represent the product of a single structural gene.

The evidence from several studies (Shepherd, 1968, Wrigley and Shepherd, 1973, and Payne et al., 1982) indicate that the genes controlling gliadin proteins are located on six of the 21 chromosomes in wheat, the short arms of 1A, 1B, and 1D, and 6A, 6B, and 6D. Inheritance studies have indicated that gliadin genes occur in tightly linked clusters that are usually inherited as unit blocks (Sozinov and Poperelya, 1980, Mecham et al., 1978, and Baker and Bushuk, 1978).

According to Kasarda et al. (1974a), there are hundreds of different gliadin components which can be identified by electrophoretic techniques. This seems to be due to the fact that the structure and function of these proteins are not crucially interrelated so that gene mutations for gliadin components are not as deleterious as those for metabolic enzymes. Another theory in relation to the multiplicity of subunits has been presented by Mecham et al. (1978) who favored the hypothesis of gene duplication followed by asymmetrical crossing over. Subsequently, the modified genes may have undergone further events such as DNA amplification leading to formation of new types of gliadin components (Cole et al., 1981).

A cDNA clone bank has been constructed to messenger RNA harvested from developing wheat endosperms (Bartels and Thompson, 1983). More than 90% of these clones code for gliadin or HMW glutenin polypeptides, the ratio between the two groups being about

10 to 1. Experiments using DNA hybridization have indicated the existence of sequence homology between gliadins of the large molecular weight range, for example, between the delta and omega gliadin families. Thus, many of the grain proteins are specified by sequence related genes although the DNA clones specifying the gliadin do not show homology with those specifying HMW glutenin subunits (Thompson et al., 1983).

It has been difficult to correlate the presence of a specific gliadin subunit with bread-making quality. However, some positive associations between blocks of gliadin components and quality were reported by Sozinov and Poperelya (1980) and Wrigley et al. (1977).

The Glutenin Proteins

One of the preferred techniques to separate and classify glutenin subunits (since its conception by Shapiro et al., 1967) has been electrophoresis using polyacrylamide gels in the presence of sodium dodecyl sulphate (SDS-PAGE). Shapiro et al. (1967) reported a linear relationship between log of MW and relative mobility of protein treated by SDS. The popularity of SDS-PAGE is due to its rapidity, reproducibility, relatively low cost, versatility and small amount of sample needed. Recently, two dimensional (2D) electrophoresis, combining isoelectric focusing in one direction with SDS-PAGE in the other has been used to increase resolution among HMW glutenins (Brown et al., 1981a, 1981b, and Cole et al., 1982).

To investigate how many different types of subunits dissociated

from the glutenin aggregates, Payne and Corfield, (1979a) prepared glutenin by gel filtration chromatography or by differential solubility They found more subunits in the case of differential solubility. The findings were in general agreement with the work of Huebner and Wall (1976) and the additional bands (found by SDS-PAGE) are probably contamination by albumins, globulins and gliadins not completely extracted prior to dissolving the glutenin fraction.

The twelve major subunits found in the gel filtration glutenin fraction fall conveniently into three groups which Payne and Corfield (1979a) designated A, B, and C. Group A has a MW between 140,000 and 95,000 daltons (measured by SDS-PAGE), group B a MW of 51,000 to 40,000 daltons and group C between 36,000 and 31,000 daltons. The group A subunits are generally referred to as the high molecular weight (HMW) subunits.

All the wheat varieties examined by Lawrence and Shepherd (1980) and by Payne et al. (1980 and 1981a) possess differences in their HMW glutenin banding patterns and up to 20 different bands have been identified using a discontinuous system of SDS-PAGE (Laemmli, 1970). It has been shown that the genes controlling these bands are located on the long arms of chromosomes 1A, 1B and 1D (Bietz et al., 1980, Brown et al., 1979, Lawrence and Shepherd, 1980, and Payne et al., 1980). Lawrence and Shepherd (1981b) and Payne et al. (1980 and 1981a) have demonstrated that chromosome 1D controls two closely linked HMW bands and 4 different allelic forms of this pair of loci have been identified. Chromosome 1B was found to control either one or two major HMW subunits. Nine different forms were reported by

Lawrence et al. (1980) and nine by Payne et al (1981a). Though some forms were unique to each study, chromosome 1A only shows 3 forms, two of these consist of single bands while the third is a null form.

A summary of the chromosomal location of the storage protein genes of the wheat endosperm is provided in Appendix Table 2 (Flavell et al., 1984). Notice that only two homoeologous chromosome series contain genes which control storage protein synthesis. These results have been confirmed by hybridization of the gliadin and glutenin cDNA clones to DNAs extracted from euploid plants and from the plants lacking individual chromosomes (Harberd, unpublished). The cDNA specifying HMW glutenin subunits hybridizes to similar extent to sequences only on the long arm of chromosomes 1A, 1B, and 1D, showing that the homeoallelic genes are clearly related and different from at least most gliadin genes.

In inheritance studies (Lawrence and Shepherd, 1981a and Payne et al., 1981b), different forms of the same subpattern have always segregated as alternative to each other, thus supporting the assumption that the different forms are controlled by allelic genes. The two genes on chromosome 1D that controlled HMW glutenin subunits are closely linked as are the two genes on chromosome 1B, since no recombinant individuals were detected among 496 test cross progenies (Lawrence and Shepherd, 1981a) or among several lines derived from F2 plants of various crosses (Payne et al., 1981b).

The physical and molecular basis of viscoelasticity is not known in detail. Elasticity (dough strength) is principally due to the long glutenin molecules, thought to be built up from HMW (and

probably LMW) subunits being linked together end to end by disulphide bonds (Ewart, 1977 and Miflin et al., 1983). The protein sequence data currently available for HMW glutenin subunits are consistent with this hypothetical structure. The amino terminal sequences include two cysteine residues in the first ten residues and the carboxyl terminal sequences of two cDNA glutenin clones each contain a single cysteine (Thompson et al., 1983).

Protein quality of a flour for bread-making appears to be directly proportional to 1) the amount of glutenin insoluable in 3M urea (Pommeranz, 1965), or 2) dilute acetic acid (Orth and Bushuk, 1972), and 3) the mean molecular weight of the glutenin aggregates (Huebner and Wall, 1976). Attributing the important properties of elasticity to HMW glutenin protein does not imply that gliadins play no part in bread-making. Indeed, being viscous and imparting extensibility, they are very much involved in expansion of the dough during fermentation. However, the intervarietal variation in dough strength is probably due to differences in the mean molecular weight of the glutenin aggregates which in turn is due to the structural variation in the different glutenin subunits (Payne et al., 1982). Payne et al. (1979b) found a positive correlation between the presence of a HMW glutenin subunit controlled by chromosome 1A and bread-making quality. Later, Payne et al. (1980) correlated the bread-making properties with presence of two subunits (5 and 10) both controlled by genes on chromosome 1D. The order of decreasing quality association for chromosome 1D subunits is 5 and 10 > 2 and 12 = 3 and 12 > 4 and 12 (Payne et al., 1982). Bournouf and Bouriquet

(1980) found that the bread-making quality of 47 genetically related varieties was correlated with two subunits of MW 108,000 and 122,000 daltons.

Genetic Control of Protein Content

Genetic variability for grain protein exists in hexaploid wheats, based on analysis of more than 20,000 hexaploid, tetraploid and diploid accessions in the USDA world collection and other research done at the University of Nebraska (Johnson and Mattern, 1979). However, the nature of genetic control is controversial, although all scientists agree that it is undoubtedly a complex subject and one that is difficult to study due to a strong influence of the environment. Aamodt and Torrie (1935) and Stuber et al.(1962) contend that grain protein content is governed by a complex polygenic system with genes distributed in all chromosomes. However, Johnson and Matterns (1979) reported two major dominant genes for high protein in Atlas 66, with one located on chromosome 5D. Nap Hal, another important genetic source for high protein, has different major genes from those found in Atlas 66 (Johnson et al, 1979). Halloran (1975) has also suggested the presence of major genes involved with many minor genes controlling the intensity of expression. Further evidence of the presence of minor genes has come from the work of Klepper (1975), who was able to select high protein lines from parents with intermediate protein levels.

That protein content is controlled by genes which act in an

additive manner, has been suggested by a large number of researchers (Stuber et al., 1962; Kaul and Susulski, 1965; Hsu and Susulski, 1969; Bhullar et al., 1978 and Knauft et al., 1980). Non-additive gene action seems to be of minor importance, though statistically significant (Chapman and McNeal, 1970; Barriga and Fuentalba, 1979; and Arora and Shandra, 1980). Transgressive segregation for the expression of protein content in F2 population has been reported by Johnson and Mattern (1979), Stuber et al. (1962), Hsu and Susulski (1969), Schumaker (1980), and Hazar (1982).

Broad and narrow sense heritability estimates also provide for contrasting opinions. Heritability estimates have been reported ranging anywhere from 0.15-0.26 (Saunderman et al., 1965) to 0.90 (Kaul and Susulski, 1965). Intermediate values were reported by Davis et al. (1961), Haunold et al., (1962), Stuber et al., (1962), Lofgren et al., (1968), Hsu and Susulski (1969), Ram and Srivastava (1975), and El-Sayed et al.(1979). Johnson et al. (1975) found that the size of the caryopsis does not affect protein content. Favret et al. (1970) and Jain et al. (1975) suggested that protein content should be expressed as the amount in one seed if high heritability values are to be obtained.

Effects of Yield on Grain Protein

According to Penning De Vries et al. (1974) the negative genetic correlation between grain yield and a high grain protein content can be partly explained by bioenergetic reasons. They calculated that

one gram of glucose produced by photosynthesis can be used by the crop to produce 0.83 grams of carbohydrate or alternatively 0.40 grams of protein. Bathia and Rabson (1976) have reported that the gross energy in the dry matter of high protein grain was higher than in a low protein cultivar and the net overall increase in photosynthesis to obtain 1% more of protein would be roughly of 1%. To provide this extra supply of energy they proposed 1) creating additional leaf area (LAI), 2) extending the period of photosynthesis activity (leaf area duration), and 3) maximizing mobilization of photosyntates into the grain. As Klepper (1974) noted, high yielding high protein wheats required enough photosynthetic capacity to provide energy to reduce CO2 and NO3. In other words, photosynthesis is needed for several interrelated processes as those mentioned by Austin et al. (1977): 1) nitrogen uptake by the roots, 2) greater plant weight that increases nitrogen uptake, 3) reduction of NO_3 to NH_4, and 4) maintenance of electroneutrality to compensate NO_3 reduction.

Johnson et al. (1975) pointed out that although high wheat yields are often accompanied by depressed protein content of the grain, these observations have been often interpreted incorrectly. Selection of grain protein independently of grain yield is likely to be ineffective (Johnson and Mattern, 1979), but protein differences among equally productive rows, on the other hand, are a reliable indication of true genetic differences. Moreover, productive high protein varieties of wheat like "Lancota" (Schmidt et al., 1979) have been developed and released, which suggests that the theoretical

calculation of energy constraints to protein production in wheat may need to be reconsidered.

Focke et al. (1980) reported concomitant progress in breeding for yield and protein between 1969 and 1978 in the German Democratic Republic. They have now reached an average of 5.6 tons/ha with 14.8% protein relying mainly on an increased vegetative reserve of protein before anthesis and active translocation to the grain. Recent evidence presented by Law et al. (1982) seems to indicate that if a single chromosome or even if a piece of a chromosome containing the regulator genes for the high protein traits are introduced in a high-yielding variety, then it is possible to achieve high protein coupled to an acceptable high yield.

According to Kramer (1979), cultivar differences in grain protein content can be caused in a number of ways, 1) differences in the absorption capacity of nitrogen from the soil per unit of biomass, 2) differences in the activity of the root system during grain filling period, 3) differences in the efficiency of the translocation of nitrogen substances from the vegetative tissues to the kernels, and 4) differences in harvest index.

Bremner (1972) has pointed out, when high protein results from greater uptake, a longer period of development before flowering is usually associated with greater uptake and content of nitrogen in the grain. Stuber et al. (1962) reported a positive correlation between grain protein content and days to flowering. Recently Randhawe and Gill (1978) and El-Sayed and Stolen (1979) have provided similar results regarding the relationship between days to flowering and

protein content.

Austin et al. (1977) reported that genetic variation exists for all traits determining nitrogen uptake and they concluded that light strawed genotypes were not suitable to produce selections having the nitrogen uptake necessary to permit high-yielding, high protein grain.

McNeal et al. (1971) suggested that plant breeders must be especially careful when selecting short varieties or they may be sacrificing protein. They found a positive correlation between grain protein content, plant height, and the amount of top growth regulating nutrient uptake. Vegetative growth protein was positively correlated with grain protein content. However, Johnson and Mattern (1979) presented data from international trials showing that there is not a consistent relationship between plant height and seed protein. Most of the high protein cultivars were semidwarf types. Desai and Bathia (1978) have pointed out that plant nitrogen content is an indication of nitrogen uptake. A positive correlation was found between plant nitrogen, grain yield and biological yield.

Under conditions where nitrogen uptake can continue throughout the grain filling period, with greater nitrogen soil availability or application of nitrogen fertilizer, both protein and starch content may increase linearly until maturity. More than half of the total grain protein content may be derived from nitrogen absorbed during the grain filling period (Bremner, 1972). Ellen and Spiertz (1975) concluded that if grain protein content depends on nitrogen uptake during grain filling period, a delay in leaf senescence will provide

the photosynthetic energy required for continuous NO_3 absorption, reduction, and storage. Austin et al. (1977) noticed that nitrogen absorption during grain filling was greater in those varieties which lost less dry matter from stem and leaves during that period. They found that Atlas 66 grain protein content could be explained in that way.

Yielding potential of a variety is usually associated with increased harvest index. Several examples are cited in the article of Donald and Hambling (1976). Some of the characteristics associated with this increase in harvest index are: 1) shorter straw, 2) earlier maturity, 3) reduced tillering and better tiller survival, and 4) smaller, upright leaves.

As Kramer (1979) reported, the effect of an increase in harvest index is twofold. The amount of straw and leaves (= nitrogen reservoir) is decreased, and at the same time, a larger quantity of grain biomass is formed so that a smaller amount of nitrogen has to be distributed to a larger amount of grain. On the average, the grain protein content appears to be 0.35% higher for every 1% decrease in harvest index. Negative correlation between grain protein content and harvest index were reported by McNeal et al. (1972), Bathia (1975), Desai and Bathia (1978), Knauft (1980), and Loffler and Busch (1982).

Khokhlov (1979) divided the grain content into, 1) the carbohydrate constituent (which is associated with harvest index) and 2) the nitrogen component (related to nitrogen translocation and its use in the synthesis of protein). The inverse relation between yield

and protein is largely due to the effect of the carbohydrate constituent. He also found little genetic variability in the nitrogen component.

Triticum turgidum ssp. dicoccoides

According to Konzak (1977), Triticum turgidum (L). Thell spp. dicoccoides (Korn) Thell (wild tetraploid emmer wheat), which carries the A and B genome is the wild ancestor of the cultivated emmer wheats. The A genome might come form T. monococcum ssp. boeticum (perhaps through Triticum urartu). The B genome and cytoplasm are yet of unknown origin.

Villegas et al. (1970) analyzed the protein content in different wheat species and accessions of wild emmer were notable for high grain protein content (27%) and for variability in this trait. In 1978, Avivi reported the high grain protein content of wild emmer. The general tendency of the more primitive or wild types for higher protein content already claimed by Harlan (1976) corresponds to the data of Avivi who found values of about 24% in seeds collected in a natural environment and values around 33% in seeds of greenhouses grown plants. Avivi also confirmed the high variability present in wild emmer with values of protein content ranging from 17% to 28% under field conditions and between 24% and 43% in the greenhouse. Finally, a positive correlation was found between protein content and seed weight and between protein and lysine content. Sharma et al. (1981) found averages of 28.5% and 29.3% for wild emmer grown under

irrigation and dryland respectively. Cole et al. (1981) believed that the protein content and quality of wild emmer may indicate a contribution to the B genome of this tetraploid by T. monococcum ssp. boeticum, T. urartu, or Aegilops squarrosa.

Wheat improvement by transferring desirable genes from wild emmer to cultivated species began in Israel in 1965 with the observation that wild emmer was a valuable source of stripe rust resistance (Gerechter Amitae and Stubbs, 1970). Gerechter-Amitai and Grama (1977) evaluated the possibility of introducing genes for high protein from wild emmer into hexaploid varieties. The chromosomes of wild emmer pair completely with the homologous chromosomes of cultivated wheats and transfer of genes is possible by crossing over. Several lines of common wheat containing genes from wild emmer have been developed in Israel which combine good yield, high protein level, and resistance to local rust disease.

Kushnir (1982) in Australia was able to increase the protein content of the Australian varieties Warrigal, and Barke, by crossing them with pentaploids derived from wild emmer. In that study, the very high protein content of wild emmer was interpreted as being due in part to the predominance of promoter genes for protein content in its A and B genomes and/or the absence of the D genome suppression of high protein reported by Welsh and Watson (1965), Mattern et al. (1978), and Bhat et Goud (1978).

Eight-hundred and fifty accessions of wild emmer were examined at Pullman, Washington using SDS-PAGE (Mansur-Vergara et al., 1984). Great genetic variability was observed for the glutenin and gliadin

fractions, particularly for bands which have been implicated in bread-making quality. In this study, no electrophoretically detectable gene markers were associated with the gene or genes controlling high protein content.

MATERIALS AND METHODS

Experimental material selected for this research represented a diverse source of wheat germplasm for both quality and quantity of protein, growth habit, and agronomic characteristics. Six Hard Red Spring Wheat lines (lines 15, 16, 17, 18, 19 and 20), developed by Criadero Buck in Argentina were used for their grain yield potential and good breadmaking properties. Three spring wheat hexaploid lines derived from Triticum turgidum (L.) Thell ssp. dicoccoides (Korn) Thell (tetraploid wild emmer wheat) developed at the Valcanic Institute in Israel were used as potential sources of high protein. They are secondary hexaploid derivatives from T.durum x T.dicoccoides / T.aestivum * 2, and are noted as lines 11, 13 and 14 in this study. McKay and Borah developed by scientists at the Idaho Research Center and at Washington State University respectively, were employed as locally adapted Hard Red Spring Wheat checks.

Cultivars representing the winter growth habit included "Bounty" (noted as line 21) which was released from the Plant Breeding Institute in Cambridge, England, and four advanced lines (noted as lines 23, 4, 6, and 10), of the Oregon State University Winter x Spring International Wheat Improvement Program. Stephens and Wanser, developed by scientists at the Oregon State University and at the Washington State University respectively, were employed as the locally adapted winter wheat checks.

Pedigrees and some agronomic data for the experimental material and checks are presented in Appendix Table 3. This collection of

germplasm was selected to identify the appropriate breeding tools and strategies which could assist the wheat breeder in developing high yielding, Hard Red Winter and Spring cultivars with good loaf volume. Five different studies were conducted to identify genetic and environmental factors affecting the performance of selected germplasm in Oregon.

Study 1

Evaluation of Laboratory Techniques for Identification of Desired Protein Quality Factors.

Due to the limited amount of seed, and to gain preliminary information about the experimental materials, the 17 lines were planted at Hyslop Agronomy Farm, near Corvallis, Oregon. Two-row plots, 3 meters long were harvested during the summer of 1983. The seed was used to establish two experiments. Winter lines were planted at the Hyslop Agronomy Farm during the fall of 1983. The second experiment involving the spring material was sown in Madras, Oregon, in April, 1984, and grown under irrigation. The materials were planted in two-row plots, 2 meters long in a completely randomized block design with eight replications. At the Hyslop site, the soil type is a Woodburn silt loam. A total of 170 kg/ha/growing season of nitrogen was applied in five split applications using either urea (46-0-0), ammonium chloride (21-0-0), or ammonium nitrate (23-0-0). Weeds were controlled with a fall application of Diuron (1.68 kg AI/ha) and by hoeing. At the Madras site, the soil is a

sandy loam. A total of 160 kg/ha/growing season of nitrogen in the form of urea (46-0-0) applied prior to planting. Weeds were controlled with an application of bromoxynil (0.5 kg AI/ha). Climatological records for these sites are given in Appendix Tables 4 and 5, respectively.

Plots at both locations were hand-sickled and threshed with a "Vogel" thresher. Grain yield was obtained by weighing the total amount of seed produced per plot. Twenty grams samples were ground in a Udy cyclone mill using a 0.5 mm. mesh sieve. The wholemeal flour produced was utilized to determine the grain protein content by near-infrared reflectance spectroscopy using a Technicon Infralyser 400. Breadmaking quality was evaluated by the "Sodium Dodecyl Sulphate Sedimentation Test" (SDSS test) proposed by Axford et al. (1978). With this method, the volume of material which precipitates is measured, after mixing flour with a solution of SDS and lactic acid. Samples with large SDSS values are reported to have high loaf volume.

The SDSS test was originally designed to evaluate European wheat cultivars for breadmaking quality. Thus, it was necessary to test the reliability of this methodology in relation to the germplasm selected for the present research. Five hundred gram seed samples of all 17 selections were sent to the Western Wheat Quality Laboratory at Pullman, Washington, to be evaluated for loaf volume. Five of these lines (lines 13, 18, 15, 16, and 11), chosen according to their intermediate to very high loaf volumes, were used to determine the appropriate combination of reactants to perform the SDSS test. A

factorial experiment was performed with four different SDS concentrations (1% to 4% SDS), four different lactic acid concentrations (10 to 40 ml/l of 9.6% lactate solution) and two sedimentation reading times (30 and 40 minutes) for each of the five lines (13, 18, 15, 16, 11). Treatment means were then correlated with the loaf volume results provided by the Western Regional Quality Laboratory.

According to Axford et al. (1979), Blackman et al. (1979), and Preston et al. (1982), results of the SDSS test are independent of growing conditions, and in particular, of variation in protein content. In order to test this statement, the 17 lines were planted in individual 15-cm pots of silt loam in the greenhouse during the fall of 1982. They were exposed to a range of nitrogen (0, 3, 6, 9, 12 g of Peters fertilizer 20-20-20) and irrigation treatments (daily, every two, three, and four days, respectively) so as to generate a broad range of grain protein contents. Greenhouse temperature of 24-30 C and the daylength of 18 h were maintained during this period. The seed from each treatment was harvested during the spring of 1983, and ground with a Udy cyclone mill (0.5 mm mesh sieve). Wholemeal flour was utilized to determine grain protein content by near-infrared reflectance spectroscopy and to estimate loaf volume by the SDSS test. The regression of SDSS values on grain protein content was calculated for the different treatments.

The 17 lines were also classified according to their electrophoretic banding patterns of the high molecular weight (HMW) glutenin subunits. The electrophoretic technique used was sodium

dodecyl sulphate polyacrylamide gel electrophoresis (SDS-PAGE) and the experimental procedure was adapted from the method described by Laemmli (1970) with the modifications proposed by Fullington et al. (1980), Hames (1981), Payne et al. (1981b) and Vieira (1985). Proteins were extracted with 0.062 M Tris-HCL buffer (pH 6.8) containing 2% (W/V) SDS, 5% (V/V) 2-mercaptoethanol, 0.001% (W/V) bromophenol blue and 10% (V/V) glycerol. Samples were placed in a hot water bath (95-100 C) for 3 min and stored at 4 C until used. The Bio-Rad dual slab system was used for SDS-PAGE. Electrophoresis was carried out in vertical slab gels (160 x 140 x 1.5 mm) with 15 wells. The separating gel contained 10% (W/V) acrylamide, 0.13% (W/V) bis-acrylamide, 0.1% (W/V) SDS and 0.375 M Tris-HCL (pH 8.8). The stacking gel contained 3.75% (W/V) acrylamide, 0.1% (W/V) bis-acrylamide, 0.1% (W/V) SDS and 0.125 M Tris-HCL (pH 6.8). Both gels were polimerized with TEMED and ammonium persulphate. Each column was loaded with 25 ul of sample. A constant current of 7.5 mA was applied for 17-18 hours. Gels were stained for 2-3 days in 0.02% Coomassie blue and destained with 10% TCA (Lawrence and Payne, 1983).

Study 2

Qualitative and Quantitative Inheritance Studies of Loaf Volume.

Two segregating populations were developed for this study. Line 15 from Argentina was crossed to lines 13 and 14 from Israel. The crosses were made in the greenhouse in the spring of 1983 and the F1s (1513,F1 and 1514,F1) were harvested in the summer of 1983. F1 seed

from both crosses was immediately planted in the greenhouse to produce the F2 generation (1513,F2 and 1514,F2) and the backcrosses to both parents (1513/15, 1513/13, 1514/15 and 1514/13).

The seed of the F2 and backcrosses generations was harvested in the winter of 1984 and a genetic study including parents, F1s, F2s and backcrosses was planted in the greenhouse on March, 1984. Each population consisted of 20 plants of each parental line, 20 F1 plants, 80 F2 plants and 40 plants for each backcross, resulting in a total of 220 plants/cross. Individual plants were grown in 15 cm pots of silt loam amended with 11 g of lime and 5 g of Peters fertilizer 20-20-20. The greenhouse temperatures varied between 18-24 C and the daylength was maintained at 14 h. The light duration was increased to 18 h and temperature raised to 24-30 C at jointing stage. Pots were fertilized twice with a total of 5 g of Peters fertilizer 20-20-20. Plants were harvested in August, 1985 and the grain samples ground in a Udy cyclone mill (0.5 mm mesh sieve). The wholemeal flour produced was used to measure SDSS values and to perform an electrophoretic analysis of the HMW glutenin subunits.

The distribution of SDSS values of the F3 grain from the F2 plants was determined. F3 samples were also classified into three quality groups: 1) SDSS values as low or lower than the poorest parental line ("low SDSS values"), 2) SDSS values intermediate between both parental lines ("intermediate SDSS values"), and 3) SDSS values as high or higher than the best parental line ("high SDSS values"). Correlations of these three groups with the presence or absence of specific HMW subunits of glutenins in the A, B, and D

genome were determined. The F3 material was also classified into different quality groups depending on the presence or absence of specific banding patterns in the three genomes. Mean sedimentation volume of the samples which fell into each of the groups was then calculated and differences in the means of the compared subunits were tested for significance with Student's "t" test.

The SDSS data were used to calculate heritability estimates for loaf volume. Two methods of estimation were considered : Warner's method of components of variance (Warner, 1952), [h2 = 2 x VF2 - (VBC1 + VBC2) / VF2] and an approximation of nonheritable variance from genetically uniform populations to estimate total genetic variance [h2 = VF2 - {1/3 (VF1 + VP1 + VP2)} / VF2] (Burton, 1953). To evaluate possible heterotic response, a t-test was used to compare mid-parental means with F1 means for each cross.

A random sample of three seeds from each F2 and backcross plant (160 plants per cross) was planted in the greenhouse (the three seeds in a 15-cm. pot) during the fall of 1984. The F3 generation was advanced using a modified single seed descent procedure. Cultural practices in the greenhouse were the same as those previously noted. The F4 seed was harvested in March 1985 and sown in Madras, April, 1985. Forty F4 entries per cross including parental lines were planted in randomized complete block design with two replications. Plots were one row, 2-meters long with 30 cm between rows. The soil was amended with 320 kg of urea / ha before planting time. Weeds were controlled with bromoxynil (0.5 kg AI/ha) and irrigation was supplied (30 mm/week) each week until late milk stage.

Climatological records for this site are given in Appendix table 6. The F5 seed was harvested in August, 1985 and the wholemeal obtained with the Udy mill was utilized to repeat the genetic evaluation of protein quality in the latter generation. Heritabilities for SDSS values were estimated utilizing parent-offspring regression of F2 derived F4 rows on F2 individual plants (Frey and Horner, 1957). Electrophoretic data were analysed following procedures noted previously.

Study 3

Inheritance of Grain Protein Content and Grain Hardness.

Nine crosses were made to study the inheritance of grain protein content and grain hardness. Three Argentine lines (lines 15, 16, and 18) were crossed to three lines from Israel (lines 11, 13, and 14). The F1, F2 and backcrosses to both parental lines were obtained following a similar strategy as described for crosses 1513 and 1514 in study 2. This genetic study was planted in the greenhouse in March, 1984, and the nine populations (crosses 1511, 1513, 1514, 1611, 1613, 1614, 1811, 1813, and 1814) were handled in a similar manner except that half the number of plants per cross were analysed due to greenhouse space limitations.

Plants were harvested during the month of August, 1984. The grain was ground as previously described to determine grain protein and grain hardness by infrared reflectance spectroscopy (Bruinsma et al., 1979). Crosses were analysed independently and estimates of

heritability and heterosis for percent grain protein, and grain hardness obtained as in study 2. F1 and F2 generations of the nine crosses were also analysed together as a factorial design where the three lines from Argentina represented one factor and the those from Israel a second factor. The purpose of this analysis was to evaluate the importance of main treatment effects and possible interactions.

Parental lines and F1 plants from the nine crosses were also planted at the Linn farm near Albany, Oregon, during the spring of 1984. Each population consisted of 10 plants per each parental line and 10 F1 plants. These plants were arranged in a complete randomized design and planted in April, 1984. The soil was a Woodburn silt loam and the plots were fertilized with 100 kg of urea /ha prior to planting and an additional 200 kg/ha more was applied at the tillering stage. Weeds were controlled by hand-hoeing. Climatological records for this site are given in Appendix Table 4. Plants were harvested during August, 1984, and estimates of heterosis were calculated as previously noted.

To obtain latter generation data, F2 and backcross plants were advanced one more generation in the greenhouse, using a single seed descent procedure. F4 seed harvested in the greenhouse was planted in plant-rows in Madras, in April, 1985 under the same experimental arrangement and cultural management as noted in study 2. The experiment was harvested in August, 1985 and grain yield per plot was determined. Twenty grams seed samples per entry were ground with a Udy mill to determine percent grain protein content, SDSS values, and grain hardness. Heritabilities for grain protein content and grain

hardness were calculated using parent-offspring regression of the F2-derived F4 segregating lines on the F2 individual plants (Frey and Horner, 1957). F4 plant-rows were compared with parental lines and checks to have preliminary results about the performance of the segregating F4 lines in relation to the three traits of interest, grain yield, grain protein content, and SDSS values.

Study 4

Identification of Possible Agronomic Traits which are Phenotypically Correlated with Grain Yield, Grain Protein Content, and SDSS Values

Hard Red Winter Wheat lines were planted under four fertilizer combinations in 1983-84 and four different fertilizer combinations in 1984-85, resulting in a total of eight environments. In the fall of 1983 two-rows plots, 2 meter long, were planted at the Hyslop Agronomy Farm. Entries were arranged in a complete randomized block design with three replications. Hard red winter lines 4, 6, 10, 21, and 25 were included in each of the four treatments and cultivars Wanser and Stephens were added as local checks. Weeds were controlled with fall application of Diuron (1.68 kg AI/ha) and by hand-hoeing. Fertilizer combinations for each of the four treatments are presented in Table 1.

In the Fall of 1984 an additional trial was planted at the Hyslop Agronomy Farm using the same experimental design. This time the plots were six-rows wide, 16 feet long with the two central rows being harvested. Fertilizer information is presented in Table 2.

Table 1. Fertilizer applications used in the experiment conducted at the Hyslop Agronomy Farm during the 1983-84 growing season.

Treatment 1	Oct/83 : 30	kg N/ha (urea)
	Jan/84 : 40	kg N/ha (ammonium nitrate)
	Feb/84 : 10	kg N/ha (ammonium nitrate)
	10	kg N/ha (ammonium chloride)
Treatment 2	Same basic fertilizer application as #1 plus:	
	Mar/84 : 80	kg N/ha (urea)
Treatment 3	Same basic fertilizer application as #1 plus:	
	Heading: 80	kg N/ha (urea)
Treatment 4	Same basic fertilizer application as #1 plus:	
	Mar/84 : 40	kg N/ha (urea)
	Heading: 40	kg N/ha (urea)

Table 2. Fertilizer applications used in the trial conducted at the Hyslop Agronomy Farm during the 1984-85 growing season.

Treatment 1	Oct/84	30 kg N/ha (urea)
	Jan/85	30 kg N/ha (ammonium nitrate)
	Feb/85	30 kg N/ha (ammonium nitrate)
	Mar/85	30 kg N/ha (urea)
Treatment 2	Oct/84	30 kg N/ha (urea)
	Jan/85	30 kg N/ha (ammonium nitrate)
	Mar/85	60 kg N/ha (urea)
Treatment 3	Oct/84	30 kg N/ha (urea)
	Feb/85	30 kg N/ha (ammonium nitrate)
	Mar/85	60 kg N/ha (urea)
Treatment 4	Oct/84	30 kg N/ha (urea)
	Mar/85	90 kg N/ha (urea)

Cultural practices and the lines included in the four experiments were the same as in the previous year.

Traits measured or calculated from each plot included:

Days to heading: number of days from emergency to 50% of the spikes were headed.

Days to physiological maturity: number of days from emergency to complete loss of the green color of all the spikes and peduncles.

Grain filling period: days to physiological maturity minus days to heading.

Plant height: measured at harvest time as the distance (cm) between the soil surface and the tip of the highest spikes, excluding the awns.

Biological yield per plot: total weight of the plant biomass above the ground level. Plots were sickled and the whole plot bundle was used for the measurement.

Grain yield per plot: the plot bundles were threshed using a "Vogel" thresher and the harvested seed was weighed to determine total grain yield per plot.

Harvest index: grain yield per plot divided by biological yield per plot.

1000 kernel weight

Grain hardness: measured by near-infrared reflectance spectroscopy using Udy ground wholemeal flour (0.5 mm mesh sieve).

Percent grain protein content: measured by near-infrared reflectance spectroscopy using Udy ground wholemeal flour.

Protein yield per plot: grain yield per plot x percent grain protein

content.

SDSS value: same experimental procedure utilized in study 1.

Broad sense heritability estimates for the previous twelve traits were calculated using variance components method (Comstock and Robinson, 1952). Phenotypic correlations among three traits, grain yield, grain protein content, and SDSS values, with nine other traits were calculated using cultivar means for each of the eight fertilizer treatments.

A total of six environments were utilized to evaluate the Hard Red Spring Wheat germplasm. In the spring of 1984, the spring lines were planted under two fertilizer combinations in Madras. Two seeding rates at the Linn farm and two seeding rates in Madras were established in the spring of 1985. In 1984, two-rows plots, 2 meters long with 30 cm between rows were planted in four replications in each experiment. Hard Red Spring Wheat lines 11, 13, 14, 15, 16, 17, 18, 19 and 20 as well as McKay and Borah were all included in the experiments. The two fertilizer combinations consisted of 1) a preplanting application of 200 kg urea / ha, and 2) a preplanting application of 180 kg of urea / ha plus 60 kg of urea / ha at heading stage. Weeds were controlled with bromoxynil (0.5 kg AI/ha).

The Linn and Madras plots in 1985 were six rows wide and 5 meters long. Seeding rates were 100 kg/ha or 50 kg/ha in both experimental sites. Lines were the same as the previous year and fertilizer applications were 320 kg of urea /ha at Madras and 300 kg of urea /ha at the Linn Farm. Climatological records for the Albany site during 1985 are given in Appendix Table 7. Plots were combined

except for a row, 4 meters long, which was sickled in advance to measure harvest index. The traits measured as well as the statistical analysis were identical to those used for the winter wheat cultivars.

To determine whether any of these twelve traits could be selected for on an individual plant basis, nine plants of each cultivar were grown in the greenhouse in a complete randomized design during the 1983/84 growing season. Winter materials were planted in vermicullite flats and allowed to germinate for seven days. Seedlings were then vernalized for eight weeks in a growth chamber at 8-10 C and a daylenght of 8 h. The plants were transplanted into 15 cm pots of silt loam amended with 11 g of lime and 5 g of Peters fertilizer 20-20-20 and put into the greenhouse at 18-24 C and a daylength of 14 h. At jointing stage, the light duration was increased to 18 h and temperature increased to 24-30 C. Pots were fertilized twice with a total of 5 g of Peters fertilizer 20-20-20. The spring material was started at the time when the winter seedlings were finishing their vernalization period. The same twelve traits were measured on a plant basis and the corresponding phenotypic correlations calculated.

Study 5

Fertilizer Management Practices to Improve Protein Content of Hard Red Winter Wheat Lines in the Willamette Valley, Oregon.

Agronomic studies were conducted during two consecutive years at

the Hyslop Agronomy Farm. The main objective was to find the best fertilizer strategy to maintain an acceptable level of grain protein content required for a Hard Red Winter Wheat cultivar to satisfy market and industry standards. A split plot was designed with fertilizer as main plot treatment and varieties as subplot treatment. Experimental lines 4, 6, 10, 21, and 25 and the two checks Wanser and Stephens were planted in two-rows plots, 2 meters long, with 30 cm. between rows and three replications. Fertilizer treatments and cultural practices are outlined in Table 1. Even though grain protein content was the trait of interest, all other eleven traits measured in study 4 were also considered in this study to find out how they were affected by the fertilizer treatments. Results were analysed in the standard split-plot fashion.

On the basis of the information collected during 1984, a similar experiment with some changes in the fertilizer treatments was repeated at the Hyslop Agronomy Farm during 1985. The 1985 rates and times of application are provided in Table 2. Varieties, weed control practices, and the traits measured were the same as the previous year. However, this year, the plots were 5 meters long with six rows, 15 cm apart. Only the central two rows were harvested and results were analysed in the same way as the previous year.

RESULTS

The results will be presented based on the five experiments conducted with no attempt made to interrelate the studies until the discussion section.

Study 1

This study was diverted towards an evaluation of the laboratory techniques, sodium dodecyl sulphate sedimentation (SDSS) test, and sodium dodecyl sulphate polyacrylamide gel electrophoresis (SDS-PAGE), for their reliability in identifying the desired protein quality factors.

A summary of the SDSS test calibration results is presented in Table 3. Thirty two treatments were imposed, but for the purpose of illustration only eight of the most representative are presented. The precipitate increased as the SDS detergent concentration increased from 1% to 4%. Within each SDS concentration, the precipitate decreased as the amount of lactic acid increased from 10 to 40 ml/l of 9.6% lactate solution. In treatment combination 7 and 8, the low SDS concentration (1%) and the high amount of lactic acid (30 ml/l) are responsible for the low SDSS values obtained for all selections, and for the low correlation coefficients. Significant correlation coefficient values were also observed for the other treatments. Treatment 11 and 12 distinguished between the higher and lower loaf volume values in contrast to treatment 3 and 4. In

Table 3. Relationship between loaf volumes and sodium dodecyl sulphate sedimentation (SDSS) values obtained with different combinations of SDS, lactate solution, and reading times, in five selected Hard Red Spring Wheat lines (lines 11, 13, 15, 16, and 18).

Selected Lines	SDSS Values (ml) in Treatment Combinations†								Loaf Volume § Values (cc)
	3	4	7	8	11	12	13	14	
11	31	30	16	16	79	77	63	60	1145
13	21	20	16	16	41	39	36	34	770
15	29	28	16	16	73	70	58	54	1040
16	30	29	16	16	78	76	59	55	1060
18	26	25	15	15	60	58	49	46	905
"r"values	.98**	.98**	.30	.30	.97*	.97*	.99**	.99**	

*, ** significance at the 0.05 and 0.01 probabilty levels, respectively (N = 5).

† The combinations in each treatment are the following :

T.3 : 1% SDS - 10ml/l lact - 30'
T.4 : 1% SDS - 10ml/l lact - 40'
T.7 : 1% SDS - 30ml/l lact - 30'
T.8 : 1% SDS - 30ml/l lact - 40'
(lact = 9.6% lactate solution)

T.11 : 2% SDS - 10ml/l lact - 30'
T.12 : 2% SDS - 10ml/l lact - 40'
T.13 : 2% SDS - 20ml/l lact - 30'
T.14 : 2% SDS - 20ml/l lact - 40'
(30' = 30 minutes reading time)

§ Loaf volume data provided by the Western Wheat Quality Laboratory.

treatment 11, the difference in SDSS values between line 11 (loaf volume = 1145 cc) and line 13 (loaf volume = 770 cc) is 38 points, whereas in treatment 3 the difference is only 10 points. According to the data, the best treatment is 2% SDS, 10 ml/l of 9.6% lactate solution, and 30 minutes to reading time.

To test the hypothesis that SDSS values are independent of protein content, the regressions of SDSS values on protein content were studied in eight selected lines grown in the greenhouse. The eight genotypes were those that had the broadest range of grain protein. Figure 1 illustrates the relationship between SDSS values and protein content for Wanser, where grain protein ranged from 10.2% to 14.9%. There is a significant increase in SDSS values when protein content varies within these limits ($r = +0.629^{**}$). Figure 2 and Figure 3 show the relationship between SDSS values and protein content for lines 10 and 14, respectively. Protein contents varies from 12.6% to 17.4% for selection 10 and from 15.0% to 18.4% for selection 14. Within that range of protein contents, there was a significant decrease in SDSS values when protein content increased (for example, line 10 : $r = -0.847^{**}$ and line 14 : $r = -0.672^{**}$). The correlation values between SDSS and protein content for the rest of the selected lines (lines 11, 15, 16, 18, and 23) are provided in Appendix Figures 1 to 5. A numerical summary of the results for the eight selections is presented in Table 4. At higher grain protein levels, relationships between SDSS values and protein content were negative.

Sodium dodecyl sulphate polyacrylamide gel electrophoresis (SDS-

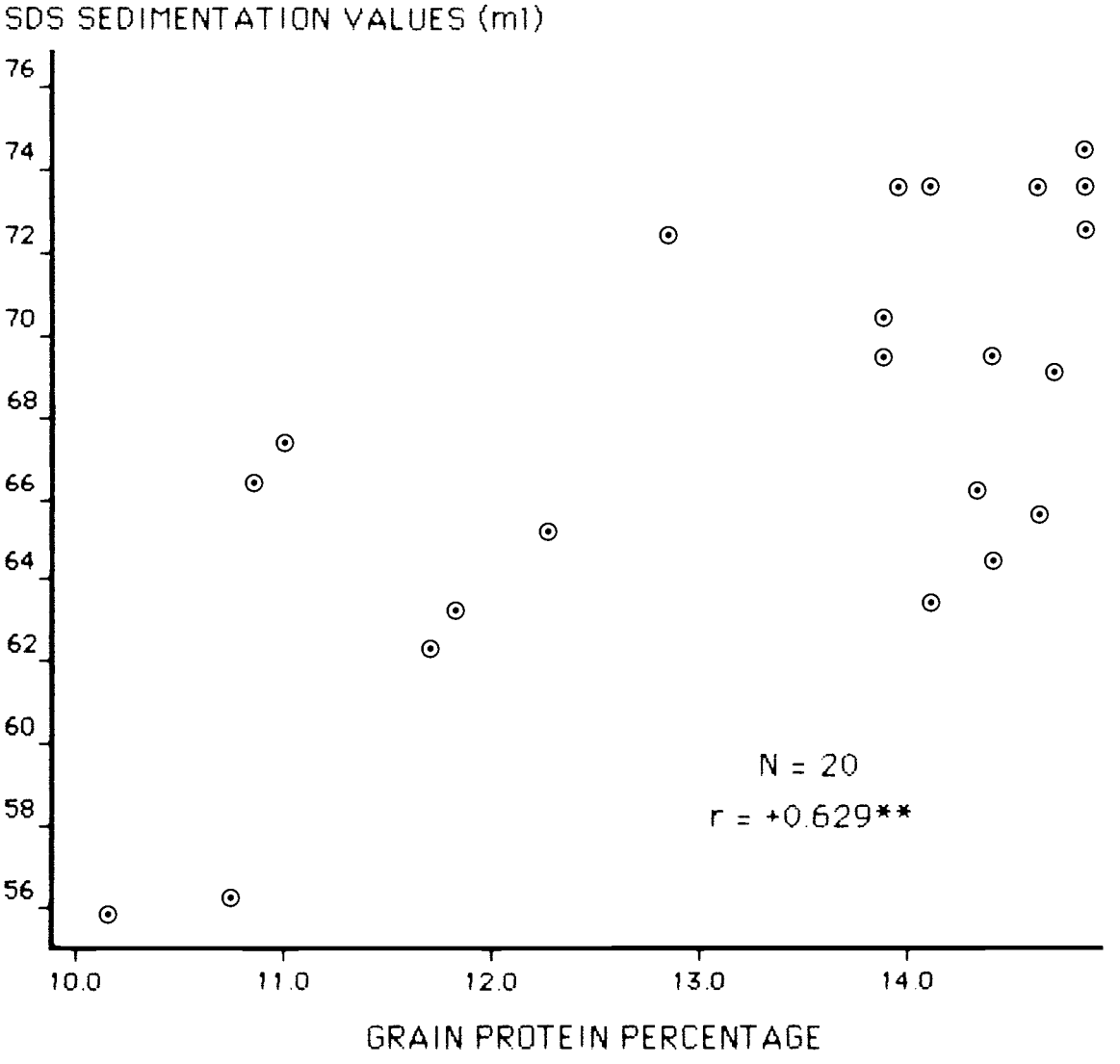

Figure 1. Relationship between grain protein content and sodium dodecyl sulphate (SDS) sedimentation values in Wanser (greenhouse, 1983).

** significance at the 0.01 probability level.

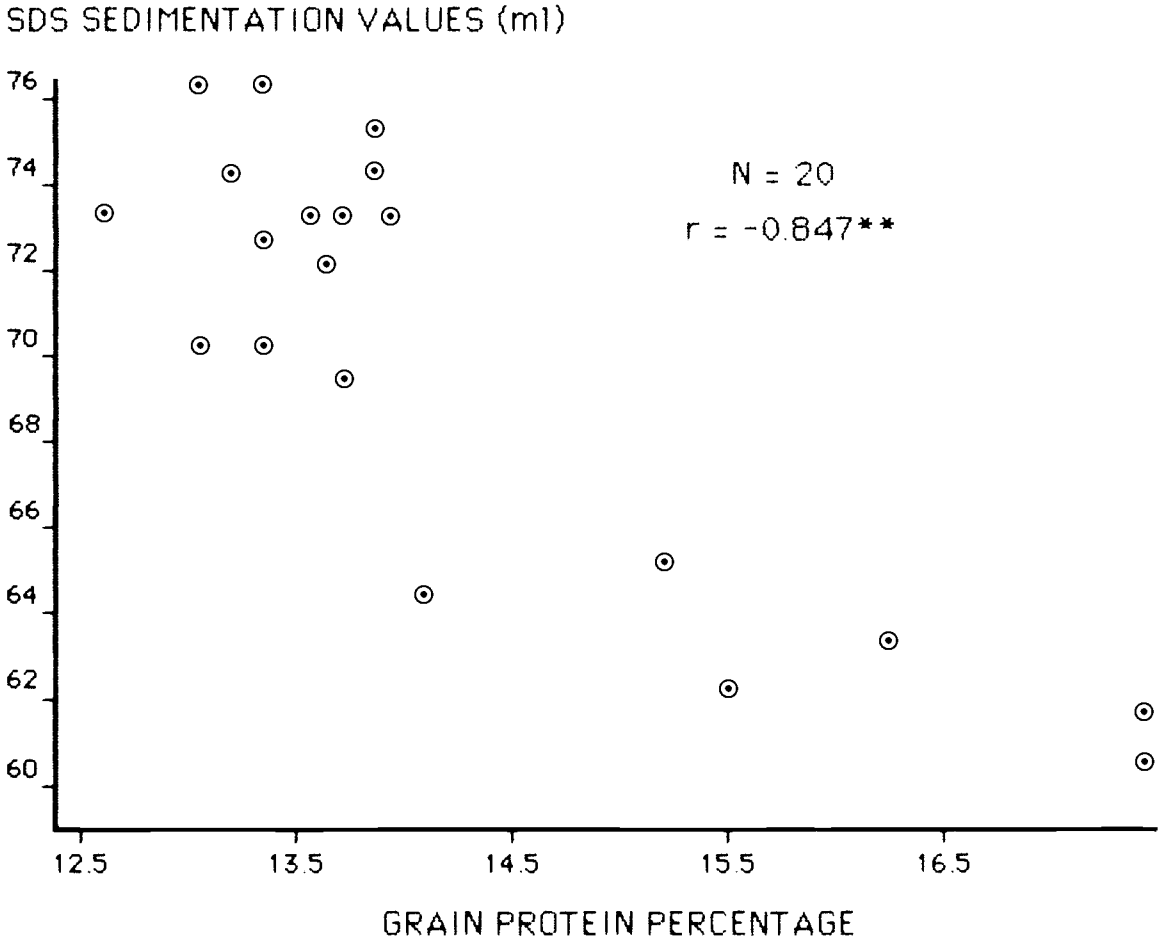

Figure 2. Relationship between grain protein content and sodium dodecyl sulphate (SDS) sedimentation values in Hard Red Winter Wheat line 10 (greenhouse, 1983).

** significance at the 0.01 probability level.

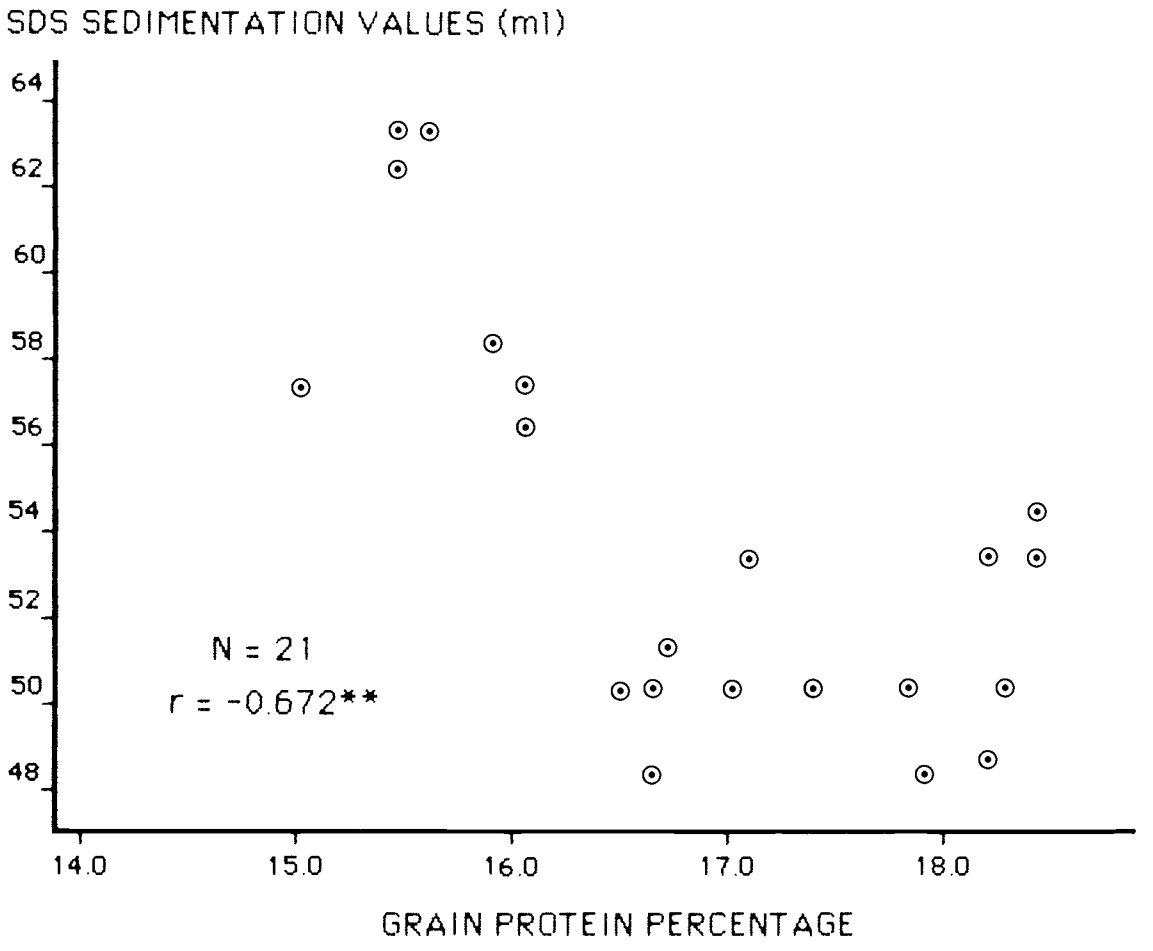

Figure 3. Relationship between grain protein content and sodium dodecyl sulphate (SDS) sedimentation values in Hard Red Spring Wheat line 14 (greenhouse, 1983).

** significance at the 0.01 probability level.

Table 4. Relationship between grain protein content and sodium dodecyl sulphate (SDS) sedimentation values in selected Hard Red Spring and Winter Wheat lines (greenhouse, 1983).

Cultivars	Percent Protein Range (%)	SDS Sedimentation Range (ml)	Correlation Coefficients
Line 11	14.0 - 19.3	72 - 59	-0.487*
Line 14	15.0 - 18.4	63 - 48	-0.672**
Line 15	13.0 - 18.3	67 - 56	-0.438*
Line 16	13.5 - 18.8	75 - 58	-0.512*
Line 18	13.5 - 18.4	63 - 44	-0.519*
Line 23	13.0 - 18.0	81 - 68	-0.686**
Line 10	12.6 - 17.4	76 - 57	-0.847**
Wanser	10.2 - 14.9	52 - 74	0.629**

*, ** significance at the 0.05 and 0.01 probability levels, respectively (N = 20).

PAGE) was the second laboratory technique evaluated for its potential applications to plant breeding. Once the SDS-PAGE experimental procedure for the high molecular weight (HMW) glutenins was adjusted, the reliability of the technique was tested. A control gel (Figure 4) was run utilizing the selected line 13 in every column, but differing in the amount of protein content from 13.9% to 22.0%. As can be noted in Figure 4, the locations of the HMW glutenin bands on the gel were not affected by protein concentration in the flour samples.

Electrophoretic banding patterns of lines 11, 13, 15, 16, 18, 4, 6, 10, 23, and of Wanser and Stephens are shown in Figure 5. The numbering system used to identify the HMW glutenin subunits is the same employed by Payne and his associates at the Plant Breeding Institute, in Cambridge, England (Payne, 1981a). According to Payne et al. (1981a), the HMW glutenin genes are found on the long arm of chromosome 1, as a pair of closely linked coding sequences near the centromere. On chromosome 1D, a pair of genes are responsible for bands 5-10 (lines 11 and 15, as an example), 2-12 (Stephens) and 3-12 (line 13). On chromosome 1B, the allelic forms are protein bands 7-8 (lines 11 and 15), 17-18 (lines 16 and 13), 7-9 (line 18 and Wanser), 13-19 (line 14) and 7 (Stephens). The glutenin gene on chromosome 1A is coding for protein band 1 (lines 11 and 15), or 2* (lines 13 and 16). Some wheat cultivars, like Stephens or line 23, do not present any glutenin gene product synthesised on chromosome 1A.

The Hard Red Winter and Spring Wheat materials were characterized for grain yield, grain protein content and loaf volume.

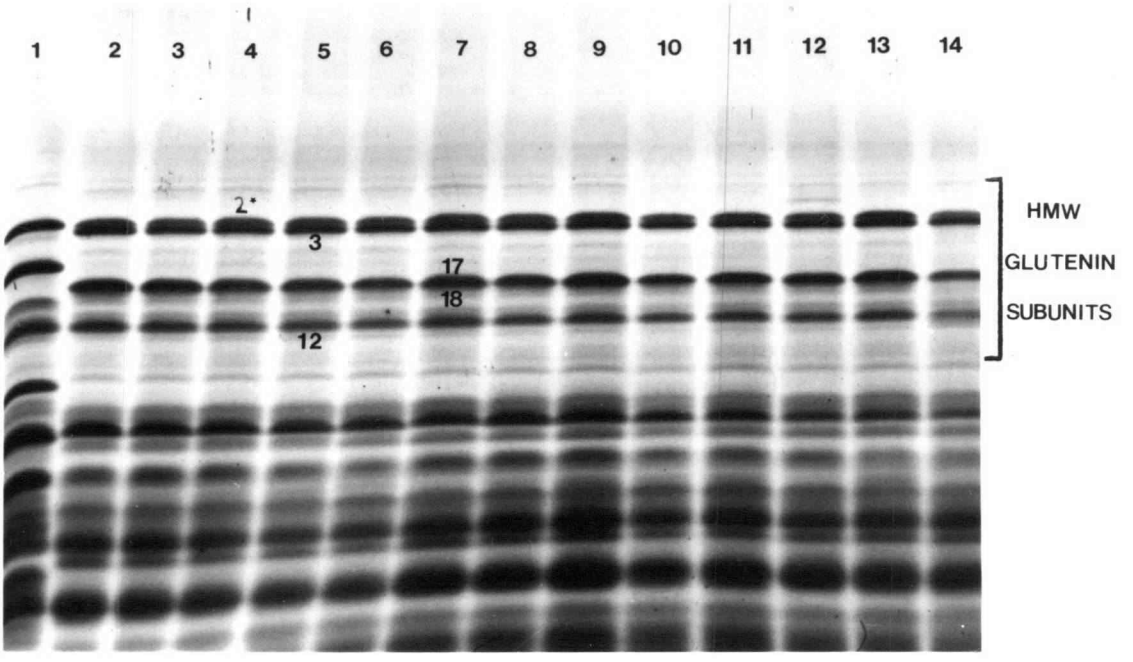

Figure 4. Relationship between flour protein content and SDS-PAG electrophoretic banding patterns of the high molecular weight (HMW) glutenin subunits in Hard Red Spring Wheat line 13 carrying bands 2* / 17-18 / 3-12.

Lane 1 : Chinese Spring
Lane 2 : 22.0% protein
Lane 3 : 21.5% protein
Lane 4 : 20.9% protein
Lane 5 : 20.2% protein
Lane 6 : 19.4% protein
Lane 7 : 18.6% protein
Lane 8 : 16.9% protein
Lane 9 : 16.8% protein
Lane 10 : 16.4% protein
Lane 11 : 16.0% protein
Lane 12 : 15.9% protein
Lane 13 : 15.7% protein
Lane 14 : 13.9% protein

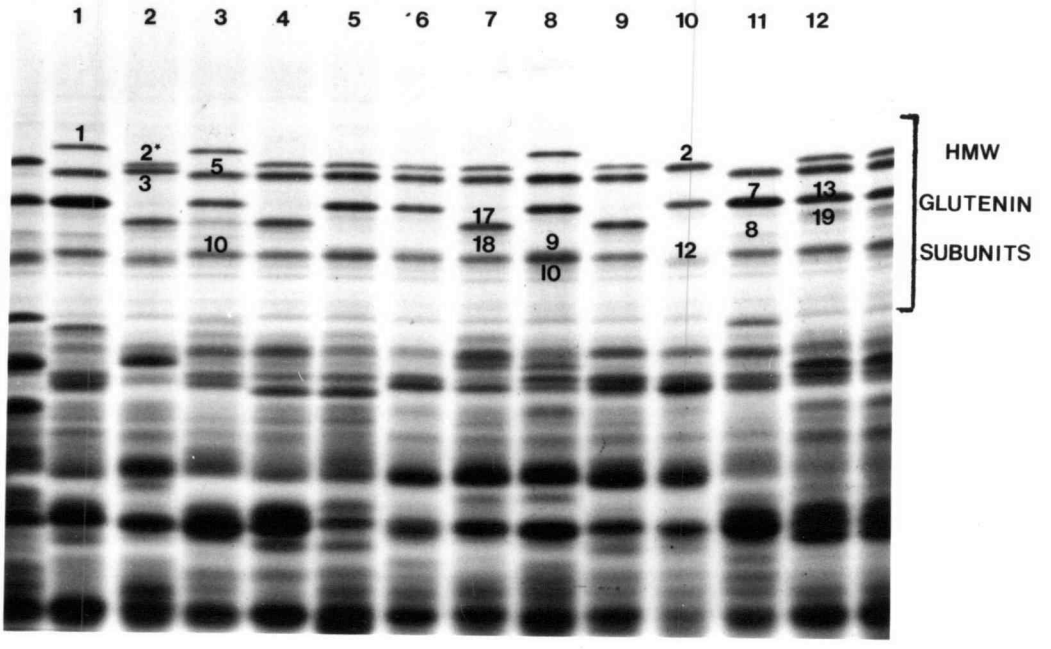

Figure 5. Electrophoretic banding pattern of the high molecular weight (HMW) glutenin subunits in selected Hard Red Spring and Winter Wheat lines used in this study.

	Cultivars	AA	BB	DD
Lane 1:	11	1	7-8	5-10
Lane 2:	13	2*	17-18	3-12
Lane 3:	15	1	7-8	5-10
Lane 4:	16	2*	17-18	5-10
Lane 5:	18	2*	7-9	5-10
Lane 6:	Wanser	2*	7-9	5-10

	Cultivars	AA	BB	DD
Lane 7:	4	2*	17-18	5-10
Lane 8:	6	1	7-9	5-10
Lane 9:	10	2*	17-18	5-10
Lane 10:	Stephens	-	7	2-12
Lane 11:	23	-	7-8	5-10
Lane 12:	14	2*	13-19	5-10

Data on the previous three traits as well as the relationship of loaf volume with SDSS values and SDS-PAGE banding patterns are summarized in Tables 5 and 6. In the winter group, there are two lines, 6 and 10, which were higher in grain yield than the check Stephens. Two others, lines 4 and 23, were not different from the same check. Lines 4 and 10 were also superior in protein content and SDSS values to the quality check Wanser. Their banding pattern (2* / 17-18 / 5-10) confirmed the quality determinations obtained with the SDSS test at the OSU laboratory and the loaf volume results received from the Western Wheat Quality Laboratory at Pullman, Washington.

Hard Red Spring data are summarized in Table 6. No checks are included in the table, as neither Borah nor Mckay were planted at Madras in the spring of 1984. The lines from Israel (lines 11, 13 and 14) were significantly lower in grain yield when compared with most of the Argentine entries. With the exception of line 19 from Argentina, the selections from Israel were significantly higher than the Argentine lines in grain protein content. Breadmaking quality data represented by the SDSS values, the loaf volume determinations, and the electrophoretic banding patterns, reveals that there were good quality lines among both groups of germplasm (line 11 from Israel, lines 15, 16, 17, 19, 20 from Argentina). There was also a good association among the three quality parameters, protein content, SDSS values, and HMW glutenin proteins. Protein bands 3-12 in the D genome, and protein bands 7-9 and 13-16 in the B genome appears to confer poor quality properties on the selection carrying them.

Table 5. Characterization of the Hard Red Winter Wheat lines for grain yield, grain protein content, and loaf volume (Hyslop, 1984-85).

Selection Number	Grain Yield (ton/ha)	Grain Protein Content (%)	SDSS (ml)§	Loaf Vol (cc)¶	HMW glutenins AA	BB	DD#
6	10.9 a †	12.6 b	59 d	910	1	7-9	5-10
10	10.7 a	13.2 a	74 a	955	2*	17-18	5-10
23	10.5 ab	12.6 b	73 a	915	-	7-8	5-10
4	10.3 ab	13.4 a	65 b	930	2*	17-18	5-10
Stephens	9.9 b	11.1 c	31 e	-	-	7	2-12
Bounty	8.7 c	13.5 a	58 d	925	1	7	2-12
Wanser	7.7 d	12.6 b	63 c	872	2*	7-9	5-10
LSD (0.05)	0.7	0.3	2				

† Treatment means with the same letter are not significantly different at the 0.05 probability level.

§ SDSS = sodium dodecyl sulphate sedimentation values
¶ Loaf Vol = Loaf volume values
# HMW = high molecular weight

Table 6. Characterization of the Hard Red Spring Wheat lines for grain yield, grain protein content, and loaf volume (Madras, 1984-85).

Selection Number	Grain Yield (ton/ha)	Grain Protein Content (%)	SDSS (ml)§	Loaf Vol (cc)¶	HMW glutenins AA	BB	DD#
16	4.8 a †	14.9 d	64 a	1050	2*	17-18	5-10
20	4.6 ab	15.7 c	50 d	1066	2*	7-8	5-10
17	4.5 b	14.4 e	57 c	1015	1	17-18	5-10
15	4.4 b	14.1 e	60 b	1040	1	7-8	5-10
18	4.3 bc	15.2 d	49 d	905	2*	7-9	5-10
19	4.1 cd	17.1 a	57 c	1085	2*	17-18	5-10
14	4.0 de	16.2 b	49 d	1065	2*	13-19	5-10
11	3.8 de	16.8 a	65 a	1145	1	7-8	5-10
13	3.6 e	16.2 b	40 e	770	2*	17-18	3-12
LSD (0.05)	0.3	0.4	2				

† Treatment means with the same letter are not significantly different at the 0.05 probability level.

§ SDSS = sodium dodecyl sulphate sedimentation values.
¶ Loaf Vol = Loaf volume values.
# HMW = high molecular weight.

Study 2

Qualitative and quantitative inheritance studies of loaf volume were conducted utilizing gel electrophoresis and SDS sedimentation test. The two crosses evaluated, 1513 and 1514, were selected based on the information in Table 6. First, they are crosses between high yielding Argentine lines and high protein lines from Israel. Second, the banding pattern in both crosses allows for a maximum number of glutenin protein combinations among the lines used in this study. Third, both crosses are spring x spring combinations which allows for a faster generation turnover time (Table 6).

Electrophoretic banding patterns of parental lines 13, 14, and 15 and their corresponding F1 combinations can be observed in Figure 6. Four other F1 lines and their parents are also presented in the same figure. This gel illustrates that all the HMW glutenin gene products from the parents are being expressed in the the F1 progenies. For example, in 1513,F1 (lane 1), protein bands 1, 7-8, and 5-10 provided by line 15 and protein bands 2*, 17-18, and 3-12 contributed by line 13 appear together in the same column.

F3 grain harvested on individual F2 plants belonging to crosses 1513 and 1514 was ground with a Udy cyclone. The wholemeal flour obtained was used to determine SDSS values. Frequency distributions of the SDSS values for each cross are presented in Figures 7 and 8. A normal distribution was obtained with the majority of the samples being intermediate between the SDSS values obtained for the two parents in each cross. Sedimentation values for both F1s are also

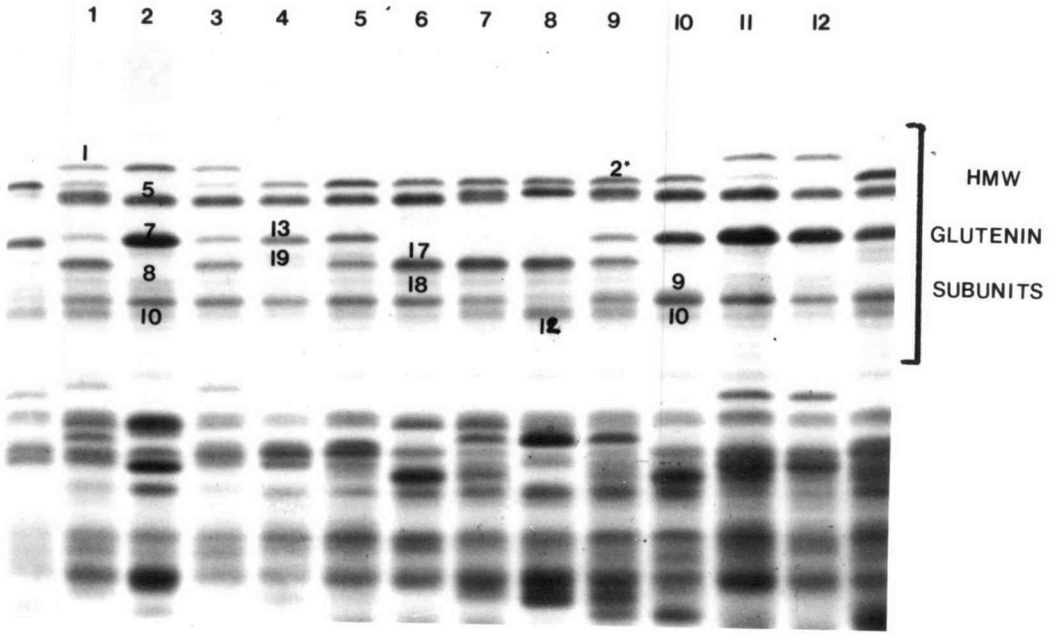

Figure 6. The SDS-PAGE banding pattern of the high molecular weight (HMW) glutenin subunits for six F1 combinations and their corresponding parental lines.

	AA	BB	DD
Lane 1: F1 1513	1	7-8	5-10
	2*	17-18	3-12
Lane 2: P.15	1	7-8	5-10
Lane 3: F1 1514	1	7-8	5-10
	2*	13-19	5-10
Lane 4: P.14	2*	13-19	5-10
Lane 5: F1 1614	2*	17-18	5-10
	2*	13-19	5-10
Lane 6: P.16	2*	17-18	5-10
Lane 7: F1 1613	2*	17-18	5-10
	2*	17-18	3-12
Lane 8: P.13	2*	17-18	3-12
Lane 9: F1 1813	2*	7-9	5-10
	2*	17-18	3-12
Lane 10: P.18	2*	7-9	5-10
Lane 11: F1 1811	2*	7-9	5-10
	1	7-8	5-10
Lane 12: P.11	1	7-8	5-10

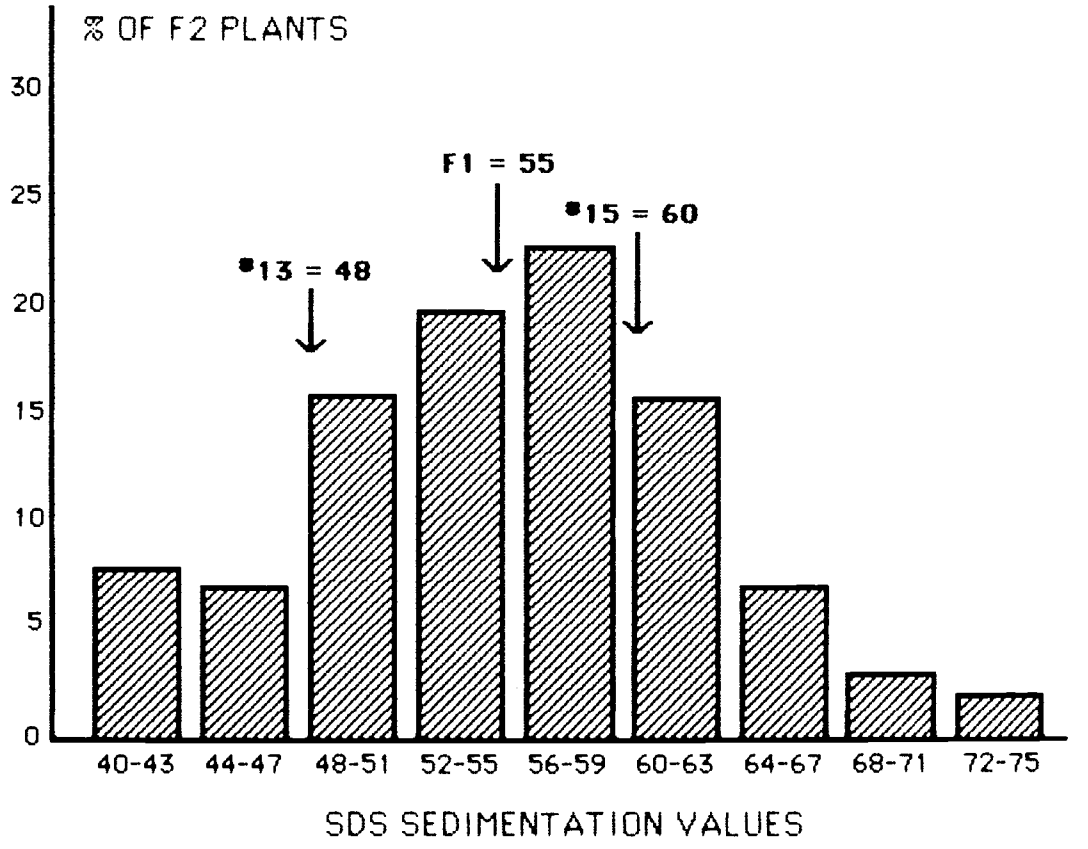

Figure 7. Frequency distribution of loaf volumes as measured by sodium dodecyl sulphate (SDS) sedimentation test in the F2 plants from cross 1513 (greenhouse, 1984).

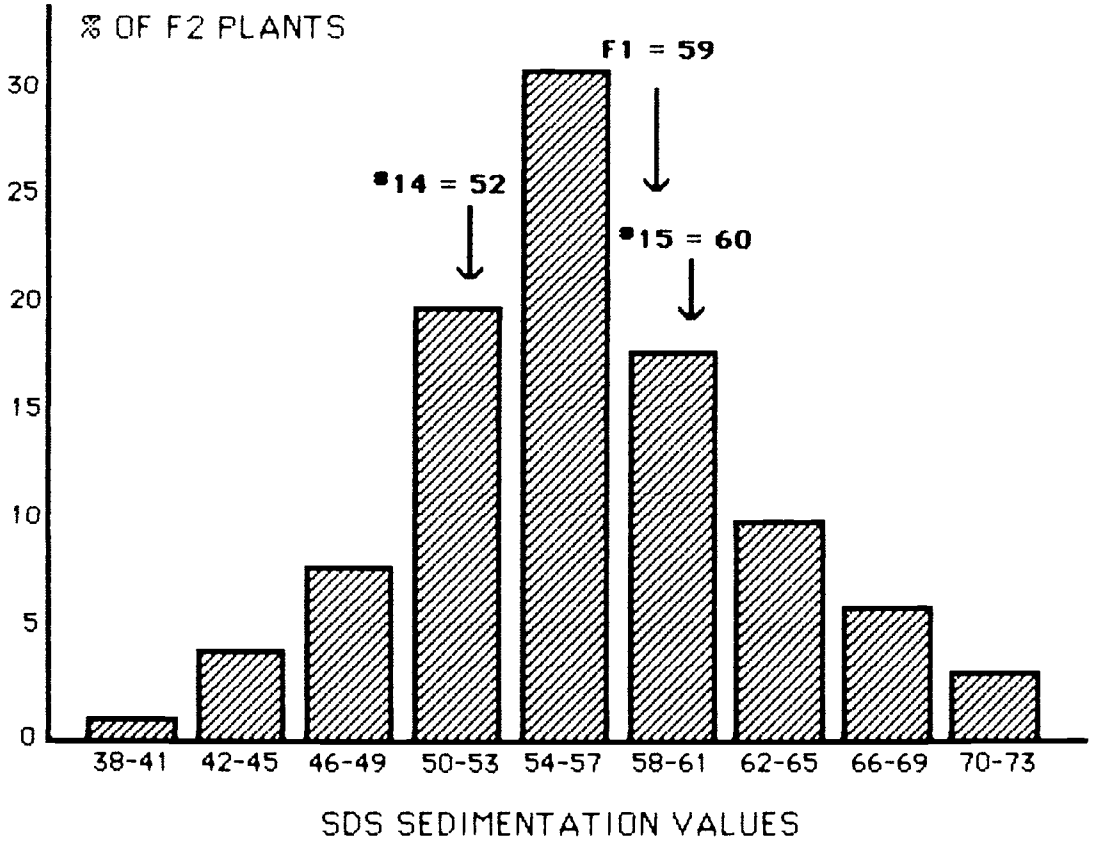

Figure 8. Frequency distribution of loaf volumes as measured by sodium dodecyl sulphate (SDS) sedimentation test in the F2 plants from cross 1514 (greenhouse, 1984).

intermediate between the parents although not necessarily coinciding with the midparental values. The wholemeal flour obtained from F3 grain harvested on individual F2 plants was also utilized to analyze the electrophoretic banding patterns for the HMW glutenin subunits. Figure 9 shows the banding patterns for the F3 grain samples from cross 1514. Parental lines 15 and 14 are included as reference points. F3 grain samples on lanes 2, 4, 5, 7, 8, 9, and 13 are still segregating for the HMW glutenin alleles on chromosome 1A. Grain samples on lanes 1, 3, 11, and 12 have already reached homozygosity for bands 1 or 2*. Similar rationale can be applied with the HMW glutenin proteins coded by the 1B chromosomes.

Bar graphs (Figures 10 and 11) show the relationship between the HMW glutenin protein electrophoretic bands and SDSS values. In Figure 10, the relationship is provided for the F2 individual plants of the cross 1513. F2 plants were classified into three groups according to their SDSS values. Then the frequency of plants carrying each banding combination for each genome was calculated within each SDSS group. In the D genome, bands 5-10 were absent in the low quality group. Frequency of plants carrying the bands 5-10 increased as the SDSS values increased. F2 plants carrying bands 3-12 were more abundant in the low quality group. In the A genome, the frequency of band 1 increased and the frequency of band 2* decreased as the SDSS values improved. The most abundant class in the high quality group, however, was the combination of bands 1 and 2* in the same F2 individual plant sample. In the B genome there was an increase in bands 7-8 and a decrease in bands 17-18 as the SDSS

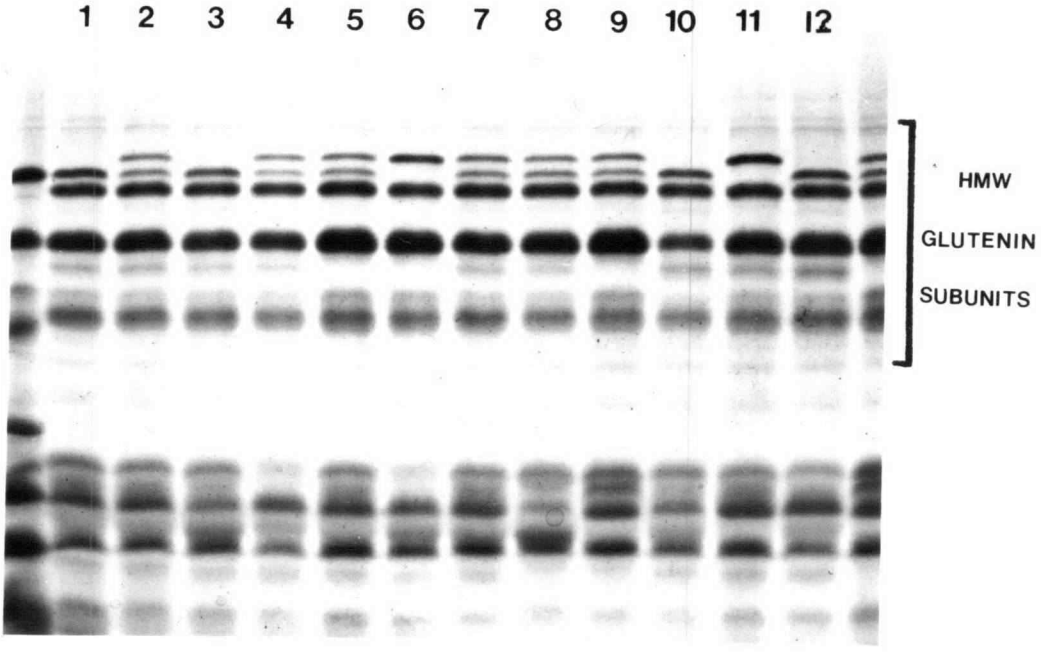

Figure 9. SDS-PAGE banding pattern of the high molecular weight (HMW) glutenin subunits for parents and F3 progeny harvested from individual F2 plants of cross 1514.

	AA	BB
Lane 1: F2 1514	2*	7-8/13-19
Lane 2: F2 1514	1/2*	7-8/13-19
Lane 3: F2 1514	2*	7-8/13-19
Lane 4: F2 1514	1/2*	7-8/13-19
Lane 5: F2 1514	1/2*	7-8
Lane 6: P.15	1	7-8

	AA	BB
Lane 7: F2 1514	1/2*	7-8/13-19
Lane 8: F2 1514	1/2*	7-8/13-19
Lane 9: F2 1514	1/2*	7-8
Lane 10: P.14	2*	13-19
Lane 11: F2 1514	1	7-8/13-19
Lane 12: F2 1514	2*	7-8/13-19

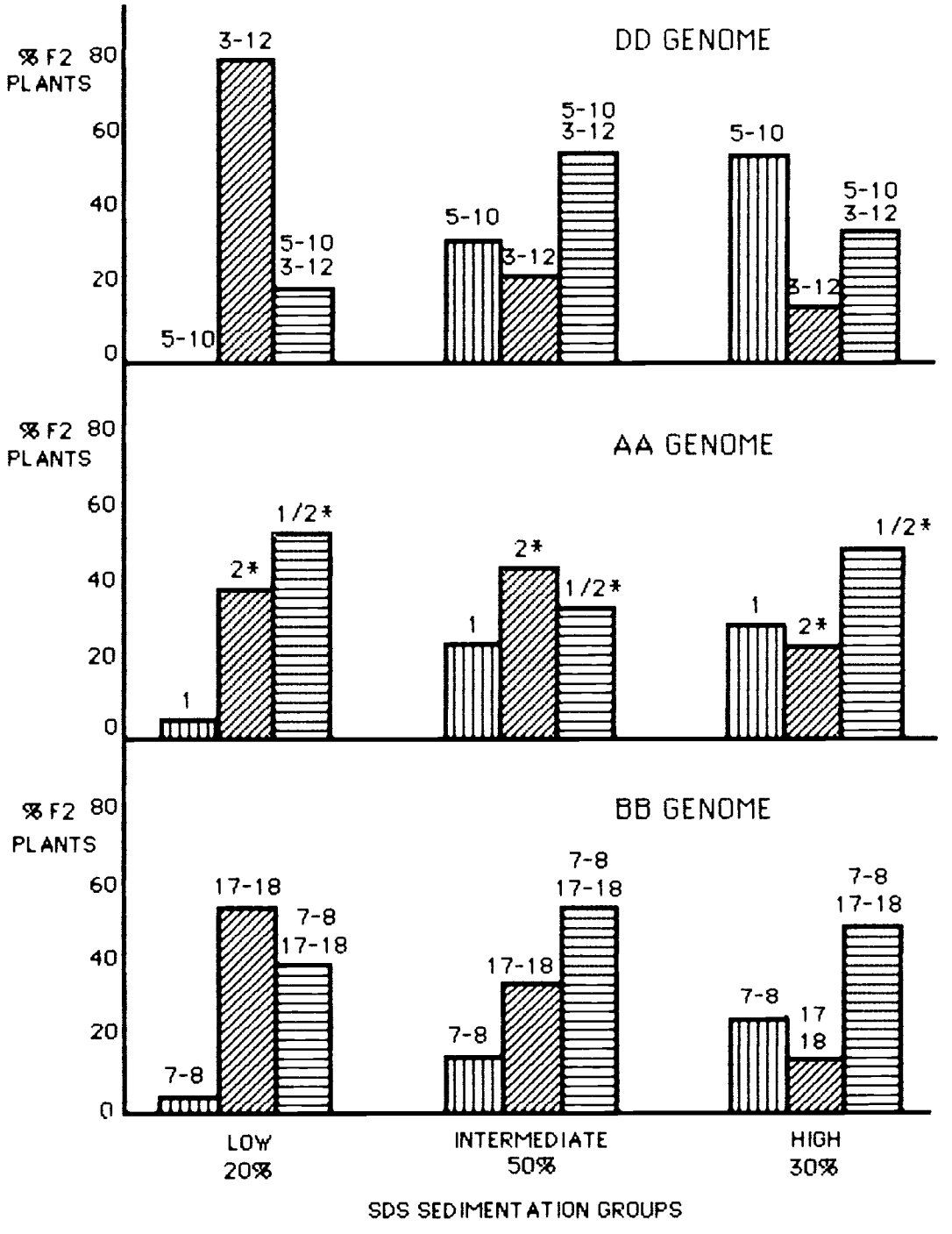

Figure 10. Relationship between the electrophoretic banding pattern of the high molecular weight glutenin subunits and sodium dodecyl sulphate (SDS) sedimentation values among individual F2 plants from cross 1513 (greenhouse, 1984).

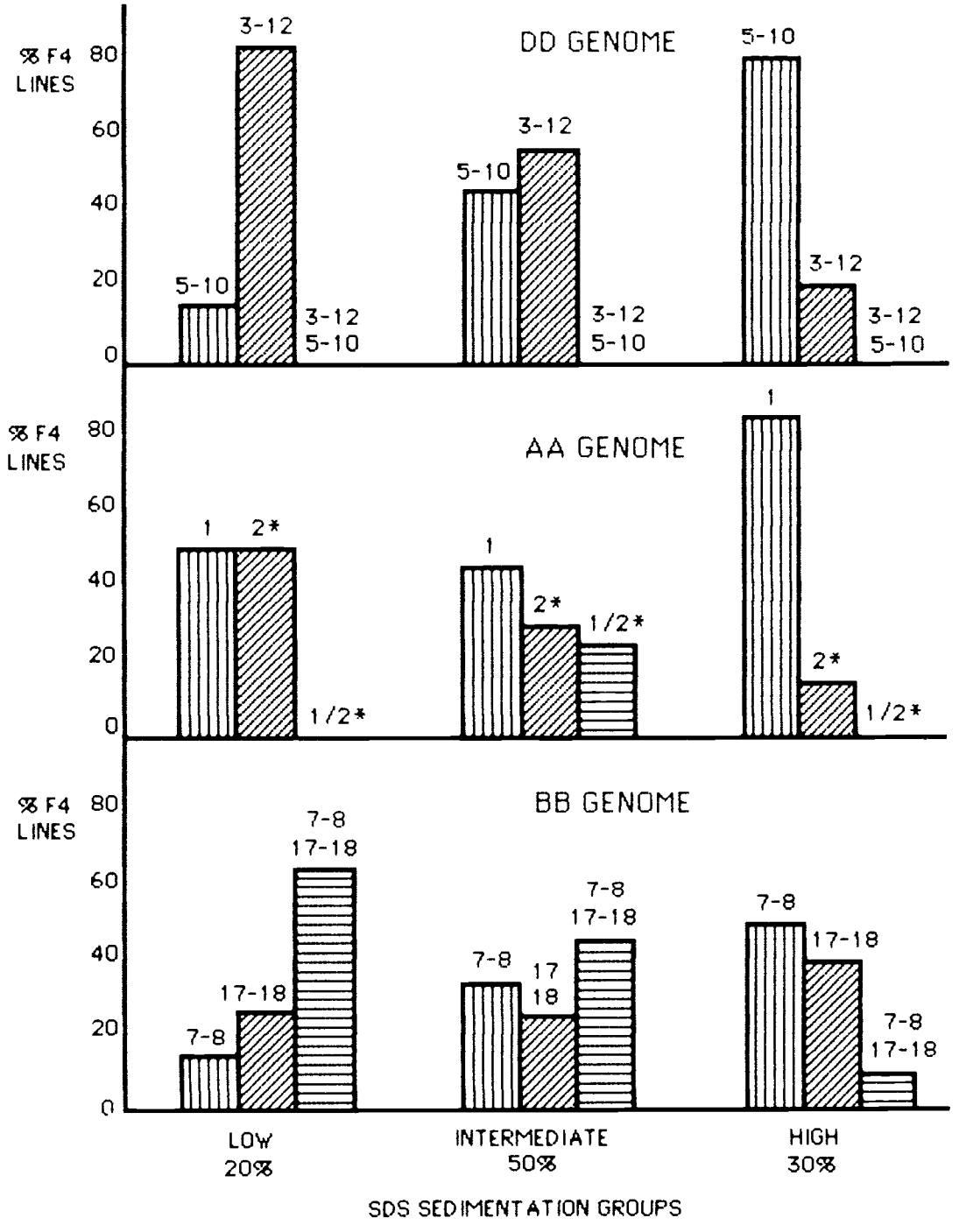

Figure 11. Relationship between the electrophoretic banding pattern of the high molecular weight glutenin subunits and sodium dodecyl sulphate (SDS) sedimentation values among F2-derived F4 rows from cross 1513 (Madras, 1985).

values improved. Again the combination of the four bands (7-8, 17-18) was the most frequent condition among the high quality group.

A similar presentation is provided in Figure 11 with the F2-derived F4 segregating lines from cross 1513 planted at Madras during the spring of 1985. The same trend previously noted for the bands in the three genomes was observed in this second analysis. There was greater homogeneity within the lines for the different glutenin loci. F4 lines in the high quality groups were preferentially carrying bands 5-10 in the D genome, band 1 in the A genome and bands 7-8 in the B genome.

Cross 1514 was studied to evaluate the importance of the HMW glutenin genes in the A and B genome when the D genome bands 5-10 remains constant. Figure 12 deals with the F2 generation and Figure 13 with the F2-derived F4 generation. Again the trend was for an increase in bands 1 and 7-8 in the A and B genome, respectively and a decrease in bands 2* and 13-19 as the quality improved.

Alternative ways of examining the relationship between HMW glutenins and SDSS values are presented in Tables 7, 8, 9, and 10. The F2 individual plants and the F2-derived F4 segregating lines of crosses 1513 and 1514 were classified according to the presence or absence of the different HMW glutenin subunits in each genome. For example, plants or lines from cross 1513 carrying the 5-10 band combination in the D genome are classified in one group, those carrying the 3-12 combination in a second group and those segregating for bands 5-10 and 3-12 in a third group. Ninety five percent confidence intervals for the mean SDSS values in each group were

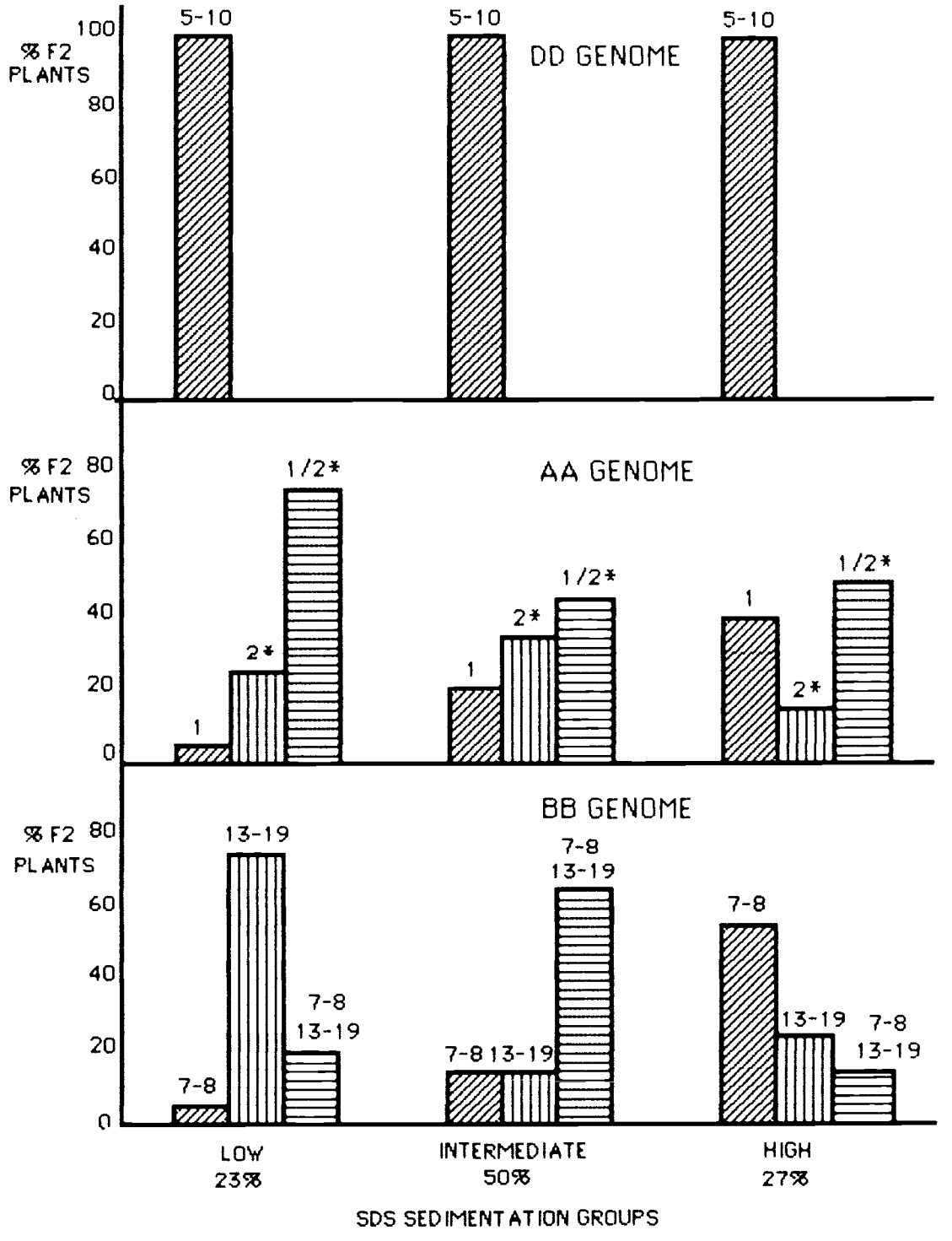

Figure 12. Relationship between the electrophoretic banding pattern of the high molecular weight glutenin subunits and sodium dodecyl sulphate (SDS) sedimentation values among individual F2 plants from cross 1514 (greenhouse, 1984).

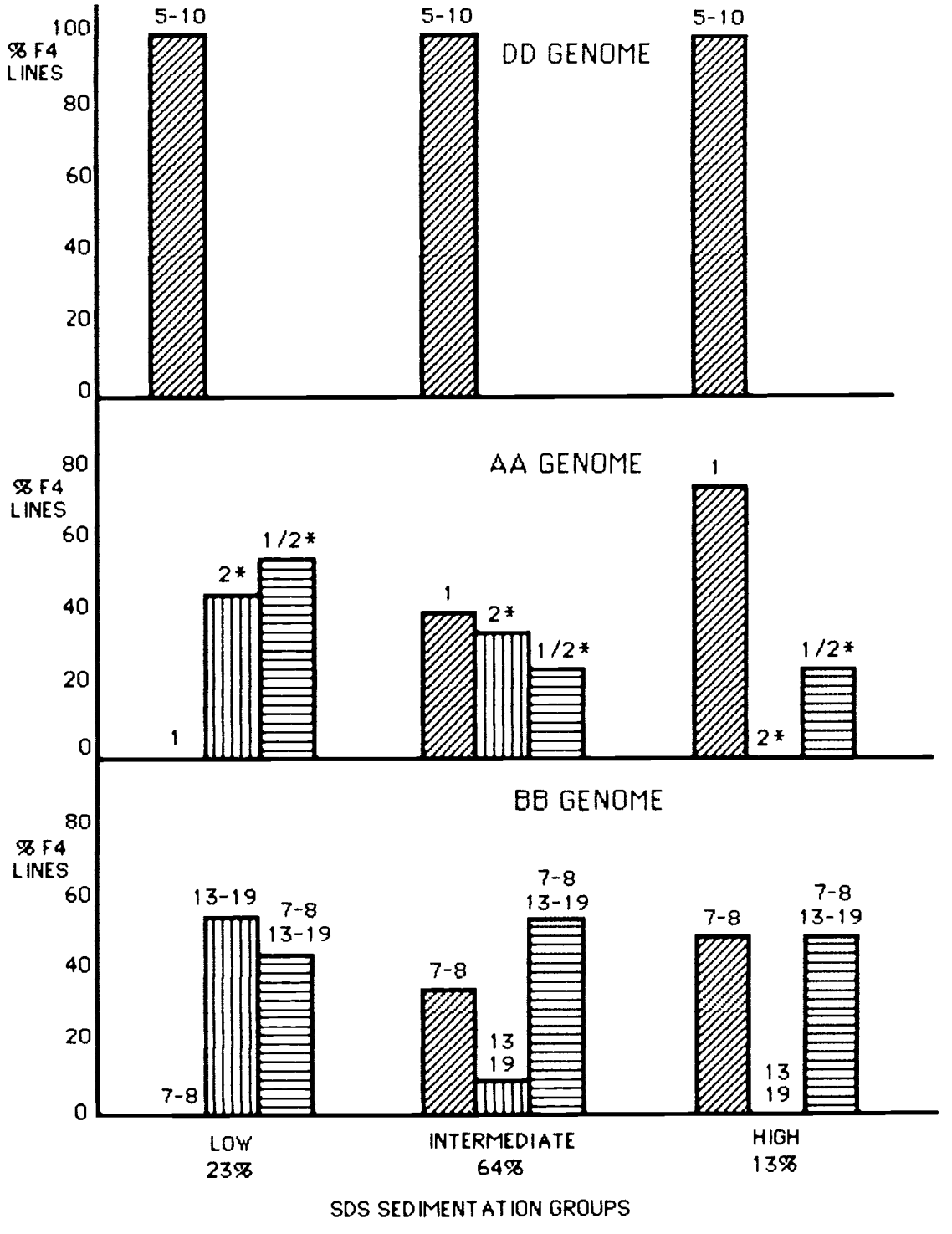

Figure 13. Relationship between the electrophoretic banding pattern of the high molecular weight glutenin subunits and sodium dodecyl sulphate (SDS) sedimentation values among F2-derived F4 lines from cross 1514 (Madras, 1985).

calculated.

The results for specific banding patterns of the F2 individual plants from cross 1513 are presented in Table 7. In the D genome, plants carrying the 5-10 combination were superior in SDSS values than those carrying bands 3-12 or those with the 5-10 + 3-12 combination. In the A genome, band 1 was associated with a higher SDSS value than band 2* alone. There were no differences among the banding groups in the B genome. Thirty six percent of the plants were still segregating for the glutenin genes in the D genome, 44% for the A genome and 52% for the B genome. Table 8 deals with the F2-derived F4 lines from cross 1513. The number of segregating lines was much lower for every genome. Glutenin genes in the D genome have already reached fixation. Once again, bands 5-10 were associated with higher SDSS values than bands 3-12 in the D genome, band 1 was superior to band 2* in the A genome and bands 7-8 to bands 17-18 in the B genome.

The data for cross 1514 are presented in Tables 9 and 10. Lines 15 and 14 are both carrying bands 5-10 in the D genome. In the A genome, there was no difference among the F2 plants or the F4 lines carrying either bands 1 or 2* with regards to SDSS values. The simultaneous presence of bands 1 and 2* in the same flour sample resulted in lower SDSS values than either of the two bands considered separately. In the B genome, the combination 7-8 resulted in a higher SDSS values than when bands 13-19 were present.

Heritability estimates for loaf volume utilizing SDSS values are shown in Table 11. Cross 1513 and 1514 heritability estimates

Table 7. Classification of F2 plants from cross 1513 into quality groups depending on the presence or absence of specific glutenin banding patterns and their relationship with loaf volume as measured by the sodium dodecyl sulphate sedimentation (SDSS) test (greenhouse, 1984).

Banding Pattern Quality Groups	Number of Plants/group	Genotypic Frequencies	0.95 Interval Estimate of the Mean SDSS values
DD Genome: 5-10	51	0.32	57.06 < 59.33 < 61.60
DD Genome: 3-12	51	0.32	46.57 < 50.29 < 54.01
DD Gen:5-10/3-12	58	0.36	48.40 < 53.40 < 58.40
	160	1.00	
AA Genome: 1	34	0.21	53.34 < 57.50 < 61.66
AA Genome: 2*	56	0.35	49.89 < 53.23 < 56.57
AA Genome: 1/2*	70	0.44	52.32 < 55.45 < 58.58
	160	1.00	
BB Genome: 7-8	24	0.15	52.91 < 59.36 < 65.80
BB Genome: 17-18	53	0.33	49.84 < 53.04 < 56.24
BB Gen:7-8/17-18	83	0.52	52.57 < 55.23 < 57.89
	160	1.00	

Table 8. Classification of F2-derived F4 segregating lines from cross 1513 into quality groups depending on the presence or absence of specific glutenin banding patterns and their relationship with loaf volume as measured by the sodium dodecyl sulphate sedimentation (SDSS) test (Madras, 1985).

Banding Pattern Quality Groups	Number of Plants/group	Genotypic Frequencies	0.95 Interval Estimate of the Mean SDSS values
DD Genome: 5-10	19	0.47	55.41 < 58.88 < 62.35
DD Genome: 3-12	21	0.53	48.62 < 52.63 < 56.64
DD Gen:5-10/3-12	--	--	---
	40	1.00	
AA Genome: 1	20	0.50	56.56 < 58.83 < 61.09
AA Genome: 2*	12	0.30	47.11 < 52.18 < 57.25
AA Genome: 1/2*	8	0.20	51.86 < 56.53 < 61.20
	40	1.00	
BB Genome: 7-8	12	0.30	55.92 < 59.91 < 63.90
BB Genome: 17-18	16	0.40	47.44 < 52.86 < 58.28
BB Gen:7-8/17-18	12	0.30	49.87 < 54.73 < 59.59
	40	1.00	

Table 9. Classification of F2 plants from cross 1514 into quality groups depending on the presence or absence of specific glutenin banding patterns and their relationship with loaf volume as measured by the sodium dodecyl sulphate sedimentation (SDSS) test (greenhouse, 1984).

Banding Pattern Quality Groups	Number of Plants/group	Genotypic Frequencies	0.95 Interval Estimate of the Mean SDSS values
DD Genome: 5-10	160	1.00	53.04 < 56.32 < 50.60
AA Genome: 1	40	0.25	55.44 < 58.92 < 62.39
AA Genome: 2*	34	0.21	50.20 < 55.60 < 61.00
AA Genome: 1/2*	86	0.54	52.43 < 55.23 < 58.03
	160	1.00	
BB Genome: 7-8	35	0.22	56.30 < 61.08 < 65.85
BB Genome: 13-19	32	0.20	47.16 < 53.17 < 59.18
BB Gen:7-8/13-19	93	0.58	52.88 < 54.88 < 56.88
	160	1.00	

Table 10. Classification of F2-derived F4 segregating lines from cross 1514 into quality groups depending on the presence or absence of specific glutenin banding patterns and their relationship with loaf volume as measured by the sodium dodecyl sulphate sedimentation (SDSS) test (Madras, 1985).

Banding Pattern Quality Groups	Number of Plants/group	Genotypic Frequencies	0.95 Interval Estimate of the Mean SDSS values
DD Genome: 5-10	40	1.00	52.40 < 54.41 < 56.42
AA Genome: 1	16	0.40	55.09 < 57.50 < 59.91
AA Genome: 2*	12	0.30	50.93 < 54.30 < 57.67
AA Genome: 1/2*	12	0.30	46.29 < 50.80 < 55.31
	40	1.00	
BB Genome: 7-8	11	0.28	54.80 < 57.00 < 59.20
BB Genome: 13-19	9	0.22	44.83 < 50.28 < 55.73
BB Gen:7-8/13-19	20	0.50	51.71 < 54.75 < 57.79
	40	1.00	

Table 11. Heritability estimates for loaf volume as measured by the sodium dodecyl sulphate (SDS) sedimentation test and heterotic response of the F1 combinations from crosses 1513 and 1514 (greenhouse, 1984).

Method of Estimation	Generations Involved in the Analysis	Heritability Estimates Cross 1513	Cross 1514
Warner(1952)	F2 - BC1 - BC2	0.014	-0.680
Burton(1953)	P1 - P2 - F1 - F2	0.860	0.560
Frey-Horner(1957)	F4 - F2	0.723**	0.546**

Method of Estimation	Generations Involved in the Analysis	SDS sedimentation values Cross 1513	Cross 1514
"t" - values	Parent 15	59.56 +3.91	59.56 +3.91
	Parent 13	48.11 +1.69	
	Parent 14		52.11 +4.31
	Midparental-value	53.83 +2.92	55.83 +3.99
	F1 value	55.13 +1.83	59.11 +3.06
	Heterotic response	+1.3	+3.28*

*, ** significance at the 0.05 and 0.01 probability levels, respectively

obtained with Burton's method (broad sense heritability) and with Frey and Horner's method were high. Results obtained with Warner's variance components method were erratic, probably due to large sampling errors. The heterotic response of the F1 SDSS values in relation to the midparental values are presented in Table 11 for both crosses. Sedimentation value for 1514,F1 was higher than the midparental value. Similar results were found in cross 1513, although the differences were not statistically significant.

Grain protein content was determined on the F2-derived F4 segregating lines planted at Madras in the Spring of 1985. The relationships between grain protein content and SDSS values are presented in Figures 14 and 15. For both crosses, significant negative "r" values were observed. With a protein contents varying from 14.9% to 18.5%, SDSS values decreased with an increase in protein content.

Study 3

The inheritance of grain protein content and grain hardness was studied in nine crosses made between selected lines from Argentina and Israel. Information in Table 6 was used to decide which were the appropriate parents to be used in the crosses. The "dicoccoides" derivative lines 11, 13, and 14 from Israel were higher in grain protein content than most other spring selections. Lines 11 and 14 also had good SDSS values. Lines 11 and 13 are Hard Red Spring Wheats and line 14 is a Soft Red selection. Selections 15, 16, and

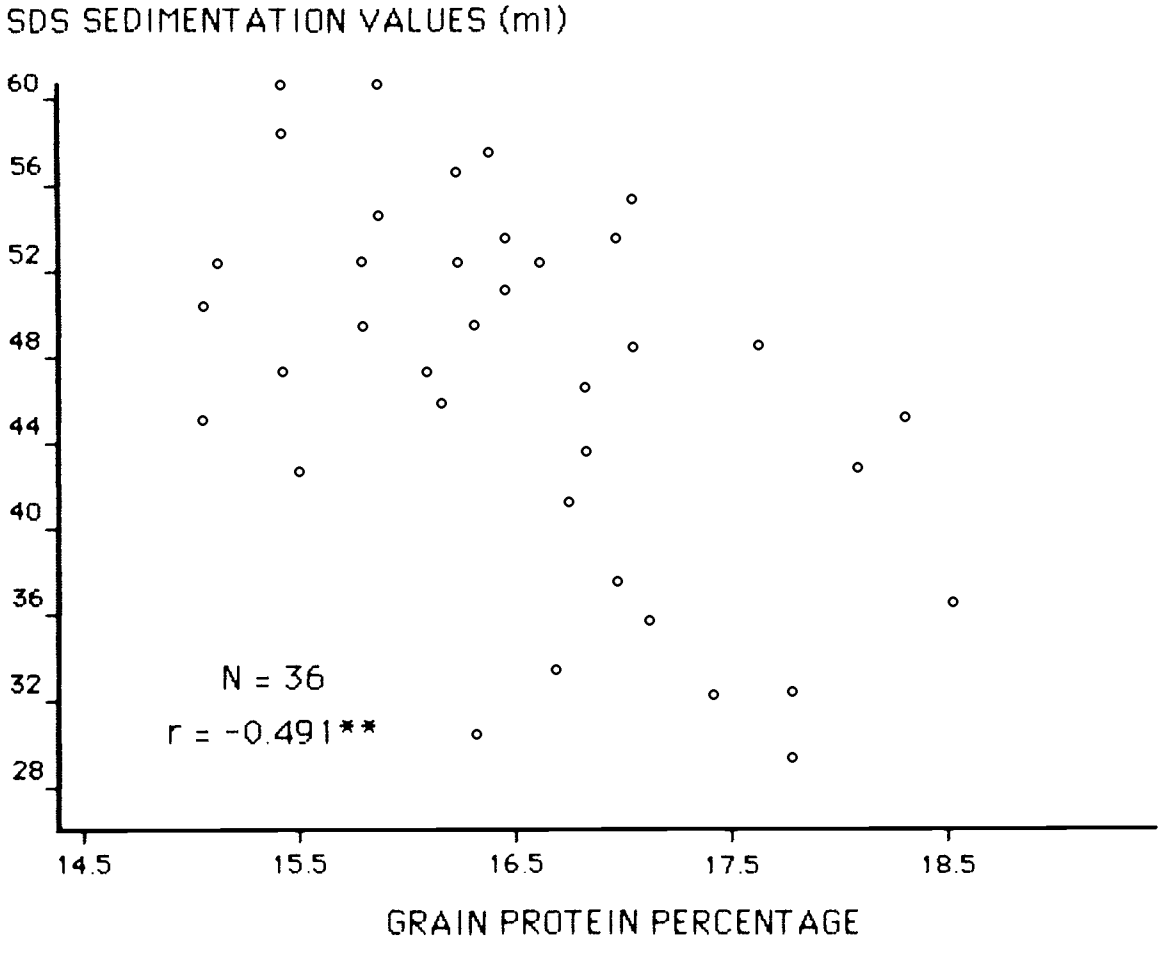

Figure 14. Relationship between grain protein content and sodium dodecyl sulphate (SDS) sedimentation values in the F4 segregating lines from cross 1513 (Madras, 1985).

** significance at the 0.01 probability level.

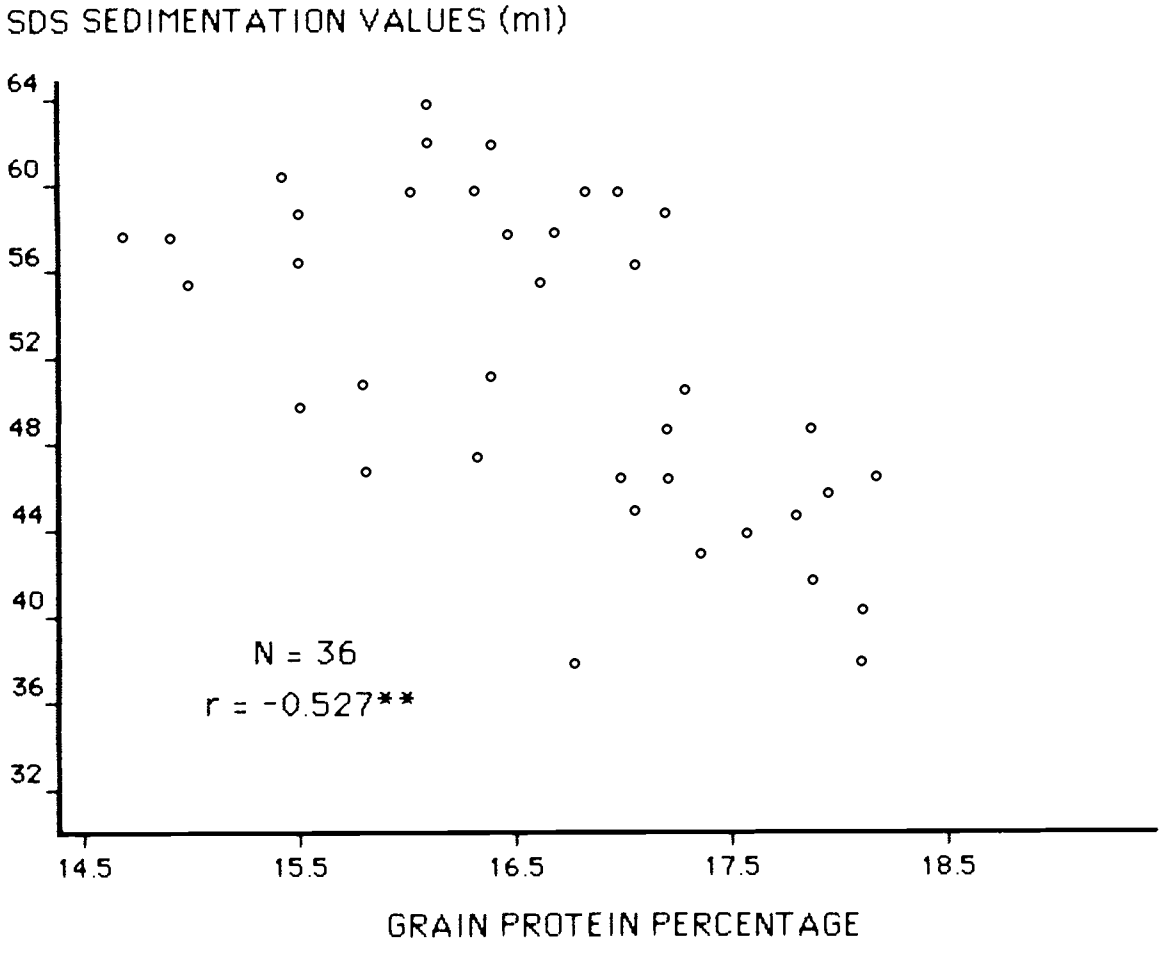

Figure 15. Relationship between grain protein content and sodium dodecyl sulphate (SDS) sedimentation values in the F4 segregating lines from cross 1514 (Madras, 1985).

** significance at the 0.01 probability level.

18 from Argentina were higher in grain yield than the lines from Israel. Lines 15 and 16 are Hard Reds with good loaf volume and line 18 was intermediate both in grain hardness and in breadmaking quality. The main goal was to combine the high yielding attributes of the Argentine selections with the high protein potential of the lines from Israel. A desirable end product would be a high yielding, high protein Hard Red Spring Wheat line with acceptable breadmaking quality.

Heritability estimates for grain protein content in each individual cross are presented in Table 12. No general trend could be defined with any of the three methods used. According to Burton's method, crosses 1513, 1613, 1811, 1813, and 1814 showed relatively high heritability values for protein content. When those crosses were evaluated under Warner's variance components method, only crosses 1513, 1613, and 1811 presented relatively high heritability values. However, none of the three crosses, 1513, 1613, or 1811, presented high heritabilities when estimates were calculated by Frey and Horner's procedure.

Protein content data from the nine crosses were analyzed together in a factorial experiment in which the lines from Argentina represented one factor and the lines from Israel the second factor. The analysis of variance tables for the F1 and F2 generations in the greenhouse are presented in Table 13. Due to the significant interaction between Argentine x Israel, attention was focused on specific crosses rather than on main effects.

Heritability estimates for grain hardness are presented in Table

Table 12. Heritability estimates for grain protein content in crosses 1511, 1513, 1514, 1611, 1613, 1614, 1811, 1813, and 1814 (greenhouse, 1984, and Madras, 1985)

Cross Number	Method of estimation		
	Burton (1953)	Warner (1952)	Frey-Horner (1957)
1511	0.16	-1.02	0.102
1513	0.89	1.23	0.001
1514	0.26	-0.99	-0.012
1611	0.13	0.74	-0.186
1613	0.60	0.81	-0.122
1614	0.41	0.68	0.328*
1811	0.85	0.45	0.100
1813	0.63	-0.14	-0.151
1814	0.74	-0.06	0.249

* significance at the 0.05 probability levels.

Table 13. Analysis of variance tables for grain protein content of the factorial experiments where the lines from Argentina represent one factor and lines from Israel the second factor (F1 and F2 generations, greenhouse, 1984).

Sources of Variation	Degrees of Freedom	F1 Generation "F"Values	Degrees of Freedom	F2 Generation "F"Values
Replications	8	2.15*	39	0.91
Argentina	2	8.78**	2	16.54**
Israel	2	23.66**	2	16.63**
Arg X Israel	4	6.69**	4	3.24*
Residual	64		312	

*, ** significance at the 0.05 and 0.01 probability levels, respectively.

Table 14. Heritability estimates for grain hardness in crosses 1511, 1513, 1514, 1611, 1613, 1614, 1811, 1813, and 1814 (greenhouse, 1984, and Madras, 1985)

Cross Number	Method of estimation		
	Burton (1953)	Warner (1952)	Frey-Horner (1957)
1511	0.64	0.48	0.649**
1513	0.66	0.50	0.542**
1514	0.95	0.82	0.835**
1611	0.71	0.70	0.480**
1613	0.74	0.70	0.585**
1614	0.94	0.81	0.833**
1811	0.78	0.11	0.434**
1813	0.79	0.66	0.344*
1814	0.85	0.72	0.579**

*, ** significance at the 0.05 and 0.01 probability levels, respectively.

14. Higher estimates for all the crosses were obtained with Burton's method (broad sense heritability estimate). Narrow sense heritability estimates provided by Warner's procedure were intermediate to high, with cross 1811 being the one exception. Regression values of F2-derived F4 lines on F2 individual plants were significant with the exception of cross 1813.

The frequency distribution of grain hardness in crosses 1614 (hard x soft), 1514 (hard x soft), and 1814 (intermediate x soft) are presented in Figures 16 through 18. F2 progeny from crosses 1614 and 1514 suggested a bimodal distribution with peaks at 43-52, 83-92, and 39-51, 104-116 respectively.

The heterotic responses for grain protein content and SDSS values were examined for each individual cross grown in the greenhouse and at the Linn farm during 1984. Results for grain protein content are shown in Table 15. There was a tendency for the F1 protein values to be lower than the midparental values. However, there were some exceptions. Differences between the F1s and the midparental values were positive and significant for crosses 1511 and 1811 when grown in the greenhouse. Results for SDSS values are presented in Table 16. Most of the crosses showed some degree of heterosis in favor of the high quality parent. Crosses 1611 and 1813, under field conditions, and 1813 and 1814, in the greenhouse, resulted in the F1s having higher SDSS values than the highest quality parent.

Grain yield per plot was measured on the F2-derived F4 segregating lines planted in Madras during the spring of 1984. Grain

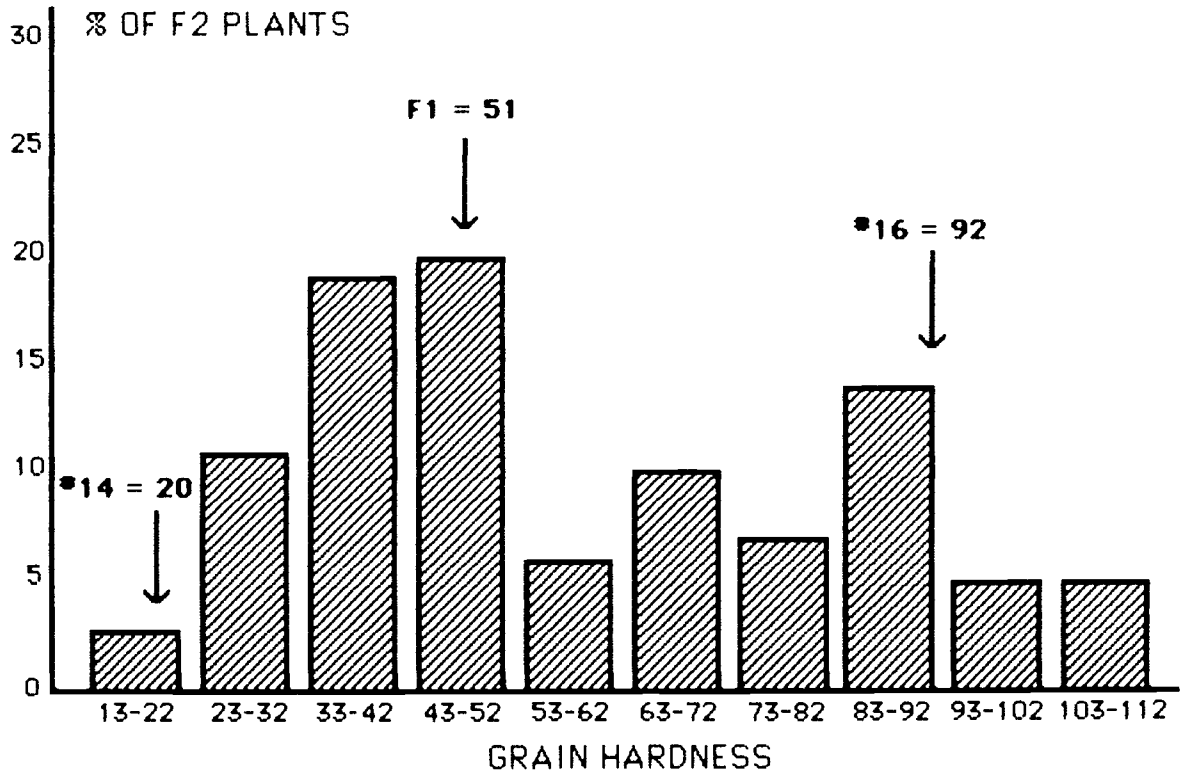

Figure 16. Frequency distribution of grain hardness values mesured on F3 grain samples harvested on individual F2 plants from cross 1614 (greenhouse, 1984).

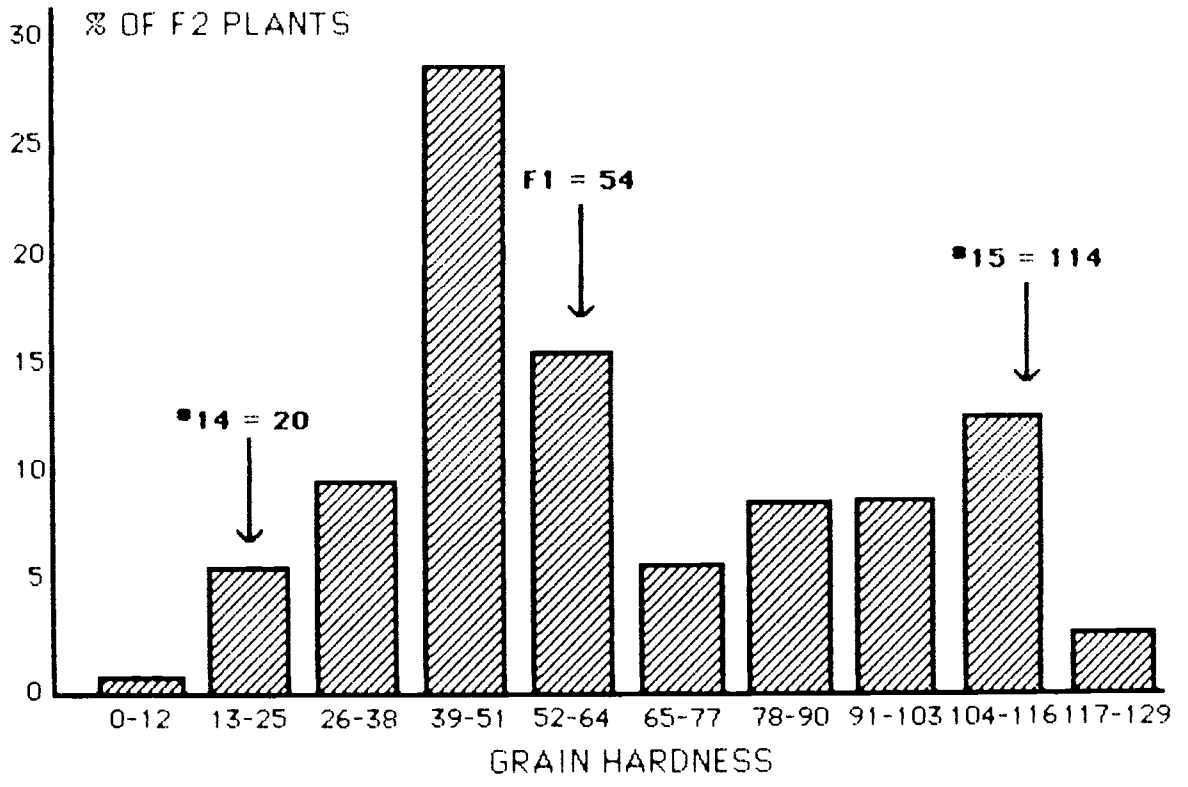

Figure 17. Frequency distribution of grain hardness values measured on F3 grain samples harvested on individual F2 plants from cross 1514 (greenhouse, 1984).

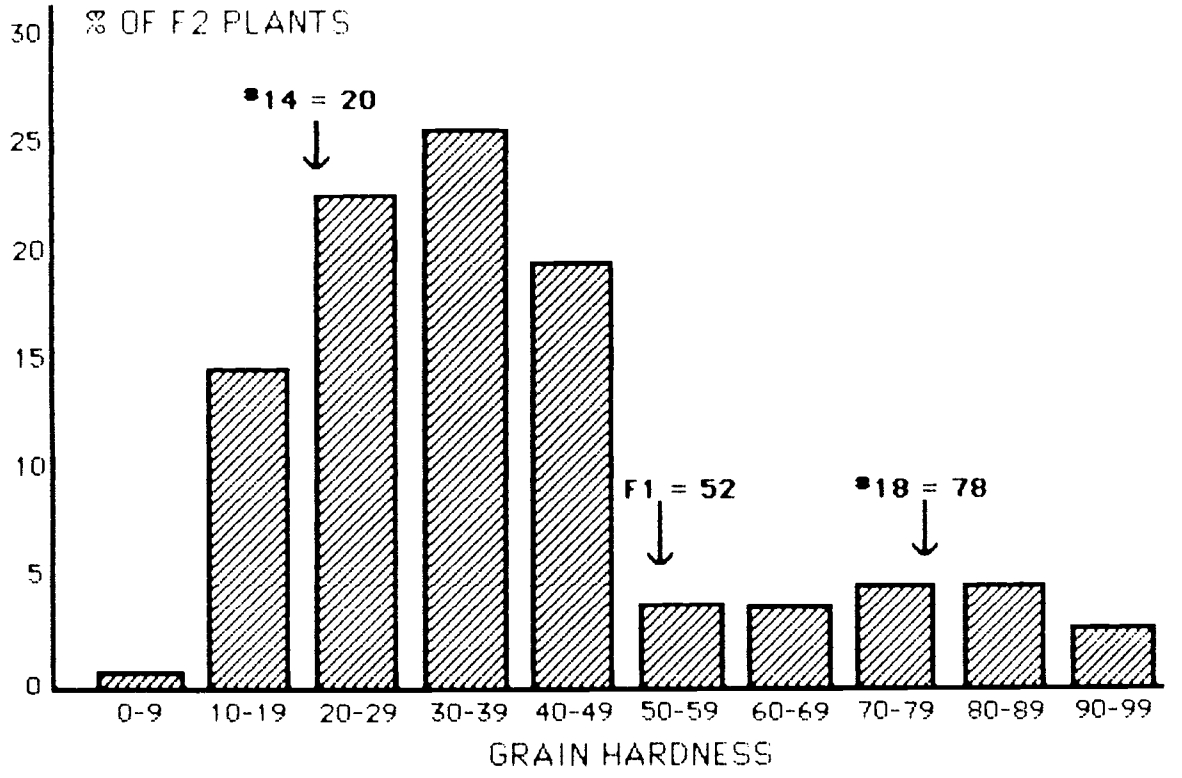

Figure 18. Frequency distribution of grain hardness values measured on F3 grain samples harvested on individual F2 plants from cross 1814 (greenhouse, 1984).

Table 15. Heterotic response for grain protein content of the F1 generations from crosses 1511, 1513, 1514, 1611, 1613, 1614, 1811, 1813, and 1814 (greenhouse, 1984, Linn's farm, 1984)

Cross Number	Argentine Parent	Israel Parent	Midparental Values	F1 Values	Differences (Heterosis)
1511-G	17.83+0.92	18.87+0.82	18.35+0.84	19.41+1.34	+1.06*
1511-L	15.91+0.80	18.27+0.74	17.09+0.75	16.76+1.40	-0.33
1513-G	17.83+0.92	20.36+0.41	19.09+0.69	19.34+0.47	+0.25
1513-L	15.91+0.80	17.04+0.87	16.47+0.81	16.00+1.15	-0.47
1514-G	17.83+0.92	18.27+0.76	18.05+0.82	16.78+0.69	-1.27*
1514-L	15.91+0.80	15.63+0.22	15.77+0.57	15.69+0.77	-0.08
1611-G	18.19+0.95	18.87+0.82	18.53+0.86	17.45+0.90	-1.08**
1611-L	14.81+0.06	18.27+0.74	16.54+0.51	14.98+0.88	-1.56**
1613-G	18.19+0.95	20.36+0.41	19.27+0.71	18.94+1.02	-0.33
1613-L	14.81+0.06	17.04+0.87	15.92+0.60	15.57+0.59	-0.35
1614-G	18.19+0.95	18.27+0.76	18.23+0.83	17.02+1.36	-1.21**
1614-L	14.81+0.06	15.63+0.22	15.22+0.16	15.47+0.61	+0.25
1811-G	18.50+0.73	18.87+0.82	18.68+0.75	19.32+0.57	+0.64*
1811-L	16.03+0.80	18.27+0.74	17.15+0.75	15.90+1.12	-1.25**
1813-G	18.50+0.73	20.36+0.41	19.43+0.57	18.77+1.23	-0.66
1813-L	16.03+0.80	17.04+0.87	16.53+0.81	15.83+0.39	-0.70*
1814-G	18.50+0.73	18.27+0.76	18.38+0.72	18.41+0.74	+0.03
1814-L	16.03+0.80	15.63+0.22	15.83+0.57	15.70+0.48	-0.13

*, ** significance at the 0.05 and 0.01 probability levels, respectively.

G = greenhouse, 1984
L = Linn's farm, 1984

Table 16. Heterotic response for sodium dodecyl sulphate sedimentation value of the F1 generations from crosses 1511, 1513, 1514, 1611, 1613, 1614, 1811, 1813, and 1814 (greenhouse, 1984, Linn's farm, 1984)

Cross Number	Argentine Parent	Israel Parent	Midparental Values	F1 Values	Differences (Heterosis)
1511-G	59.56+3.91	67.89+2.09	63.72+3.04	60.89+2.57	-2.83*
1511-L	65.56+1.33	68.89+2.37	67.22+1.80	67.44+6.31	+0.22
1513-G	59.56+3.91	48.11+1.69	53.83+2.92	55.13+1.83	+1.30
1513-L	65.56+1.33	54.11+2.93	59.83+2.21	64.33+4.15	+4.50**
1514-G	59.56+3.91	52.11+4.31	55.83+3.99	59.11+3.06	+3.28*
1514-L	65.56+1.33	61.00+2.45	63.28+1.91	64.00+1.94	+0.72
1611-G	62.78+3.93	67.89+2.09	65.33+3.05	66.78+1.72	+1.45
1611-L	74.89+1.90	68.89+2.37	71.89+2.08	75.89+3.92	+4.00**
1613-G	62.78+3.93	48.11+1.69	55.44+2.93	56.56+2.79	+1.12
1613-L	74.89+1.90	54.11+2.93	64.50+2.39	68.89+2.76	+4.39**
1614-G	62.78+3.93	52.11+4.31	57.44+4.00	61.22+1.20	+3.78*
1614-L	74.89+1.90	61.00+2.45	67.94+2.13	68.87+3.81	+0.93
1811-G	45.78+2.95	67.89+2.09	56.83+2.48	57.44+2.46	+0.61
1811-L	60.00+4.24	68.89+2.37	64.44+3.33	66.78+2.44	+2.34
1813-G	45.78+2.95	48.11+1.69	46.94+2.33	51.11+1.36	+4.17**
1813-L	60.00+4.24	54.11+2.93	57.05+3.53	63.33+3.50	+6.28**
1814-G	45.78+2.95	52.11+4.31	48.94+3.58	51.56+2.13	+2.62
1814-L	60.00+4.24	61.00+2.45	60.50+3.35	64.22+2.44	+3.72**

*, ** significance at the 0.05 and 0.01 probability levels, respectively.

G = greenhouse, 1984
L = Linn's farm, 1984

yield, grain protein, and grain hardness of the F4 lines were utilized to calculate phenotypic correlations. Results for each individual cross are presented in Table 17. The relationship between protein content and grain yield per plot was negative in every cross. For grain hardness and protein content, the relationship was either non-existent or it was positive and significant in crosses 1811 and 1813. The relationship between grain yield per plot and grain hardness was erratic with both negative and positive non significant "r" values being observed.

As noted previously, the desirable end product is a high yielding, high protein Hard Red Spring Wheat line with acceptable breadmaking quality. Yield, protein content, and quality data collected among the F4 segregating lines can provide a preliminary insight on the probability of the success in obtaining the appropriate genetic combinations from these populations. Table 18 summarizes the information for the nine crosses. Grain yield was regarded as the most important trait. Only those lines yielding as much or more than the highest yielding checks were classified as satisfactory. Among those selections, some lines were identified as being superior in protein content to the Argentine parental line used in the cross. Finally, the high yielding, high protein lines were selected for loaf volume by looking at the HMW glutenin subunits. For example, in cross 1511 there were 11 segregating F4 lines with yields not significantly different from the highest check. Among those high yielding lines, ten have a higher protein content than line 15. All ten lines have the right HMW glutenin banding pattern

Table 17. Phenotypic correlations among grain yield, grain protein content, and grain hardness in the Argentina X Israel F4 segregating lines planted in Madras in the spring of 1985.

Cross Number	Grain Yield Protein Content	Grain Hardness Protein Content	Grain Yield Grain Hardness
1511	-0.234	-0.073	0.106
1513	-0.084	0.307	-0.264
1514	-0.107	-0.084	-0.172
1611	-0.001	-0.041	0.177
1613	-0.404*	0.383*	-0.217
1614	-0.221	0.194	0.042
1811	-0.605**	0.636**	-0.253
1813	-0.489**	0.537**	-0.244
1814	-0.395*	0.372*	0.188

*, ** significance at the 0.05 and 0.01 probability levels, respectively (N = 36).

Table 18. Number of F4 lines which exceed the local checks and Argentine parents for grain yield, grain protein content and loaf volume as predicted by high molecular weight (HMW) glutenin subunits (Madras, 1985).

Cross Number	Number of F4 Lines Selected for		
	Grain Yield †	Grain Protein Content §	HMW Glutenins ¶
1511	11	10	10
1513	29	13	5
1514	27	16	12
1611	11	6	6
1613	14	3	1
1614	11	5	2
1811	24	12	7
1813	22	12	3
1814	16	1	-

† Number of lines with yields as high or higher than the highest yielding check (local check or Argentine selection) at the 0.05 probability level.

§ Number of high yielding lines with a higher protein content than the Argentine parent of the cross at the 0.05 probability level.

¶ Number of high yielding, high protein lines with the appropriate HMW glutenin banding pattern.

(1/7-8/5-10). The results for the other crosses can be interpreted in a similar way. A total of 46 F4 lines out of 324 have been identified as potential high yielding, high protein, and good quality selections.

Study 4

It was the objective in study 4 to identify possible highly heritable traits that are phenotypically correlated with grain yield, grain protein content, and SDSS values. Broad sense heritability estimates and variance components for the twelve agronomic traits measured are presented in Table 19 for the Hard Red Spring Wheat lines and in Table 20 for the Hard Red Winter Wheat selections. Among the spring wheat lines, protein yield, biological yield, and grain yield showed the lowest heritability values. Estimates for harvest index and grain protein content were intermediate while days to heading, days to maturity, grain filling period, plant height, 1000 kernel weight, grain hardness, and SDSS values had high heritability estimates.

Heritability values were relatively higher among the winter wheat selections. Grain yield, biological yield, and grain protein content were the traits with the lowest heritability values. Heritability estimates for duration of grain filling period, harvest index, and protein yield were intermediate while estimates were high for days to heading, days to maturity, plant height, 1000 kernel weight, grain hardness, and SDSS value.

Table 19. Components of variance and broad sense heritability estimates for twelve selected traits of breeding importance in Hard Red Spring Wheat lines (Madras, 1984-1985 and Linn's farm, 1985)

Traits Measured	Variance Components			Broad Sense Heritability
	Genetic	Gen x Env	Error	
Days to Heading	30.18**	1.41**	0.89	0.99
Days to Maturity	10.83**	0.90**	2.46	0.97
Grain Filling Period	9.07**	2.96**	2.96	0.92
Plant Height	180.72**	13.17**	9.51	0.98
Biological Yield	142307.50	948118.50**	900834.79	0.38
Grain Yield	28739.75*	65306.35**	95691.01	0.60
Harvest Index	5.99**	5.39**	3.25	0.84
1000 Kernel Weight	18.07**	5.41**	4.12	0.93
Grain Hardness	1352.11**	26.86**	39.95	0.99
Grain Protein	148.07**	84.87**	86.86	0.87
Protein Yield	53.92	1308.82**	2357.95	0.12
SDS Sedimentation	131.99**	13.06**	3.62	0.98

*, ** two means squares used to estimate interaction component differed significantly at the 0.05 and 0.01 probability levels, respectively.

Table 20. Components of variance and broad sense heritability estimates for twelve selected traits of breeding importance in Hard Red Winter Wheat lines (Hyslop, 1984-85).

Traits Measured	Variance Components			Broad Sense Heritability
	Genetic	Gen x Env	Error	
Days to Heading	6.30**	1.16**	0579	0.97
Days to Maturity	6.09**	2.50**	0.26	0.95
Grain Filling Period	3.29**	3.66**	0.66	0.91
Plant Height	169.25**	1.06	6.22	0.99
Biological Yield	241489.36**	123246.38**	237891.85	0.89
Grain Yield	28644.83**	24835.09**	23625.10	0.86
Harvest Index	17.96**	6.38**	4.04	0.94
1000 Kernel Weight	19.69*	4.03**	3.43	0.96
Grain Hardness	1067.00**	26.33**	47.64	0.99
Grain Protein	84.96**	96.66**	27.12	0.86
Protein Yield	696.93**	275.34**	466.10	0.92
SDS Sedimentation	302.01**	13.47**	4.58	0.99

*, ** two means squares used to estimate interaction component differed significantly at the 0.05 and 0.01 probability levels, respectively.

Phenotypic correlations among the twelve traits are presented in Table 21 for the spring materials and in Table 22 for the winter selections. Among the spring wheat selections, grain yield was positively correlated with days to maturity, duration of grain filling period, biological yield, harvest index, 1000 kernel weight, protein yield, and SDSS values. There was a negative correlation between grain yield and grain protein content. Grain protein content was negatively correlated with days to maturity, duration of grain filling period, biological yield, grain yield, harvest index, 1000 kernel weight, and protein yield. The SDSS value was positively associated with grain yield, harvest index, and protein yield and negatively associated with days to heading time and plant height.

The association found among the winter materials is presented in Table 22. Grain yield was positively correlated with biological yield, harvest index and protein yield. There was a negative association between grain yield and plant height. Grain protein was positively correlated with biological yield, grain hardness, protein yield and SDSS values and negatively associated with harvest index and 1000 kernel weight. The SDSS value was positively associated with plant height, biological yield, grain hardness, percent protein content, and protein yield and negatively correlated with harvest index and 1000 kernel weight.

All the previous correlations were calculated among genetically fixed materials planted in solid stands. To find out whether those phenotypic correlations still held among individual plants, the spring lines were planted in the greenhouse and at the Linn farm and

Table 21. Phenotypic correlations among twelve selected traits of breeding importance in Hard Red Spring Wheat lines (Madras, 1984-85 and Linn's farm, 1985).

	Grain Yield	Grain Protein	SDS Sedimentation
Days to Heading	0.064	0.131	-0.298
Days to Maturity	0.635**	-0.556**	-0.054
Grain Filling Period	0.404**	-0.492**	0.160
Plant Height	-0.070	0.262	-0.349*
Biological Yield	0.986**	-0.532**	0.288
Grain Yield	-----	-0.554**	0.360**
Harvest Index	0.475**	-0.371**	0.498**
1000 Kernel Weight	0.358**	-0.291*	-0.086
Grain Hardness	-0.121	-0.013	0.082
Grain Protein	-0.554**	-----	-0.255
Protein Yield	0.982**	-0.408**	0.352*
SDS Sedimentation	0.360**	-0.255	-----

*, ** significance at the 0.05 and 0.01 probability levels, respectively (N = 54)

Table 22. Phenotypic correlations among twelve selected traits of breeding importance in Hard Red Winter Wheat lines (Hyslop, 1984-85).

	Grain Yield	Grain Protein	SDS Sedimentation
Days to Heading	0.182	0.052	-0.175
Days to Maturity	0.233	0.071	-0.126
Grain Filling Period	0.163	0.056	0.066
Plant Height	-0.313*	0.053	0.397**
Biological Yield	0.696**	0.274*	0.304*
Grain Yield	-----	-0.067	0.080
Harvest Index	0.502**	-0.416**	-0.321*
1000 Kernel Weight	0.194	-0.516**	-0.412**
Grain Hardness	0.066	0.319*	0.666**
Grain Protein	-0.067	-----	0.579**
Protein Yield	0.888**	0.396**	0.340**
SDS Sedimentation	0.080	0.579**	-----

*, ** significance at the 0.05 and 0.01 probability levels, respectively (N = 54).

the corresponding "r" values are shown in Tables 23 and 24. In the greenhouse, grain yield was positively associated with days to maturity, harvest index, biological yield, and protein yield. There was a strong negative correlation between grain yield and protein content. In the field, grain yield was positively correlated with biological yield, harvest index, and SDSS value, and negatively correlated with percent protein content and protein yield. Grain protein content was negatively correlated with biological yield, grain yield, and protein yield in the greenhouse, and with biological yield, grain yield, and harvest index in the field. The SDSS value was positively associated with grain filling period and protein yield in the greenhouse, and with grain yield and harvest index in the field.

Winter wheat selection were only planted in the greenhouse. In Table 25, the "r" values calculated among individual plants are shown in Table 25. Grain yield was positively correlated with plant height, biological yield, harvest index, and protein yield and negatively correlated with 1000 kernel weight. Grain protein content was positively associated with days to maturity, biological yield, and protein yield. The SDSS value was positively associated with grain hardness and negatively associated with days to maturity.

Study 5

Experiments were conducted to evaluate the feasibility of improving the protein content of Hard Red Winter Wheat lines by

Table 23. Phenotypic correlations among twelve selected traits of breeding importance, measured on individual plants, in Hard Red Spring Wheat lines (greenhouse, 1984).

	Grain Yield	Grain Protein	SDS Sedimentation
Days to Heading	0.408	-0.378	-0.439
Days to Maturity	0.475*	-0.427	-0.328
Grain Filling Period	0.304	-0.212	0.466*
Plant Height	-0.175	0.140	0.258
Biological Yield	0.841**	-0.748**	0.328
Grain Yield	-----	-0.854**	0.437
Harvest Index	0.498*	-0.346	0.052
1000 Kernel Weight	-0.194	0.234	0.379
Grain Hardness	0.081	0.029	0.312
Grain Protein	-0.854**	-----	-0.394
Protein Yield	0.788**	-0.541*	0.498*
SDS Sedimentation	0.437	-0.394	-----

*, ** significance at the 0.05 and 0.01 probability levels, respectively (N = 20).

Table 24. Phenotypic correlations among twelve selected traits of breeding importance, measured on individual plants, in Hard Red Spring Wheat lines (Lindt's farm, 1984).

	Grain Yield	Grain Protein	SDS Sedimentation
Days to Heading	-----	-----	-----
Days to Maturity	-----	-----	-----
Grain Filling Period	-----	-----	-----
Plant Height	-0.445	0.209	-0.140
Biological Yield	0.797**	-0.638**	0.244
Grain Yield	-----	-0.735**	0.620**
Harvest Index	0.802**	-0.547*	0.739**
1000 Kernel Weight	0.069	0.115	-0.132
Grain Hardness	0.459	-0.059	0.401
Grain Protein	-0.735**	-----	-0.294
Protein Yield	-0.648**	0.085	0.452
SDS Sedimentation	0.620**	-0.294	-----

*, ** significance at the 0.05 and 0.01 probability levels, respectively (N = 20).

Table 25. Phenotypic correlations among twelve selected traits of breeding importance, measured on individual plants, in Hard Red Winter Wheat lines (greenhouse, 1984).

	Grain Yield	Grain Protein	SDS Sedimentation
Days to Heading	0.134	0.152	-0.126
Days to Maturity	0.042	0.700**	-0.481**
Grain Filling Period	0.163	0.056	-0.043
Plant Height	0.735**	-0.334	0.314
Biological Yield	0.842**	0.429**	-0.060
Grain Yield	-----	0.106	0.007
Harvest Index	0.696**	-0.359	0.045
1000 Kernel Weight	-0.570**	-0343	-0.190
Grain Hardness	0.273	-0.111	0.628**
Grain Protein	0.106	-----	-0.089
Protein Yield	0.879**	0.552**	-0.041
SDS Sedimentation	0.007	-0.089	-----

** significance at the 0.01 probability level (N = 28).

fertilizer management practices in the Willamette Valley, Oregon. Results of this agronomic studies are presented in Table 26 and 27 for the 1983-84 and the 1984-85 growing season, respectively. A combined analysis for the two crop years was not generated because different fertilizer treatments were employed in the two years (Tables 1 and 2, in Materials and Methods).

Treatment means, averaged across experimental lines are presented in Table 26. There was a significant increase in biological yield, grain yield, grain protein content, protein yield, and SDSS value, and a decrease in harvest index and 1000 kernel weight comparing treatment 1 (January and February nitrogen applications) with treatment 2 (January, February, and March nitrogen applications). Number of days to maturity and the duration of the grain filling period increased for treatments 3 (nitrogen fertilization at heading time) and 4 (nitrogen applications at the tillering and heading stages). The highest values for grain yield and biological yield were observed under treatments 2 and 4. Grain protein content, SDSS value, and 1000 kernel weight were traits not affected by the timing of fertilizer application. Days to heading and grain hardness were independent of the amount or timing of nitrogen application.

The fertilizer strategy for the 1984-85 growing season was planned based on the 1983-84 results. The total amount of nitrogen applied was constant for all treatments; however the timing of application was varied. The winter and early spring of 1985 were extremely dry affecting the response among fertilizer treatments.

Table 26. Results of the fertility trials conducted at the Hyslop Agronomy Farm during the 1983-84 growing season. Fertilizer treatments averaged across experimental lines are presented for the twelve traits measured.

Traits Measured	Fertilizer Treatments				LSD
	1	2	3	4	(0.01)
Days to Heading (days)	151 a	152 a	151 a	152 a	1.4
Days to Maturity (days)	204 a	204 a	208 b	208 b	0.3
Grain Filling (days)	53 a	53 a	57 b	56 b	1.5
Biological Yield (gr/plot)	3293 a	3979 b	3378 a	3940 b	429.5
Grain Yield (gr/plot)	1168 a	1323 b	1241 a	1403 b	152.4
Harvest Index	36 a	33 b	37 a	36 a	1.5
1000 Kernel Weight (gr)	43 a	40 b	42 ab	40 b	2.8
Grain Hardness	91 a	84 a	84 a	87 a	7.1
Grain Protein (%)	11.2 a	12.7 b	13.5 b	13.5 b	1.1
Protein Yield (gr/plot)	131 a	166 b	168 b	190 c	21.7
SDS Sedimentation (ml)	55 a	60 b	61 b	61 b	1.9

Treatment means with the same letter are not significantly different at the 0.01 probability levels.

LSD (0.01) = Least significant difference at the 0.01 probability level.

Table 27. Results of the fertility trials conducted at the Hyslop Agronomy Farm during the 1984-85 growing season. Fertilizer treatments averaged across experimental lines are presented for the twelve traits measured.

Traits Measured	Fertilizer Treatments			
	1	2	3	4
Days to Heading (days)	142	142	143	142
Days to Maturity (days)	196	196	196	197
Grain Filling (days)	54	54	53	54
Plant Height (cm)	110	112	110	110
Biological Yield (gr/plot)	3655	3599	3533	3565
Grain Yield (gr/plot)	1153	1145	1126	1148
Harvest Index	31	32	32	32
1000 Kernel Weight (gr)	44	44	43	44
Grain Hardness	99	97	98	95
Grain Protein (%)	12.4	12.3	12.5	12.5
Protein Yield (gr/plot)	141	140	140	142
SDS Sedimentation (ml)	55	55	56	55

The results are shown in Table 27. There were no significant differences for any of the treatments among the four fertilizer combinations utilized.

DISCUSSION

The viscoelastic properties of wheat are principally governed by the type and amount of protein. These two variables determine the mixing properties of the flour, and the quality for specific end-product uses. High protein bread wheats are traditionally grown in continental climates resulting in moderate grain yields, and 11% or higher grain protein content. In the maritime climates, wheat yields are high, but the grain protein percentage is low, generally less than 10% and as a result the flour is unacceptable for the milling and baking of bread.

The main objective of this research was to evaluate laboratory techniques to determine, in addition to quantity, the quality of protein. Also to suggest breeding strategies for the development of bread wheat cultivars with acceptable protein levels for maritime climates, as found in the Pacific Northwest. Results from the five studies are discussed to emphasize those aspects which are thought to be critical to the success of such a breeding program.

Sodium Dodecyl Sulphate Sedimentation Test and Breadmaking Quality.

Sodium dodecyl sulphate sedimentation (SDSS) test was developed by Axford and his associates (Axford et al., 1978) as a quick procedure to predict breadmaking quality when only small flour samples are available (a frequent situation encountered for individual plants in early segregating generations). According to

data presented by Blackman and Gill (Blackman et al., 1979) and Preston and his associates (Preston et al., 1982), SDSS values are highly correlated with loaf volume, being independent of the environment, and in particular, variations in protein content.

In this investigation, correlation coefficients obtained for the SDSS test calibration experiment confirmed the potential use of this procedure to predict loaf volumes for the genetic material evaluated (Table 3). Five grams wholemeal flour samples, using 2% SDS, 10ml/l of 9.6% lactate solution, and a reading time of 30 minutes, provided the best experimental procedure to discriminate between good and poor loaf volumes. The amount of lactate solution and the reading time were different from the values originally reported by Axford and his associates (Axford et al., 1978).

In contrast to the results reported by Blackman and Gill (1979) and Preston et al. (1982), SDSS values were found to be highly influenced by variations in protein concentrations. When protein contents were low (below 13%), an increase in protein content resulted in an increase in SDSS values (Figure 1). Gluten quality in the check cultivar Wanser improved with the amount of protein. Wanser's response to an increase in protein explains why people in the milling and baking industry has frequently paid a premium for higher protein wheats to insure the quality of their end-product.

Results observed in this study, however, suggest that at higher protein levels (above 14%), SDSS values are negatively correlated with the concentration of protein in the grain (Table 4 and Figures 2, 3, 14, and 15). An explanation for the lower SDSS values is that

the concentration of SDS in the test (2%) is not enough to dissolve the higher amount of protein present in the flour sample. It is also possible that the additional protein synthesized at the higher protein levels may not contribute to the viscoelastic properties of the dough, resulting in lower SDSS values.

According to the data provided in Figures 1 and 2, and in Appendix Figures 1 through 5, the higher SDSS values were found between 12.0% and 14.0% protein. These data suggest that SDSS values should not be interpreted as a measurement of loaf volume unless the corresponding protein determinations are available (Table 4). Within certain protein percentages (Tables 5 and 6), the association between SDSS values and loaf volumes was adequate for early generation progeny screening of the experimental materials used in this study. Before employing this technique in a bread breeding program, it would be important to calibrate the test according to the existing germplasm and quality standards.

High Molecular Weight Glutenin Subunits and Protein Quality

Limitations of the SDSS test in predicting loaf volume are common to many baking tests described in the literature (Zeleny test, Pelshenke, Alveograph, and Mixograph). Measurements obtained with these procedures are the results of an interaction between protein quality and quantity. Due to the confounding effect of protein quantity, genetic studies on the inheritance of protein quality using any of these techniques have been difficult to interpret. Most

baking tests require relatively large number of kernels which have to be sacrificed for the flour sample. A method to avoid some of these problems involves the identification of the high molecular weight (HMW) glutenin subunits.

Sodium dodecyl sulphate polyacrylamide gel electrophoresis (SDS-PAGE) technique was adopted in this study to separate and classify glutenin storage proteins into their HMW subunits. One of the advantages of this technique is the small amount of flour sample required (20-30 mg of wholemeal flour per column). It can be performed with the endosperm of on individual kernel without sacrificing the corresponding embryo. Within a broad protein range, the SDS-PAGE glutenin banding pattern was shown in this study to be independent of protein content in the flour sample (Figure 4).

According to Payne (Payne et al, 1981b), the presence of bands 5-10 in the D genome, bands 7-8 or 17-18 in the B genome and bands 1 or 2* in the A genome guarantees good breadmaking properties. To test this conclusion, the associations between glutenin subunits, loaf volumes and SDSS values were studied (Table 5 and 6). Lines 11, 15, 16, 4, and 10 had the best quality scores (highest loaf volumes and SDSS values) which were predicted by their HMW glutenin banding patterns. However, the HMW glutenin banding pattern failed to predict the quality response in Bounty (noted as selection 21 in Table 5). Bounty has a poor banding combination in the D genome (bands 2-12), and still has a relatively high loaf volume. Grain protein content in Bounty was higher than in the other experimental materials, and, probably, compensated for a poor protein quality.

High molecular weight glutenin subunits could help in identifying good breadmaking quality (high loaf volumes) in low protein environments. This technique might not be so reliable in continental climates where loaf volume can be the result of a high protein content.

The contribution of the different glutenin bands to breadmaking quality was studied using SDSS values as a measurement of loaf volume. Line 15 from Argentina (1/7-8/5-10) x Line 13 from Israel (2*/17-18/5-10), noted as cross 1513, represented a combination between two lines with high and low SDSS values, respectively. When the relative importance of individual subunits were evaluated (Tables 7 and 8), bands 5-10 were superior to bands 3-12 in the D genome, band 1 exceeded band 2* in the A genome, and bands 7-8 proved better than bands 17-18 in the B genome. The heterozygous condition in the three genomes (for example, 3-12 + 5-10 in the D genome) always resulted in intermediate SDSS values.

F2 Individuals and F4 lines were classified according to SDSS values (high, intermediate, and low) to determine possible glutenin subunits interactions among and within the three genomes. Bands 5-10, 1, and 7-8 were more frequent than bands 3-12, 2*, and 17-18, respectively in the high SDSS group. However, individuals heterozygous for the A and B genome (1 + 2* and 7-8 + 17-18, respectively) were more abundant than either of the homozygous alternatives among the higher SDSS group. Intraallelic interactions among bands in an heterozygous state are not relevant for the traditional wheat breeder interested in developing homozygous

cultivars. Hybrid wheat breeders will have to evaluate the most favorable intra-allelic combinations for their F1 products.

Since most of the F2 plants and F4 lines in the high SDSS group (Figures 10 and 11) carry band 1 rather than 2*, bands 7-8 instead of 17-18 and bands 5-10 in contrast to 3-12, one might assume that bands 1, 7-8, and 5-10 are associated with higher loaf volumes. However, this conclusion may not be necessarily true. The HMW glutenin banding pattern for line 15 (SDSS value = 60 ml) is 1/7-8/5-10. It is possible that F2 plants carrying the glutenin subunits from line 15 have a higher SDSS value just because they resemble their parental line in coding sequences other than just for the HMW glutenins.

Line 15 from Argentina (1/7-8/5-10) x line 14 from Israel (2*/13-19/5-10), noted as cross 1514, represented a combination between two lines with the same favorable glutenin subunits at the D genome (5-10). Differences among SDSS values in the segregating populations could only be accounted for by differences in the banding patterns of the A and B genomes. Even though there was a tendency for band 1 to replace band 2* in the high SDSS group (Figures 12 and 13), there were no significant differences in their individual contributions to loaf volumes (Tables 9 and 10). Band 1 was superior to band 2* in cross 1513, but not in cross 1514. It can be concluded that the contribution of individual bands to gluten quality depends primarily on the glutenin subunits present in the other two genomes. The superiority of band 1 in relation to loaf volume might be related to the presence of bands 7-8 in the B genome, as with selection 15. A definitive answer can only be provided when bands are compared in the

same genetic background, i.e. among isogenic lines.

The work described in this section suggests that some combinations of the HMW glutenin subunits might be more effective than others in conferring good protein quality to flour. The objective, with respect to the breeding program, is to determine which allelic variants for each of the five glutenin loci on the group 1 chromosomes (1A, 1B, and 1D) correlates most strongly with loaf volume. These subunits can then be brought together by conventional breeding methods using the SDSS test as primary screen and SDS-PAGE as a secondary screen to test which of the better quality progeny possess the desired subunits.

Inheritance of Protein Quality and Quantity

Inheritance of protein quality was studied utilizing the SDS-PAGE technique. Glutenin proteins are synthesized by three pairs of closely linked genes which are inherited in a Mendelian fashion (Flavell et al., 1984). It was observed in this study that the F1s received the complete set of HMW glutenin subunits from both parents. Whether allelic forms in each glutenin loci are equally expressed cannot be answered without the appropriate densitometric analysis of the gel.

Genotypic frequencies for each pair of genes in the F2 and F4 generations are presented in Tables 7 through 10. As would be expected, heterozygosity decreases with an increase in the number of generations of selfing. For example, in cross 1514, 54% of the F2

plants are segregating for bands 1 or 2* on chromosome 1A (Table 9). In the F4 generation, 70% of the lines are homozygous for this glutenin locus (Table 10).

Simultaneously, the quantitative inheritance of loaf volume was evaluated using SDSS values. If SDSS values and HMW glutenin subunits are both measuring the same quality parameter, their inheritance patterns should be similar. Heritability estimates for SDSS values were high (Table 11), suggesting that this genetic trait is mainly under genetic control. Normal distributions for the F2 SDSS values of crosses 1513 and 1514 (Figures 7 and 8) can be interpreted as the result of the segregation of a few major genes.

When the F1 generations from the Argentine x Israel crosses were evaluated for their heterotic response involving SDSS values (Table 16), there was a tendency for the F1 to exceed the midparental values in the positive direction. Line 15 from Argentina (1/7-8/5-10) x line 11 from Israel (1/7-8/5-10), noted as cross 1511, was the only F1 where a positive heterotic response was not observed. Apparently, there is an advantage in the F1 hybrid which cannot be easily explained at the level of HMW glutenin subunits. If there were any kind of intra-allelic interaction between glutenin bands at the same locus, there is no reason why the heterozygous genotypes should always yield higher SDSS values than either of the homozygous parents. The heterotic response for protein content was also calculated among the same group of Argentine x Israel crosses. There was a tendency for the F1 hybrids to have less protein than the midparent (Table 15). If it is true that at high protein

concentrations (those levels found in parents and F1s in Table 15), SDSS values are negatively correlated with higher protein content, a positive SDSS heterotic response would be explained as the consequence of the negative heterotic response for grain protein content.

The inheritance of protein content and grain hardness were studied simultaneously on the nine crosses between selected Argentine and Israel lines. Hard endosperm wheats have been traditionally associated with high protein content and good breadmaking properties. It was of interest to learn if an association between protein and hardness existed in the experimental materials used in this study. Both traits were measured using near-infrared reflectance spectroscopy. This technique facilitates genetic studies due to the large number of individual samples that can be processed per unit of time.

Heritability estimates for grain protein content were erratic, with many negative values observed (Table 12 and 13). The negative values reflect the lack of precision of the estimates, due to a large environmental component, which is characteristic of traits with low heritabilities. There was no evidence to support the presence of major genes for protein content among the lines derived from T.turgidum ssp. dicoccoides. However, the lines from Israel proved to complement the lines from Argentina for protein content, suggesting that they were carrying different genetic sources for grain protein. The preliminary results from the F4 segregating lines (Table 18) demonstrate that the protein levels of the Argentine

materials were significantly improved by the addition of the "dicoccoides" germplasm without affecting either yield potential or loaf volume properties. A total of 46 F4 lines were selected on the basis of their yield potential, higher protein content and appropriate glutenin banding pattern, to be tested in preliminary yield trials.

When heritability estimates were calculated for grain hardness (Table 14), they were high and consistent, suggesting a qualitative type of inheritance. In Figures 16 and 17, the F2 progeny from crosses 1614 and 1514 (hard x soft) reflect a bimodal distribution, indicative of major genes undergoing segregation. This is in agreement with the findings reported by Law et al. (1978). Grain hardness was positively correlated with percent protein in some crosses (crosses 1613, 1811, 1813, and 1814). Whether grain hardness increases because protein content increases, or whether high protein content is the result of hard endosperm texture, are questions that cannot be answered based on correlation coefficients.

There is no evidence in this investigation to consider protein content, protein quality, and grain hardness as being under the same genetic mechanism of control. Hard wheat cultivars are not necessarily higher in protein content and loaf volume than soft wheats. Line 14 from Israel, is a Soft Red Spring Wheat with a high protein content, and a loaf volume of 1065 cc. It also has the right glutenin subunits for breadmaking quality on chromosomes 1A and 1D (Table 6). When line 14 (2*/13-19/5-10) was crossed to line 16 (2*/17-18/5-10), high yielding, high protein F4 segregating lines

were recovered with bands 17-18 in the B genome (along with 2* in the A genome and 5-10 in the D genome) and a soft endosperm texture (Table 18). It can be concluded that the traditional possible association among hard endosperms, high protein contents, and high loaf volumes, is nothing more than a breeding artifact, without any genetic implications.

Relationships of Selected Agronomic Traits with Grain Yield, Protein Content, and SDSS Values.

A selection criterion, other than grain protein percentage or grain yield, is often required due to the frequent negative association between these two traits. The objective of this phase of the study was to identify highly heritable traits associated with grain yield and protein content which could be used in early generation selection. Comstock and Robinson's components of variance methodology (Comstock and Robinson, 1952) was utilized to obtain broad sense heritability estimates for twelve agronomic traits in both spring and winter materials. These heritability estimates were calculated on a solid seeded plot (as unit of reference). Values were generally high for all traits (Tables 19 and 20). Moreover, the genotypic x environmental variance component was low due to the homogeneity of environments. Even so, grain yield and protein content were still among the traits which had the lowest heritability estimates.

Among the spring wheat materials (Table 21), a strong negative

associations between percent protein and grain yield was observed. Traits positively associated with grain yield were negatively associated with protein content. For example, selecting for long grain filling periods, or higher biological yields or larger kernels would result in higher yields, but would reduce protein concentration in the kernel. No single selection criterion proved of value in improving grain yield and grain protein content simultaneously in early generation. These results are in agreement with the data reported by Loffler et al. (1982).

Relationships among traits were somehow different among the winter materials (Table 22). Short stature plants, with higher biological yields, and harvest indexes resulted in high yielding selections. However, high harvest indexes resulted in lines with lower protein and a reduced loaf volume, as measured by SDSS values. The negative correlation between protein content and harvest index might have been responsible for the shortage of high yielding, high protein cultivars among the semidwarf Hard Red Winter Wheat materials. If breeders were able to obtain the yield potential through biological yield rather than harvest index, protein content could be raised without affecting yield potential.

Smaller kernels were found to have a higher protein content. High tillering selections with smaller kernels could result in high grain yield with high protein content. Biological yield and kernel weight appear to be two selection criteria which can be used to improve grain yield and protein content simultaneously in Hard Red Winter Wheat materials.

Among winter wheats, high loaf volumes could be obtained with taller plants, large biomasses, low harvest indexes and small kernels. Sedimentation values were positively correlated with protein content since the protein concentrations among the winter selections were in general lower than 14% (Table 5). As previously noted, when protein levels are low, SDSS values increase with an increase in protein content.

Data in Tables 23, 24, and 25 address the question of whether the agronomic information is valid when obtained from space planted individuals, since wheat is grown commercial in solid stands. In the pedigree breeding system, it is common to select among individual plants in early generations. The positive correlation between harvest index and grain yield, measured on solid stand yield trial plots (Tables 21 and 22), was maintained at the individual plant level. These results explain why pedigree breeders have been successful in increasing wheat grain yield in the past 30 years by manipulating the relationship between grain and straw. However, by favoring semidwarf types, they have also been selecting against protein content. Biological yield was also positively correlated with grain yield among individual plants. Selection for high biological yield can be attempted on individual plant basis in early generations, even though heritability estimates for this trait are somewhat lower than for harvest index.

Importance of Agronomic Practices in the Production of Hard Red Winter Wheats.

The negative correlation between protein content and grain yield was once attributed to bioenergetic limitations (Penning De Vries et al., 1974). High grain protein percentage may be associated with a reduced capacity to synthesize and store carbohydrates rather than with high protein storage. In high harvest index material, the problem becomes even more critical. Straw and leaves (nitrogen reservoir) are reduced in relation to grain biomass so that a smaller amount of nitrogen has to be distributed to a larger amount of grain.

A solution for this apparent dilemma was attempted in this study by manipulating the fertilizer strategy of the winter crop (Table 1). An early season (January and/or February) application of nitrogen in the form of ammonium nitrate improved the vegetative growth of the crop, thus increasing biological yield, tillering potential, the nitrogen reservoir, and reducing harvest index. A complementary spring application of fertilizer at the tillering stage, helped the crop realize its yield potential, and provided enough nitrogen to guarantee a desirable amount of storage protein in the kernel.

With a split application of nitrogen in January, February and March (treatment 2 in Table 26), a simultaneous increase in grain yield and grain protein content was obtained. This positive association observed between yield and protein could be accounted for by the increase in biological yield and the decrease in harvest index obtained with the fertilizer treatment. Under the growing conditions

in the Willamette Valley during the 1983-84 growing season, there was no advantage in delaying nitrogen applications until heading time (treatment 3).

Sedimentation values improved significantly under a split nitrogen application in January, February, and March, even though most of the Hard Red Winter Wheat lines utilized in this study carried the right HMW glutenin banding pattern. There is a minimum amount of protein required to guarantee a high loaf volume no matter which glutenin subunits are present. It is hard to define a minimum acceptable protein level based on the data generated in this study. Eleven and a half to twelve percent protein would be a first tentative estimate which requires further investigation to substantiate.

In the 1984-85 growing season, the objective of the agronomic experiment was to determine whether January or February were the optimum months for the early nitrogen applications. Unfortunately, no significant differences among treatments were obtained, perhaps due to the dry weather conditions which prevailed during the winter and early spring months. Protein contents were relatively high in the experiment, but at the expense of lower yields.

Breeding Strategies for Hard Red Winter and Spring Wheats for Non-Traditional Areas.

The development of high yielding wheat cultivars with an acceptable loaf volume at a minimum level of protein has now become a

feasible breeding goal for non-traditional areas. New techniques, such as the SDSS test and SDS-PAGE of the HMW glutenin subunits have provided the breeders with the necessary tools to select for protein quality among a large number of progenies in early generations. A better understanding of the genetic relationship among protein quantity, protein quality and grain yield, and their interactions with other traits of agronomic importance, have contributed to the development of the following breeding strategies.

If the main breeding objective is to develop Hard Red Winter Wheat cultivars, winter x spring crosses will allow the breeder to benefit from the high yield potential present in both gene pools. A first step would be to select appropriate parents for the crossing block according to the following criteria. Among the high yielding winter parents available, those with the highest biological yield and tillering potential, tallest stature, lowest harvest index, best winterhardiness and most favorable glutenin subunit combinations are preferred. Facultative spring types, as those lines coming from Argentina, could be selected according to their yield potential and electrophoretic banding pattern so as to compensate for possible deficiencies in the winter counterparts.

Spring habit is a dominant trait which allows the F1 generation to be advanced in the greenhouse without vernalization. During the same year, F2s can be planted as bulk populations in a cooler spring location to satisfy the vernalization requirements and save one breeding year. Selection should be delayed until the F3 generation when individual F3s will be space-planted in a typical winter

location. Plant selection should be concentrated on winter hardiness, biological yield, tillering potential, small kernel size, plant height, and resistance to the prevailing biotic and abiotic stresses.

F4 plant rows should then be grown in two locations with two replications per location, with split applications of nitrogen in January, February and March. Breeders can then decide which rows are agronomically superior based on the same criteria used for individual F3 plant selection. The selected plant rows should be harvested at both locations and the yield per plot recorded. In the laboratory, protein and grain hardness can be determined by near-infrared reflectance spectroscopy among the high yielding materials. A first screening for high loaf volume can be performed with the SDSS test. Those lines which look promising after SDSS can be evaluated for their HMW glutenin banding pattern by SDS-PAGE and advanced into preliminary yield trials the following year.

With spring wheats, there is no single agronomic criterion to rely upon for the simultaneous early generation selection of grain yield and protein content. Protein content and grain yield will have to be evaluated based on solid seeded plots in latter generations. A spring crossing block should include high yielding locally adapted cultivars, agronomically superior selections adapted to other spring growing areas, and high protein sources as the hexaploids lines derived from T.turgidum ssp. dicoccoides. Winter x spring crosses could also be used to benefit from the high yield potential in both gene pools.

A large number of crosses should be made. Each individual cross can be advanced as a bulk population until the F4 generation, eliminating entire crosses due to agronomic and/or disease problems. Early generation yield testing of the F4 bulks can be performed to select those populations with high yield and protein. F5 head rows can then be derived from the selected bulks in order to be evaluated for agronomic characteristics, SDSS values and electrophoretic banding pattern. The best head rows should be advanced into preliminary yield trials.

The failure in the past, of bread wheat breeding programs in non-traditional areas, can be attributed to the emphasis concentrated on the selection for semidwarf types with high harvest index. Utilizing this approach, breeders increased the yield potential of their germplasm, but reduced the protein percentages in the kernel and the quality of the flour for breadmaking. With the newer techniques, it is a possible to look at both protein quality and quantity. The trade off between carbohydrate and protein can now be avoided with the appropriate HMW glutenin subunits. The desirable glutenin combination can now be incorporated into agronomically superior cultivars with acceptable protein levels, utilizing conventional breeding methods and SDSS and SDS-PAGE as protein quality screens.

SUMMARY AND CONCLUSIONS

It was the objective of this investigation to evaluate the possibility of developing high yielding cultivars with acceptable loaf volumes at minimum protein levels for non-traditional bread wheat growing areas. Selected winter and spring germplasm was evaluated as new sources of genetic variability for quality and quantity of protein and various agronomic traits. The germplasm included hexaploid spring wheats derived from Triticum turgidum ssp. dicoccoides with high protein potential, and spring type selections from Argentina with good baking properties. Winter materials were from the Oregon State University International Winter x Spring Wheat Improvement Program.

In evaluating the potential of developing agronomically superior cultivars with acceptable quality and quantity of protein for bread flour, the following experiments were conducted: 1) evaluation of laboratory techniques (SDSS test and SDS-PAGE) for their reliability in identifying the desired quality factors, 2) characterization of selected wheat germplasm for grain yield, grain protein, and breadmaking quality, 3) identification of the inheritance patterns of factors influencing breadmaking quality, 4) identification of the inheritance pattern of factors influencing grain protein content and grain hardness in hexaploid wheat selections derived from Triticum turgidum ssp. dicoccoides, 5) determination of highly heritable traits that may be phenotypically correlated with grain yield, grain protein, and SDSS values, and 6) evaluation of agronomic practices

for the production of Hard Red Winter Wheat lines.

The following conclusions were reached based on the results of this investigation:

1. Development of high yielding bread wheat cultivars with an acceptable protein level is a legitimate breeding goal in non-traditional bread wheat growing areas. Sodium dodecyl sulphate sedimentation (SDSS) test and the SDS-PAGE of the high molecular weight glutenin subunits have provided the wheat breeder with the necessary tools to predict protein quality and loaf volume.
2. Sodium dodecyl sulphate sedimentation values were found to be highly influenced by variation in protein concentration. The higher SDSS values were concentrated between 12% and 14% protein. However, when protein content data are available, this breadmaking test can be recommended for early generation progeny screening for the following reasons: 1) good relationship with loaf volume, 2) simple, rapid procedure which requires only inexpensive laboratory equipment.
3. The SDSS test was calibrated to the existing quality standards for Hard Red Winter and Spring Wheats in the Pacific Northwest. Five grams wholemeal flour samples with 2% SDS, 10 ml/l of 9.6% lactate solution, and a reading time of 30 minutes provided the best combination to discriminate between lines with high and low loaf volumes for the experimental materials used in this study.
4. Electrophoretic analysis of the HMW glutenin is a more powerful, but also a more laborious and expensive technique to predict loaf volume in parental lines and early generations. Advantages

of this method are the following: 1) small sample size required (half a kernel) and 2) HMW glutenin banding patterns are independent of the protein percentages in the flour samples. High molecular weight glutenin subunits can help identify breadmaking quality, specially in low protein environments.

5. Glutenin proteins are synthesized by three pairs of closely linked genes which are inherited in a Mendelian fashion. F1s received the complete set of HMW glutenin proteins from the parents. When these F1s were evaluated for their SDSS heterotic response, there was a tendency for the F1s to exceed the midparental values. There was some evidence for intra-allelic interactions among HMW glutenin bands in an heterozygous state.

6. Contribution of the different glutenin subunits to gluten quality was studied using SDSS values as a measurement of loaf volume. The D genome bands 5-10 were always associated with higher loaf volumes than bands 3-12 or 2-12. Importance of individual subunits in the A and B genomes, depends on the interactions with other glutenin proteins, in a particular genetic background.

7. There was no evidence for the presence of major genes for high protein content among the hexaploid selections derived from Triticum dicoccoides. However, the incorporation of this source of germplasm into the Argentine lines resulted in improvements in grain protein percentages without a reduction in grain yield. The simultaneous improvement in yield, protein quantity, and quality among the Argentine x Israel crosses was obtained by

delaying selection until the F4 generation.

8. Inheritance studies of grain hardness revealed that this trait was qualitatively inherited. There was no evidence in this investigation to consider protein content, protein quality, and grain hardness under the same genetic mechanism of control. The traditional possible association among hard endosperms, high protein contents, and high loaf volumes, appears to be nothing more than a breeding artifact. In this study, high yielding, high protein F4 lines were recovered with the right banding pattern (2*/17-18/5-10), and a soft endosperm texture.
9. Grain yield and grain protein percentage were negatively correlated among spring wheat selections (-0.554). No single selection criterion proved of value in improving both traits simultaneously.
10. Among the winter materials, harvest index was positively associated with grain yield, but negatively associated with grain protein content. The shortage of high yielding, high protein Hard Red Winter Wheat lines might be a consequence of the breeding effort devoted to harvest index improvement in the past. Biological yield was positively correlated with both grain yield and grain protein content, thus becoming the best selection criterion to improve both traits simultaneously.
11. Protein content in Hard Red Winter Wheat cultivars could be improved by management practices without sacrificing yield potential. Early season applications of nitrate nitrogen (January and/or February), which resulted in an increase in

biological yield and a decrease in harvest index, resulted in a simultaneous increase in protein content and grain yield.

12. The availability of new laboratory techniques and a better understanding of the genetic relationships among protein quantity, protein quality, and grain yield, have contributed to identify new potential Hard Red Winter and Spring Wheat selections for non-traditional bread wheat growing areas.

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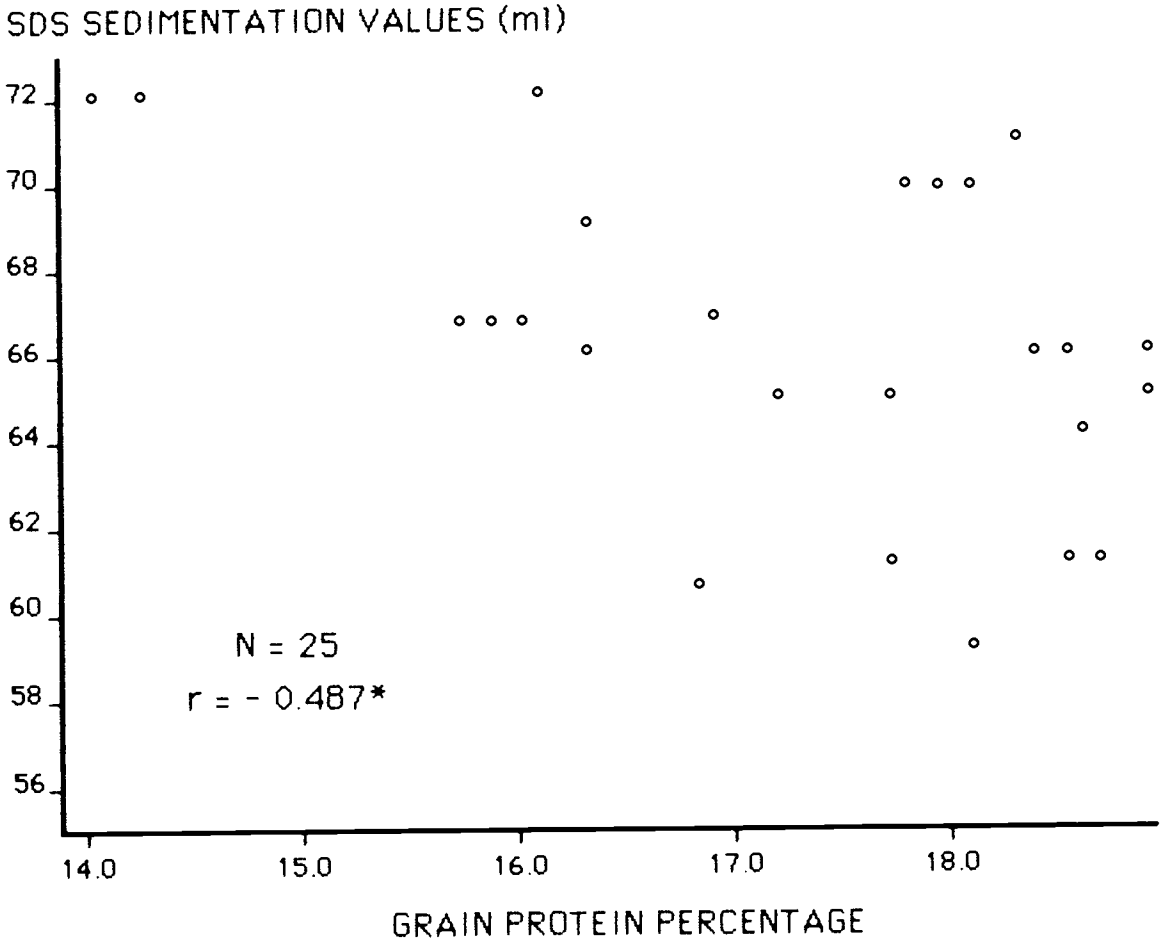
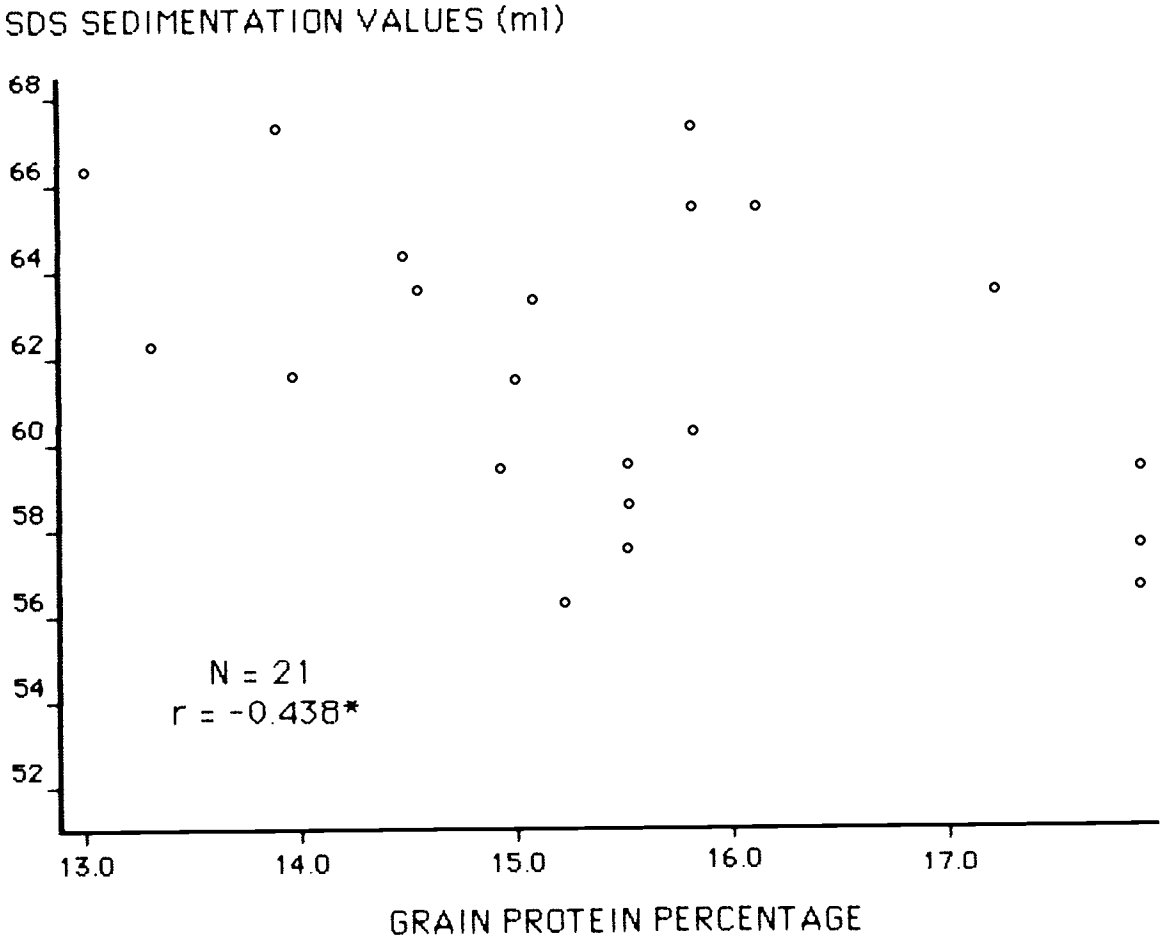
APPENDIX



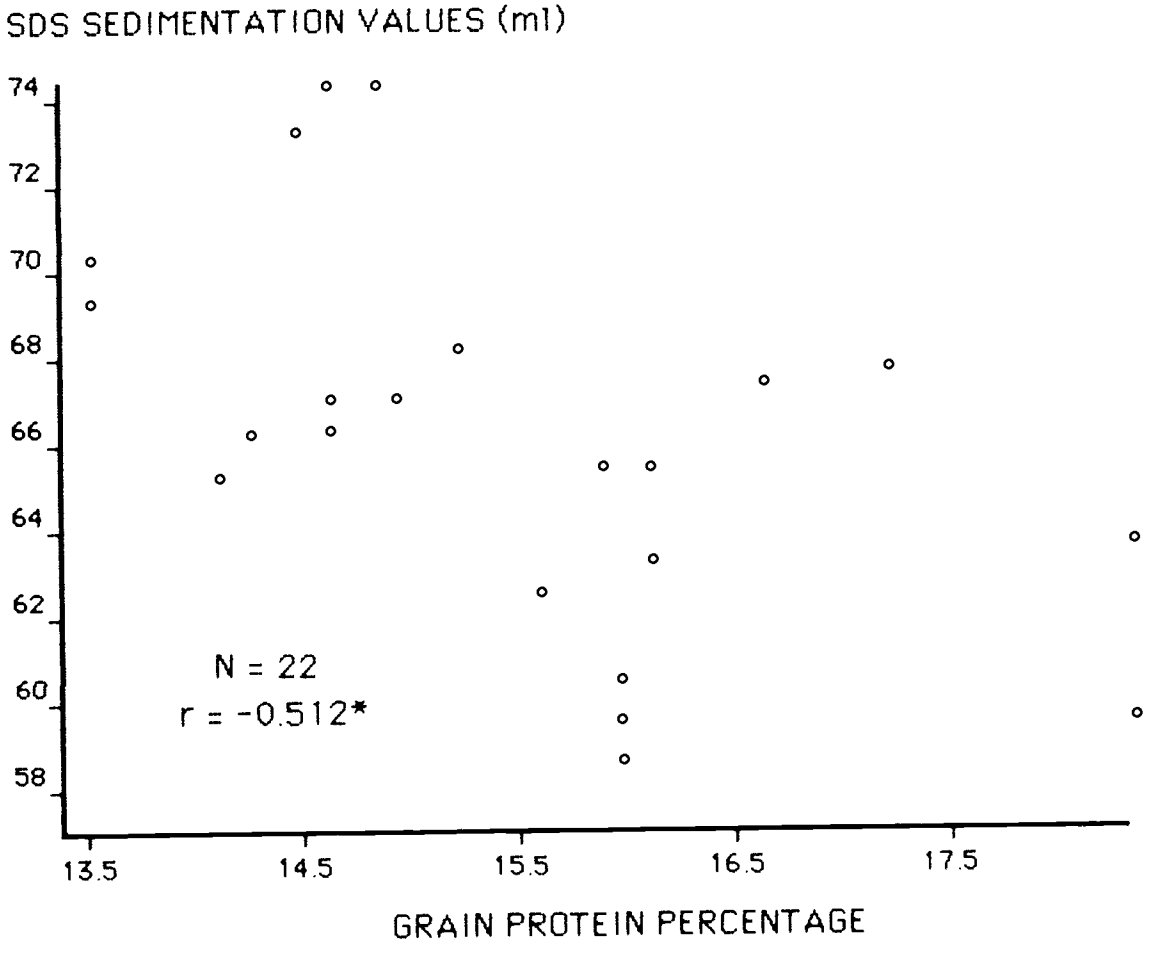
Appendix Figure 1. Relationship between grain protein content and sodium dodecyl sulphate (SDS) sedimentation values in Hard Red Spring Wheat line 11 (greenhouse, 1983).

* significance at the 0.05 probability level.



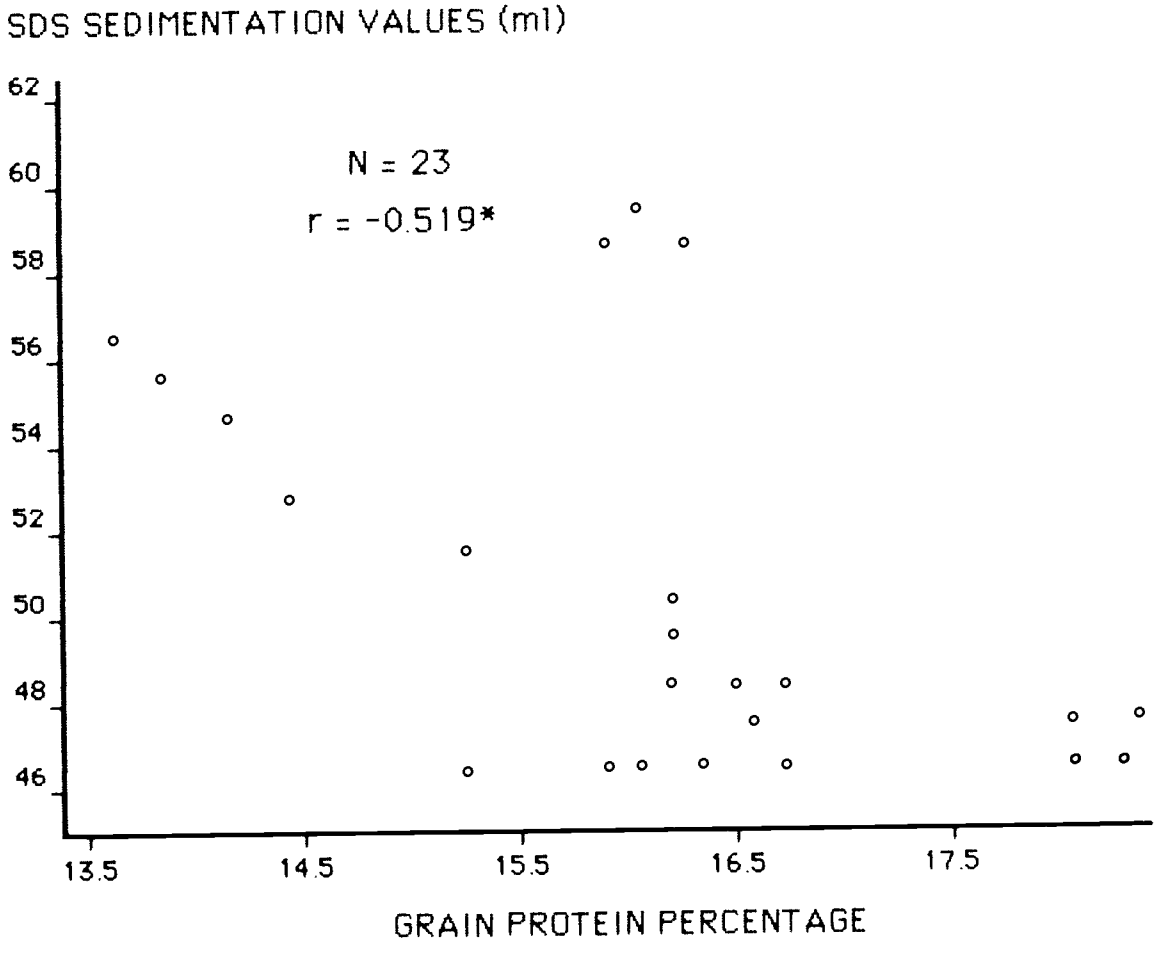
Appendix Figure 2. Relationship between grain protein content and sodium dodecyl sulphate (SDS) sedimentation values in Hard Red Spring Wheat line 15 (greenhouse, 1983).

* significance at the 0.05 probability level.



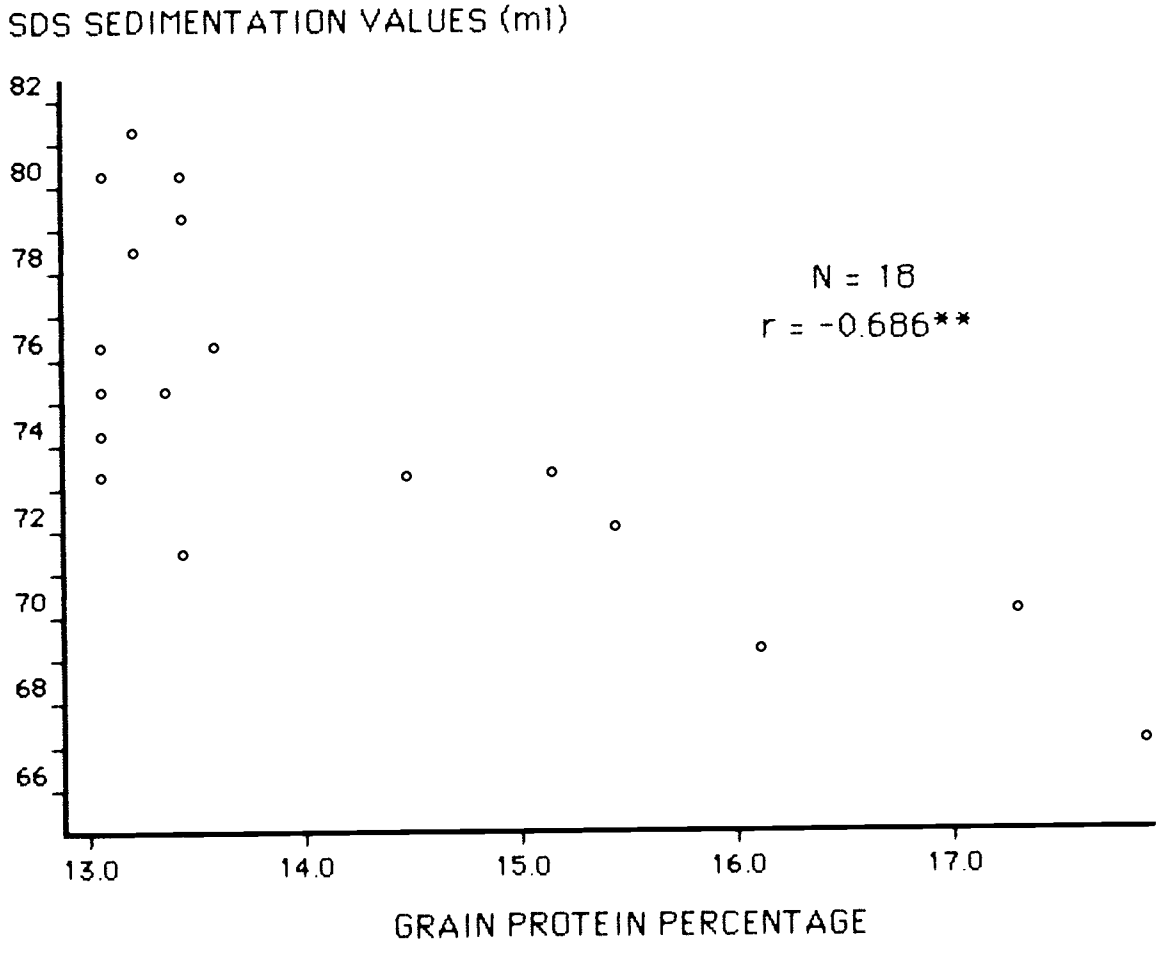
Appendix Figure 3. Relationship between grain protein content and sodium dodecyl sulphate (SDS) sedimentation values in Hard Red Spring Wheat line 16 (greenhouse, 1983).

* significance at the 0.05 probability level.



Appendix Figure 4. Relationship between grain protein content and sodium dodecyl sulphate (SDS) sedimentation values in Hard Red Spring Wheat line 18 (greenhouse, 1983).

* significance at the 0.05 probability level.



Appendix Figure 5. Relationship between grain protein content and sodium dodecyl sulphate (SDS) sedimentation values in Hard Red Winter Wheat line 23 (greenhouse, 1983).

** significance at the 0.01 probability level.

Appendix Table 1. The percentage of protein in the components of the wheat kernel (Hinton, 1953).

Kernel Components	Fraction/100gr whole grain	Protein/100gr fraction	Protein/100gr grain
Pericarp	8.0	4.4	0.3
Aleurone	7.0	19.7	1.4
Germ	1.0	33.3	0.3
Scutellum	1.5	26.7	0.4
Outer Endosperm	12.5	13.7	1.7
Middle Endosperm	12.5	8.8	1.1
Inner Endosperm	57.5	6.2	8.8
Total	100.0	100.0	14.0

Appendix Table 2. Chromosomal location of the storage protein genes of the wheat endosperm (Flavell et al., 1984).

Gene Loci	Chromosome Arm	Position on the chromosome	Storage proteins coded for
Glu-A1	1A Long	Close to centromere	HMW subunits of glutenin
Glu-B1	1B Long	Close to centromere	
Glu-D1	1D Long	Close to centromere	
Gli-A1	1A Short	Towards the end	- gliadins
Gli-B1	1B Short	Towards the end *	- gliadins and LMW glutenin subunits
Gli-D1	1D Short	Towards the end	
Gli-A2	6A Short	Towards the end	- gliadins
Gli-B2	6B Short	Towards the end *	- gliadins
Gli-D2	6D Short	Towards the end	

* The genes on these chromosomes are located on the short arm satellites (the terminal part of the chromosome arm beyond the nucleolar organizing region).

Appendix Table 3. Pedigree and description of wheat cultivars and selections included in the study.

Selection 15 : (B.Cimarron / Calidad-Tobari 66 x Bluebird-Correcaminos). A semi-dwarf hard red spring wheat cultivar released by Criadero Buck, in Argentina under the name of Buck Pucara. High tiller number, very high yielding potential and photoperiod sensitive.

Selection 16 : (B.Pangare / Rafaela MAG-B.Pampero x B.Relen). Short stature, high yielding hard red spring line from Criadero Buck, Argentina. Excellent breadmaking quality properties and photoperiod insensitive.

Selection 17 : (Pitic 62-Bapet * 2 <Caeren / Pitic 62-Eren x B.Manantial>). Short stature hard red spring line from Criadero Buck , Argentina. Photoperiod insensitive.

Selection 18 : (Kavkaz-Jaral"s" SWM 1296). Short stature hard red spring line selected at Criader Buck, Argentina, from an F2 population received from CIMMYT, Mexico . Photoperiod sensitive.

Selection 19 : (Cardenal x Ciano-Sonora 64 / B.Namuncura"s"-Rafrica). Semi-dwarf hard red spring selection from Criadero Buck, Argentina. Photoperiod sensitive and high grain protein content.

Selection 20 : (Cardenal x Ciano-Sonora 64 / B.Namuncura"s"-B.Manantial"s"). Semi-dwarf hard red spring selection from Criadero Buck, Argentina. Photoperiod sensitive.

Selection 11 : Semi-dwarf hard red spring line from the Valcanic Institute in Israel. Excellent breadmaking properties, high spike fertility and large kernel size.

Selection 13 : Relatively tall hard red spring line from the Valcanic Institute in Israel. Photoperiod insensitive.

Selection 14 : Relatively tall soft red spring line from the Valcanic Institute in Israel. Photoperiod insensitive.

Appendix Table 3. (continued)

Selection 23 : (Probstorfer Extrem / Tobari 66 = ORCR 8313). Hard red winter line from the Oregon State University Winter x Spring program. Good breadmaking properties. Photoperiod sensitive.

Selection 4 : (Stp /5/ Tob / B.Man. // BB /3/ Cdl /4/ Sx,F1 /6/ Voro = ORCR 8511). Hard red winter line from the Oregon State University Winter x Spring program. High protein content. Photoperiod sensitive.

Selection 6 : (Cno / Chr // On /5/ 53-388 /3/ An64 /PI // LR64 /4/ II18427 /6/ B = ORCR 8512). Hard red winter line from the Oregon State University Winter x Spring program. High yield potential. Photoperiod sensitive.

Selection 10 : (Pumafen // Ciano"s" / Gallo = ORCR 8414). Hard red winter line from the Oregon State University Winter x Spring program. Photoperiod sensitive.

Stephens : (Nord Desprez / Pullman Selection 101). Standard height, soft white winter wheat cultivar from Oregon State University. Medium to high tillering levels, moderate head fertility and a high seed weight. Photoperiod sensitive.

Wanser : (Burt / Itana). Tall hard red cultivar from Washington State University. Standard hard red winter variety for the Pacific Northwest. Photoperiod sensitive.

Bounty : (TJB 30/148 x Durin). Awnless, short stature soft red winter line from the Plant Breeding Institute, in England. Photoperiod sensitive.

Appendix Table 4. Summary of meterological data for Corvallis, Oregon (1983-84). *

Month	Average temperature, °C			Precipitation	Evaporation	Radiation
	Max.	Min.	Mean	mm	mm	Langley
September	22.8	8.8	15.8	13.5	127.0	414
October	17.4	4.7	11.1	26.7	49.3	232
November	11.9	5.5	8.7	252.2	----	85
December	4.8	-0.5	2.2	306.1	----	67
January	9.3	1.7	5.5	82.8	----	101
February	11.2	2.1	6.7	175.8	----	154
March	14.4	4.6	9.5	97.0	----	259
April	14.0	3.8	8.9	86.6	67.1	353
May	17.6	5.9	11.8	93.2	94.2	438
June	20.9	8.1	14.5	110.2	123.7	547
July	27.3	10.3	18.8	5.1	214.1	687
August	27.4	9.6	18.5	Trace	190.8	547
September	23.7	8.6	16.2	18.8	117.9	362

* Observations were taken from Hyslop Field Laboratory.

Appendix Table 5. Summary of meterological data for Madras, Oregon (1983-84). *

Month	Average temperature, °C			Precipitation	Evaporation
	Max.	Min.	Mean	mm	mm
September	21.3	1.8	11.5	5.6	99.6
October	17.9	1.7	9.8	25.6	50.3
November	9.3	0.5	4.9	31.2	10.2
December	-0.7	-8.2	-4.5	88.4	----
January	6.4	-4.6	0.9	5.6	----
February	8.9	-2.2	3.3	23.4	----
March	12.5	-1.3	5.6	31.7	----
April	12.2	-1.2	5.5	22.9	----
May	17.2	1.3	9.2	3.8	79.2
June	20.2	4.1	12.5	28.7	150.1
July	27.9	6.9	17.4	2.5	235.7
August	27.8	6.9	17.3	9.6	206.2
September	23.7	8.6	16.2	18.8	117.9

* Observations were taken from Redmond Field Laboratory.

Appendix Table 6. Summary of meterological data for Madras, Oregon (1984-85). *

Month	Average temperature, °C			Precipitation	Evaporation
	Max.	Min.	Mean	mm	mm
September	21.1	2.8	12.0	11.9	99.6
October	13.4	-0.7	6.3	31.2	50.3
November	7.5	-1.6	3.0	77.5	10.2
December	3.7	-6.8	-1.5	13.4	----
January	2.8	-6.9	-2.0	4.3	----
February	6.5	-6.4	0.0	5.8	----
March	10.9	-4.9	3.0	9.4	----
April	17.5	-0.7	8.4	6.3	----
May	19.4	1.5	10.4	17.5	79.2
June	20.2	4.1	12.5	28.7	150.1
July	27.9	6.9	17.4	2.5	235.7
August	27.8	6.9	17.3	9.6	206.2
September	23.7	8.6	16.2	18.8	117.9

* Observations were taken from Redmond Field Laboratory.

Appendix Table 7. Summary of meterological data for Corvallis, Oregon (1984-85). *

Month	Average temperature, °C			Precipitation	Evaporation	Radiation
	Max.	Min.	Mean	mm	mm	Langley
September	23.7	8.6	16.2	18.8	117.9	362
October	15.0	5.4	10.2	118.1	36.1	183
November	10.7	3.9	7.3	344.2	----	97
December	6.6	-0.1	3.2	101.8	----	75
January	5.8	-2.2	1.8	6.3	----	101
February	9.2	-0.1	4.5	92.7	----	169
March	11.7	1.1	6.4	125.5	----	290
April	16.8	5.5	11.1	26.7	81.0	392
May	19.6	6.0	12.8	23.9	130.6	498
June	24.1	8.6	16.3	56.4	172.0	616
July	30.6	11.3	21.0	13.7	248.7	640
August	27.4	9.6	18.5	Trace	190.8	547
September	23.7	8.6	16.2	18.8	117.9	362

* Observations were taken from Hyslop Field Laboratory.