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Title: Nature of the Inheritance of Gluten Strength and Carotenoid Pigment Content in Winter by Spring Durum Wheat Crosses (Triticum turgidum L. Var. durum).

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Dr Warren E. Kronstad

Durum wheat cultivars for North-Eastern Oregon have to be competitive in terms of their yield potential with soft white winter wheat cultivars and meet strict quality requirements of the milling industry. Combining the high yield potential of fall planted durum wheat cultivars which have an acceptable level of winter hardiness with the good quality characteristics of the spring types through winter by spring crosses is believed to be an appropriate strategy. However, to be efficient, quality traits of the breeding lines and the nature of their inheritance must be evaluated early in the breeding process. The primary objective of this study was to investigate the nature of genetic variability involving two main quality traits, namely gluten strength and carotenoid pigment content. These traits are measured by the SDS sedimentation test and by spectrophotometric analysis of pigment extracts, respectively. Total genetic variability involving grain yield, kernel weight and protein content was also studied. Combining ability analysis of a 4x4 diallel cross using two winter and two spring parents was performed according to Griffing's (1956) Model 1, method 1.

Both additive and non additive type gene action controlled all traits studied. Non additive type gene action was particularly important for grain yield and kernel weight suggesting that selection for these traits should be delayed until later generations (F5 or F6). Protein and pigment content were controlled primarily by genes functioning in an additive manner although they are also influenced by significant non additive type gene action. Reciprocal effects were significant for pigment content suggesting that some maternal effect might be involved. The predominance of additive type gene action for sedimentation volume suggests that this trait can be used to screen early generation material (F2, F3) for gluten strength.

F2 populations generated from the diallel cross were compared in terms of their genetic variances, potential transgressive segregation and were used to investigate the possible associations between the traits measured. Winter by spring crosses were usually characterized by an enhanced genetic variability for yield and gluten strength. Transgressive segregation for sedimentation volume was present in these crosses. Protein content was negatively associated with grain yield. No relationship between gluten strength and grain yield was observed. Gluten strength did not appear to be associated with total protein content of the grain. Sedimentation volume varied greatly, even in populations with low variability in protein content. Consequently, selection on the basis of sedimentation volume per se would not be result in selecting inadvertently agronomically unsuitable types.

Nature of the Inheritance of Gluten Strength and Carotenoid Pigment Content in Winter by Spring Durum Wheat Crosses (*Triticum turgidum L. Var. durum*)

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Karim Ammar

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Redacted for Privacy

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Redacted for Privacy

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Typed by Karim Ammar

In dedication to:
my parents, Najiba and Hamed,
my sister, Ilhem

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INTRODUCTION

Interest expressed by the milling industry in North Eastern Oregon for durum wheat presents a challenge to breeders trying to develop suitable durum wheat cultivars for that area. Winter type durums, due to their higher yield potential, would be more competitive with soft white winter wheat cultivars than spring type durums. However the winter durum germplasm is characterized by poor end-use quality. Consequently, in the United States, all durum cultivars are spring types. Quality is a major concern to durum breeders as the milling and pasta-manufacturing industries impose strict quality requirements. Thus, crossing winter and spring durum types to combine the yield potential of the winter types with the good quality characteristics of the spring types would appear reasonable. This strategy would require a careful monitoring, preferably in early segregating generations, of the quality characteristics in the breeding populations. It is recognized that a final evaluation of all the quality attributes of a durum line can only be achieved in the latest stages of a breeding program when adequate amounts of seeds make large scale tests feasible. However, several tests performed on smaller lots of seed have been developed and now allow breeders to evaluate their early segregating populations on an individual plant basis. Two such tests are the SDS sedimentation and the test quantifying carotenoid pigment content. These tests provide breeders with information regarding two of the most

important quality parameters in durum wheat, gluten strength and semolina color, respectively. Any information regarding the potential use of these tests in selecting plants with good quality in winter by spring crosses would be valuable to durum wheat breeders. The objectives of this study were threefold: 1) to obtain information concerning the nature of gene action involved in the inheritance of gluten strength as measured by the SDS sedimentation test and of carotenoid pigment content. Information was also sought for traits that might influence sedimentation volume, i.e. grain protein content, kernel weight and grain yield. 2) to assess the genetic variability generated for quality traits in populations derived from different gene pools, and c) to determine the possible association between sedimentation volume and grain yield, kernel weight or protein content.

LITERATURE REVIEW

PART 1: QUALITY CHARACTERISTICS AND TESTING IN DURUM WHEAT

Durum wheat fruit is a large caryopsis, generally with a large flinty endosperm. It is harder and more vitreous than most other types of wheat. For this reason it is used in the production of a coarse ground stock, namely semolina. During the milling of durum wheat, the endosperm is separated from the bran which contains the pericarp, seed coat and aleurone. Endosperm is then milled into semolina and flour. The total utilizable milled product represent about 76% of the kernel and is fractionated into semolina (63%) and clear flour (13%) (Finney et al.,1987). Qualitative requirements of durum wheat are closely related to those of its main processing industries, namely the milling and the pasta-manufacturing industries (Cubadda, 1988). Technological quality of durum wheat is evaluated at three different levels: First, the wheat is judged according to the characteristics of the kernel itself. Secondly, the milling and semolina characteristics are considered with regards to the ease of processing and to their pasta-making potential. Finally, durum wheat is judged for the quality of its resulting end-product. Numerous experimental testing procedures performed on the wheat kernel have been developed to predict the expected milling, processing and end-product quality. Although experimental testing can only approximate the commercial process, it is the best system currently available to evaluate the quality potential of durum wheat cultivars to be released (Dick and Youngs, 1988).

1- Kernel characteristics:

a- Test weight and thousand kernel weight:

Test weight is an important factor and reflects the soundness of the grain. A minimum test weight of 60 pounds per bushel is required in the United States and of 73 kilograms per hectoliter in Europe (Cubadda, 1988). Over a broad range of test weights, a significant trend exists toward higher milling yields with increasing test weights (Cubadda, 1988). A high thousand kernel weight is also considered an important characteristic of a durum wheat. Both of these traits indirectly measure the average kernel size which is closely related to milling yield. Matsuo and Dexter (1980) reported a highly significant correlation ($r=.69$) between thousand kernel weight and milling yield. They explained this result by the fact that larger kernels usually show higher endosperm to bran ratio. However, when samples were divided into 4 sub-samples according to their kernel size, no uniform trend was detected. Milling yield decreased significantly only when kernel size fell below a certain level. From the same study, it appeared that test weight is less correlated with milling yield than thousand kernel weight.

b- Vitreousness:

Kernel vitreousness have been associated with semolina granulation and grain protein content (Dick and Youngs, 1988). The presence of non vitreous (starchy) kernels does not affect total milling yield. Matsuo and Dexter (1980), using durum wheat samples with variable percentage of starchy kernels, were not able to detect any significant effect on total milling yield. However, they did find

a significant change in the relative proportions of the two milling fractions, semolina and flour. They concluded that starchy kernels reduced semolina yield in favor of flour yield. Also, non vitreous kernels have a negative effect on total protein content (Cubadda, 1988).

c- Grain protein content:

Total grain protein content may range from 14% to 22% of the grain dry weight (Blanco et al., 1988). A moderately high protein content, above 12%, is required to produce an acceptable product (Joppa and Williams, 1988). Total grain protein is strongly affected by the rainfall and the temperature prevailing at the time of grain filling, as well as by the nitrogen supply (Blanco et al., 1988). While nitrogen has a positive effect on protein content, wheat cultivars show different responses in translocating nitrogen from the leaves and the stems into the kernel (Henson and Waines, 1983). Wheat protein content can be determined accurately by the Kjeldahl method or by near infrared reflectance (NIR) analysis. Wheat proteins are highly heterogeneous and can be divided into four groups according to their solubility: The water-soluble albumins and the neutral salt-soluble globulins represent only about 20% of the total wheat protein. They are cytoplasmic proteins with enzymatic activities (Feillet, 1988). Gliadins and glutenins constitute 80% of the total protein content of durum wheat and are responsible for the viscoelastic properties of the gluten (Blanco et al., 1988). Gliadins are alcohol-soluble proteins known for their medium molecular weight (25,000 to 100,000) and their high extensibility. Glutenins are acid or base-soluble

proteins of high molecular weight (100,000 to 3,000,000) (Feillet, 1988).

d- Ash content:

Several European milling industries consider ash content to be the most important characteristic of durum wheat. In such countries, ash content of semolina is imposed by law. The yield of a given semolina with a fixed ash content varies according to the ash content of the wheat before milling (Dick and Youngs, 1988). Correlation coefficients superior to .90 were found between ash content and semolina yield when 10 samples from each of two durum cultivars were scored for both traits. Consequently, if a durum wheat is high in mineral elements, less semolina is extracted (Dexter and Matsuo, 1978). Wheat ash content varies considerably depending on the environment and the growth conditions (Matsuo, 1988).

2- Semolina characteristics:

Semolina is the main milling fraction of the durum wheat endosperm. In assessing semolina quality, attention is given to factors affecting dough development during processing and to factors associated with some of the cooking quality of the finished product.

a- Granulation:

With the generalized introduction of continuous processing which replaced batch processing, the demand for fine and uniform semolina prevails (Cubadda, 1988) . The requirements in terms of semolina granulation differ from country to country. In the United States, semolina is defined as the purified middling of

durum wheat that will pass through a No.20 U.S. sieve, of which no more than 3% will pass through a No.100 U.S. sieve (Finney et al., 1987).

b- Semolina color:

The amber color of the durum wheat kernel has been identified as the result of certain carotenoid pigments, namely, xanthophylls. Yellow color is one of the most important criteria for high quality pasta products (Johnston et al., 1983). Pasta color is determined mainly by the semolina carotenoid content. Consequently, semolina color is useful for predicting pasta color (Dick and Youngs, 1988). However, the color of the pasta product can be altered as the result of high amounts or high activity of the enzyme lipoxygenase. In fact, some of the original pigment is lost to oxidation during the processing of the semolina at a rate which is a function of the lipoxygenase activity (Lee et al., 1976). When lipoxygenase activity is controlled or eliminated (by processing under vacuum or by adding oxidation inhibitors) semolina color is highly correlated with pasta color. Semolina color can be estimated by visual rating using standard color plates. This method is found to be somewhat subjective (Johnston et al., 1981). Semolina color can be more accurately quantified by spectrophotometry of the pigment extract (AACC. method 14-50) or by the use of a reflectance color meter (Konzak et al., 1973).

c- Rheological characteristics:

Evaluation of the pasta making potential of a semolina has been attempted through rheological tests similar to those used to evaluate the suitability of soft

wheats for bread-making. The most popular rheological test is the farinograph which requires 50 or 300 grams of semolina. Farinograph curves from semolina dough can provide useful information on semolina characteristic before processing. These information include dough development time, dough strength, mixing time and other rheological characteristics (Cubadda, 1988). However, this information is inadequate for predicting cooking quality of semolina and are not as pertinent for predicting pasta quality as they are for predicting baking quality in bread wheats (Finney et al., 1987).

d- Semolina protein content:

Semolina total protein content generally is about one percentage point less than the whole wheat protein (Finney et al., 1987). The relationship between semolina protein content and several pasta quality parameters is fairly well established. Although low protein semolina can be successfully processed, stretching or even breaking of the pasta strands may occur in the later stages of pasta production. Matsuo (1988) reported that a minimum of 11 % protein in the semolina from Canadian durum cultivars is required for an adequate cooking quality of the resulting pasta. Dexter and Matsuo (1977) investigated the effect of semolina protein content on some quality parameters using wheat samples from the same cultivars but differing in their protein content. They found that an increase in protein content resulted in a decrease in farinograph mixing time and in an improvement of the consistency and tolerance index of the pasta dough. The same study suggests that cooking quality and tolerance to overcooking is

improved when protein content increases. However, these relationships are not as straightforward as suggested and caution must be used in making inferences about cooking quality of a durum wheat based on semolina protein data. In fact, Fertini (1988) showed that pasta from semolina samples in the same protein range can vary from excellent to very poor in cooking quality. Consequently, protein content alone is not sufficient to indicate the cooking quality of the resulting pasta. In predicting pasta cooking quality from semolina, one must take into account protein composition as well as protein content.

e- Gluten strength:

In durum wheat, gluten strength influences both dough mixing properties of semolina and cooking quality of pasta (Dick and Quick, 1983). Feillet (1988) stated that "differences in quality among semolina samples derived from different durum cultivars are due to the greater or lower capacity of their proteins to form, during pasta making, a network capable of retaining the other components of semolina, especially starch granules". In durum wheat, strong gluten is a major quality requirement as semolina samples with strong gluten tend to produce pasta products with superior cooking characteristics (Dexter and Matsuo, 1980). In fact, strong gluten gives pasta products a greater cooked firmness and a better tolerance to overcooking (Quick and Donnelly, 1980). Cereal chemists have developed several methods to evaluate gluten strength using relatively low amounts of semolina or of wholemeal. The mixograph (a miniature high speed dough mixer) method is routinely used in all wheat quality laboratories and the

resulting mixogram scores correlate fairly well with pasta cooked firmness. This method requires ten grams of semolina (approximately 20 grams of wheat) and is effective mainly in distinguishing wide differences in gluten quality (Leisle and Baker, 1973). In 1976, the Centro Internacional de Mejoramento de Maiz Y Trigo (CIMMYT) developed another method to distinguish wide differences in gluten strength. It consists in mixing 10 grams of semolina with a salt solution and in washing of the water and salt soluble compounds. A wet gluten ball is formed and placed on a glass sheet. Gluten strength is evaluated by the spread of the gluten ball on the glass in thirty minutes. A wholemeal, Sodium dodecyl sulfate/Lactic acid solution sedimentation test (SST) was developed for bread making quality evaluation of European bread wheats through gluten characteristics estimation. Dexter and Matsuo (1980) evaluated 30 durum wheat cultivars for mixogram scores, SDS sedimentation volumes, protein content and pasta cooked firmness. They concluded that mixogram and SDS sedimentation test were equivalent for gluten strength evaluation as they explain the same percentage of variation in cooking quality. However, only the SST was able to show cultivar by environment interaction which suggest that it would be a more reliable screening test. Using 25 F3 lines from the cross D71110/Edmore Quick and Donnelly (1980) compared the SST which requires 6 grams of wheat to the micro-mixogram test which requires 10 grams of semolina (about 20 grams of wheat). The correlation between the two tests was highly significant and the SDS test was able to account for 65% of the variation in mixogram scores. Also, Dick

and Quick (1983) described a 1 gram SDS-micro-sedimentation test (MST) which had good reproductibility and could be used routinely in early generation testing for gluten strength. Micro sedimentation test volumes were strongly correlated with mixogram scores ($r=.91$, $p<.01$). Maximum R-squared improvement regression analysis for cooked firmness (dependent variable) showed MST to be the best one-variable model as it accounted for 53% of the variation in the firmness of cooked pasta. Also, Wheat protein and MST together was the best two-variables ($R^2=71\%$) model for prediction of spaghetti cooked firmness. Whatever method is used to evaluate gluten strength, no correlation has been found between gluten strength and grain or semolina protein content (Quick and Donnelly, 1980. Dick and Quick, 1983. Autran et al., 1986).

3- Pasta product quality characteristics:

During the manufacture of the pasta products, the semolina is mixed with water to form a pasta dough that goes through a kneading step before it is extruded through dies of different shapes. Then the pasta goes through a highly critical drying process before it can be packaged and stored. At this stage, the quality characteristics of the finished product depends on its ability to give a cooked product that meets the consumer's requirements. These characteristics are genotype-dependent and include mainly yellow color, cooked firmness, tolerance to overcooking and absence of stickiness. As described previously, pasta color will depend primarily on semolina color as long as lipoxygenase activity is controlled. The other characteristics which are designated generally by "cooking

quality characteristics" will depend on the gluten properties (viscoelasticity or strength) and on the "surface characteristics" of the pasta, that is, absence of stickiness, mushiness and clumping. Autran et al.(1986) suggest that the two types of parameters, those related to gluten strength and those related to surface properties, do not seem to be related. In fact, they did not detect any significant correlation between the two types of parameters in 26 durum breeding lines.

The most reliable test for cooking quality remains the sensory test done by a taste panel (Matsuo, 1988). However, this test may be subject to some individual bias (Cubadda, 1988). Objective tests using instruments to assess cooking quality vary from country to country and measure only some of the relevant characteristics. Pasta cooked firmness can be objectively evaluated using an Instron Universal Testing Instrument (Canton, MA) equipped with a special plastic cutting edge that measures the work required to cut a pasta strand (Walsh, 1971). Surface stickiness is related to the total organic matter that can be washed off from the cooked pasta. The main constituent of this total organic matter is starch, mainly amylopectin (Cubadda, 1988). Stickiness can also be measured by a compression tester which gives values that are highly correlated with the total organic matter (Dexter et al., 1983).

PART 2: GENETIC CONTROL OF SOME QUALITY TRAITS

Genetic improvement of quality traits in durum wheat will depend on two essential factors. The first is obviously the availability of genetic variability for the

trait under improvement. A second factor that is highly critical for the genetic improvement of quality characteristics is the availability of reliable and reproducible tests that require small amounts of seed in order to be applicable to early generation material (F2 or F3 generations).

1- Thousand kernel weight:

As an indirect measure of the average kernel size, thousand kernel weight is an important milling characteristic in durum wheat. It is affected by the environment and by the number of heads during the grain filling period (Joppa and Williams, 1988). In selection experiments within two durum wheat populations, Haugerud and Cantrell (1984) reported that selection for high kernel weight in the F4 was effective in improving the population means. This improvement in kernel weight was found to be associated with a decline in the number of kernel per spike.

2- Grain protein content:

An extensive review of the literature on wheat protein content and its genetic control was done by Porceddu et al. (1983). The authors reported great variability for protein content among Triticum species and that Triticum aestivum and Triticum durum consistently had the lowest protein content. Within a sample of 3400 durum wheats from the USDA collection, the protein content varied from 7.3% to 21.3% with a mean being 12.75 ± 2.86%. Only 5% of this variation was ascribed to genetic causes. The genetic control of protein content is a complex subject and the investigations on this matter resulted in quite different

conclusions. It has been suggested that protein content is governed by a complex polygenic system with genes distributed on all the chromosomes. Some reports mention that it is under the control of few major genes with minor genes affecting the intensity of the genetic expression . Additive gene action seems to be the main source of variation although minor dominance effects were reported to be significant (Mihaljev, 1978). Heritability estimates ranging from 0.15 to 0.90 were cited (Porceddu et al., 1983). The heritability estimates depended on the experimental design, the number of generations and the material used. While it was mentioned (Joppa and Williams, 1988) that a minimum protein content in durum wheat is required for the manufacturing of good pasta products, grain protein content by itself is less of a critical factor than protein quality.

3- Gluten properties:

As stressed previously, gluten viscoelasticity or strength is a major quality requirement for durum wheat. It strongly influences the rheological properties of durum semolina as well as the cooking quality of pasta. Consequently, breeding for strong gluten has been a priority in all durum production area in the world. Numerous genetic studies were undertaken in order to investigate the inheritance of gluten strength and to assess the efficiency of selection for this trait. Braaten et al. (1961) reported heritability estimates for mixogram scores of 63%-70% and 56%-65% for broad and narrow sense respectively (narrow sense heritability estimates were derived from the regression of F5 means on F3 means). Environmental influence on the expression of the trait was significant. The

mixogram method for evaluating dough strength was judged not to be accurate enough by the authors. Nevertheless they concluded that selection in F3 for mixogram score can be effective in weeding out weak gluten individuals. More accurate indicators of gluten strength are now available which are also better predictors of pasta cooking quality (SDS sedimentation tests) and can be performed on early generations material. Quick and Donnelly (1980), reported that selection for strong gluten in 25 F3 lines from D71110/Edmore cross based on sedimentation volume (using six grams of wholemeal) was 84% as successful as selecting using mixogram (requiring 20 grams of wheat) scores.

5- Storage protein in relation to gluten strength:

The relationship between pasta making quality with particular attention to gluten strength and the electrophoretic banding pattern of the gliadin polypeptides of durum wheat was investigated by Daminaux et al.(1978). They found that good pasta quality and strong gluten were always associated with the electrophoretic band having a relative mobility of 45 (γ-gliadin band 45). On the other hand, poor gluten properties were always linked with the presence of γ-gliadin band 42. Daminaux et al. (1980) studied the inheritance of band 42 and band 45 in segregating populations over several generations (F1, F2, backcrosses) in three crosses. They reported the codominant nature of the inheritance and that the two bands are likely to be part of two gliadin blocs that are inherited as such. Furthermore, they tentatively mapped the genes coding for the two gliadin blocs to chromosome 1B. Using the same generations in a cross between two biotypes

of the cultivar Duramba (one with band 42 and the other with band 45), DuCros and Hare (1983) reported that gliadin polypeptides 42 and 45 are coded for by two alleles at the same locus. They showed that both alleles exhibited dosage effects as band 42 displayed a greater degree of dominance over band 45. Consequently, early generations seeds or lines with γ-gliadin 45 can be selected as potentially strong gluten types while lines with γ-gliadin 42 can be discarded.

DuCros et al. (1983) studied 103 F7 breeding lines from different backgrounds in an attempt to relate different durum wheat dough strength parameters as measured by mixograms to the gliadin protein composition as determined by electrophoretic banding patterns. The only relationship detected was that previously reported of gliadin groups represented by band 42 and band 45. They also reported that band 42 always occurred with bands 7, 9, 13 and 15 and that band 45 was linked to band 14. Joppa, Khan and Williams (1983) determined the chromosomal location of genes coding for nineteen out of thirty gliadin polypeptides performing Polyacrylamide gel electrophoresis on a set of "Langdon" D-genome disomic substitution lines and on some durum cultivars. Each of the aneuploid lines had a different D-genome chromosome pair from Chinese Spring substituted for a homeologous durum A- or B-genome chromosome pair. It was showed that most bands were controlled by group one chromosomes while the rest was controlled by group six chromosomes. It was demonstrated that the short arm of chromosome 1B alone controlled bands 25, 32, 34, 36, 40, 42, 45 and 64. Because unidimensional Polyacrylamide gel

electrophoresis (PAGE) is unable to assist in mapping hybrid polypeptides that are controlled by more than one chromosome, DuCros et al. (1983) capitalized on the better resolution of two-dimensional electrophoresis (PAGE in the first dimension and isoelectric focusing in the second). Aneuploid lines from cultivar Langdon were used to perform a more accurate mapping of the genes coding for gliadin polypeptides. They showed that homeologous group one controlled Ω- and γ-gliadins while chromosomes 6A and 6B controlled α- and β-gliadins. Furthermore the two dimensional electrophoresis showed that each of band 42 and 45 were actually composed of one major component and one or two minor components. If the tight association between gluten strength and gliadin band 45 is unanimously accepted, the nature of such association, until recently, was yet to be elucidated. In his early work, Daminaux (1978) recognized two possibilities to explain this association: either the γ-gliadin proteins have a direct causal, i.e functional, role in determining gluten characteristics, or the γ-gliadin bands are genetic markers for other proteins responsible for differences in quality (the genes for both groups of proteins being tightly linked). Payne et al. (1984) showed that in eight durum wheat lines (six cultivars and two biotypes of the cultivar Duramba), genes coding for γ-gliadin 45 were tightly linked to those coding for ω-gliadin 35 and to those coding for the low molecular weight glutenins designated as LMW-2. Also it was demonstrated that all lines with band 42 had also the ω-gliadin 33, 35 and 38 bands and those corresponding to the low molecular weight glutenins designated by LMW-1. The family of genes coding for the ω-gliadin, for

the γ-gliadin and for the low molecular weight subunits is referred to in bread wheat as locus Gli-B1. Furthermore, the authors reviewed the arguments supporting the fact that the low molecular weight glutenins were actually the functional proteins influencing gluten properties. These included: 1) it is the glutenin fraction alone that has some viscoelastic properties, while the gliadin fraction produces a viscous mass when hydrated, and 2) in the SDS sedimentation test which strongly correlates with the presence of γ-gliadin 45, only the large aggregates of the glutenins form the poorly soluble sediment, while the gliadin fraction is freely soluble. Consequently, and from the results of their work, they concluded that γ-gliadin 45 is just a marker, and is strongly associated with a low molecular weight glutenin which is the real cause of gluten viscoelastic properties. This conclusion was supported by the work of DuCros (1987) who detected a tight relationship between LMW glutenins and gluten quality parameters in 100 durum lines while high molecular weight glutenins appeared to be very poor indicator of gluten strength. Furthermore, an ultimate confirmation of Payne's conclusions came from the identification by Pogna et al. (1988) of a recombination within the Gli-B1 locus in the Italian durum cultivar Berillo which has the bands of the LMW-2 genes associated with the genes coding for band 42. Despite the presence of band 42, berillo had good viscoelastic properties and strong gluten.

Josephides et al.(1987) showed that chromosome 1B contained the genes that strongly influenced gluten strength. They substituted chromosome 1B of two strong gluten cultivars (Edmore and Kharkov 5) for the 1B chromosome of the

weak gluten cultivar Langdon. In all the locations were the lines were grown, the 1B substitution lines had stronger gluten when compared to Langdon. The 1B chromosome substitution into a weak gluten background was responsible for a drastic change in all characteristics associated with gluten strength such as mixogram score, pasta cooked weight, pasta cooking loss, firmness and even loaf volume when bread was baked with the durum flours.

4- Pigment content and lipoxygenase activity:

Because of the prime importance given to the color of the semolina products, several groups have investigated the mode of inheritance and the potential efficiency of selection for yellow color in semolina or pigment content in the grain. Braaten et al. (1961) investigated the inter-generation relations of pigment content in order to see if early generation selection would be effective. They evaluated, among other traits, the pigment content of granular flour samples from grain collected on F3 and F5 plants from three crosses. Transgressive segregation was observed in the F3 in two out of three crosses. Broad and narrow sense heritability estimate were found to be high, ranging from 72%-96% and from 79%-94% respectively. It was concluded that genotype by environment interactions were of little consequence and that early generation selection would eliminate most of the undesirable genotypes. Somewhat different results were reported by Lee et al. (1976) who used a 10-parent diallel analysis for wheat pigment content, lipoxydase activity and macaroni pigment content (as predicted from grain pigment content and lipoxidase activity) on material grown at two

locations. Differences in the ranking of the parental lines were observed across locations suggesting an important effect of the environment in the phenotypic expression of the three traits. Both additive and non additive components of variation were significant for all traits at the two locations. The estimation of the genetic parameters involved and the analysis of F1 data suggest that heterosis was largely environment-dependent. Absence of epistasis was consistent and the best combiners, as determined by general combining ability analysis in the F1, were different in different locations. Heritability estimate was found to be high enough (0.79) to justify mass selection for wheat pigment content in the early generations at only one location. More recently, Johnston et al. (1983) investigated the inheritance of semolina color in plants from F1, F2 and F3 generations from six durum wheat crosses and in progenies of the backcrosses to both parental lines involved in each cross. Yellow color of the semolina was evaluated using a color meter. Results suggest that semolina color is a highly heritable trait controlled primarily by additive gene effects (82% of the variability was attributed to additive effects) but whose intensity is influenced by the environment. Observation of the generation means revealed that the genotype by environment interactions consisted in changes in magnitude rather than ranking. Identification of transgressive segregants for high color was possible in four of five crosses. In summary, it should be possible to effectively select for high semolina color in early generations as long as the environment allows for a good expression of the genetic potential of the plants in terms of pigment content. The major genes

responsible for semolina color were mapped to chromosomes 2A and 2B (Joppa, unpublished, cited in Joppa and Williams, 1988).

MATERIALS AND METHODS

Experimental populations were generated by hybridizing four parental lines in all possible combinations including reciprocal crosses. The parental material used consisted of a spring cultivar Altar 84, a spring line UC606 and two winter durum lines H9072-12 and H9072-10. Altar 84 is a cultivar released by the Centro International Mejoramento Maiz Y Trigo (CIMMYT) and is widely grown in Mexico. Selection UC606 is a fixed breeding line from the University of California-Davis breeding program. Both winter parents are fixed breeding lines introduced from Turkey. A description of these lines is presented in Appendix Table 1.

Crosses were made in the greenhouse in the winter and spring of 1989. Reciprocal crosses were kept separate. Some F1 seeds were planted in the greenhouse in the spring of 1989 to produce F2 seeds. The experimental populations evaluated consisted in parental lines, F1 plants and F2 plants. The experiment was planted on October 10, 1989 at an experimental site established on a farmer's field located 15 miles Northeast of Pendleton, Oregon.

The soil type at this site is a coarse silty typic haploxeroll. Fertilization was performed according to the common practices in the area: 100 kilograms per hectare of nitrogen, 20 kilograms per hectare of phosphorus and 20 kilograms per hectare of potassium were applied before planting. Twenty kilograms per hectare of nitrogen was topdressed prior to anthesis in the spring. Weeds were controlled

by spraying 0.5 liter per hectare of Buctril and 0.5 liter per hectare of Rhomene (MCPA) in the spring while plants were at the tillering stage. The total amount of rainfall in the area was 332 millimeters from September to August. The climatic conditions that prevailed during the 1989-90 growing season are summarized in Appendix Table 2.

The experimental design used was a split plot restriction of a randomized complete block with three replications. Crosses represented main plots while parents and progenies were the sub-plots. Each main plot consisted of ten rows of ten plants each. Parental lines and F1s were represented by one row each and the F2 population consisted in seven rows. Plants were space planted with 30 cm between plants and 45 cm between rows. Randomization was performed separately between and within main plots. At maturity, each plant was harvested separately. Cleaned seeds from each plant were used to collect data on the following traits:

Grain Yield: was the total grain weight in grams per plant.

Two hundred kernel weight: was the weight in grams of two hundred seeds randomly sampled from one plant.

Grain protein content: was the total protein content of the grain expressed in percent, as determined by Near Infrared Reflectance (NIR) analysis. A detailed description of the procedure is presented in Appendix Table 3.

Gluten strength: was estimated by reading the volume in milliliters of whole meal that sedimentated in a Lactic acid/Sodium Dodecyl Sulfate solution (SDS

sedimentation test). The procedure used was that reported by Dick and Quick (1983) and is described in Appendix Table 4.

Carotenoid pigment content: was the concentration (in p.p.m.) of a pigment extract. It was determined by converting absorbance readings obtained from a spectrophotometer. A modification of A.A.C.C. method 14-50 was followed as described in Appendix Table 5.

Sub-plot means for grain protein content, sedimentation volume and pigment content were estimated for the parental lines and F1s on a row basis. Grain yield and two hundred kernel weight data were collected on an individual plant basis. Fifteen grams of seeds from each plant within the same parental or F1 row were then bulked to produce the wholemeal samples on which the other traits were measured. F2 sub-plots means were computed from data collected on single plant basis for all traits.

The following statistical analysis were performed:

1. Means and standard deviations were calculated for each trait measured.

2. Analysis of variance was used to test for significant differences of mean values among generations and crosses. Fisher's protected Less Significant Difference (LSD) test was used to identify the statistically significant differences between means.

3. Combining ability analysis was performed on parents and F1 plants of all crosses including reciprocal combinations. Because the parental lines represented a selected group of fixed lines, a fixed effect model for combining ability analysis

was used (Griffing's Model 1, method 1 (Griffing, 1956)). Estimates of General Combining Ability (GCA) effects for the four parents and of Specific Combining Ability (SCA) effects of each F1 combination were obtained. Estimates of components of variation due to non additive and to additive gene action were consequently obtained according to Griffing (1956). Gluten strength and pigment content can be considered as endospermic traits. Endosperm tissue on an F1 plant represents F2 generation tissue. Consequently, the combining ability analysis for these traits was in fact performed in the F2 generation.

4. Genetic variances were computed for all traits for the twelve crosses by subtracting the variance within the F2 populations (phenotypic variance) from the environmental variance. The environmental variance was obtained by pooling the variances computed for parent 1, parent two and the F1. Genotypic variances were used to compare the populations in term of the genetic variability generated for all traits. F2 populations data were also used to identify potential transgressive segregation.

5. Correlation coefficients between different traits were computed for each cross on F2 plants.

EXPERIMENTAL RESULTS

Results are reported from a 4x4 diallel cross involving parents, F1 and F2 plants grown under space planted conditions. Evaluation of the parental lines for the traits measured was conducted from information obtained from analysis of variance, mean values and the protected LSD test. Similarly, information was obtained concerning differences between crosses and between generations within each cross. Mean values and standard deviation for each cross and generation are presented in Appendix Tables 7-11. The nature of gene action for grain yield, kernel weight and protein content was identified through combining ability analysis using parents and the F1 generation, while parents and F2 seeds were used for sedimentation volume and pigment content. F2 plants populations were examined in terms of their genetic variances and potential transgressive segregation for kernel weight, protein content sedimentation volume and pigment content. Phenotypic correlations between the traits are also presented.

Evaluation of the parents

Observed mean squares among the parental lines computed for the traits measured are presented in Table 1. Differences were found for all traits at the 0.05 or 0.01 level of probability. Coefficients of variation values were low (< 10) for all traits with the exception of grain yield that had a coefficient of variation of 21.56%. A significant effect of blocking was observed for protein content.

Protected LSD test results for the mean values are presented in Table 2.

Table 1. Observed mean squares for the parental lines for five traits when grown under space planted conditions at Pendleton, Oregon, 1989-90.

Source of variation	df	Mean Squares				
		Grain Yield (gms)	Kernel Weight (gms)	Protein Content (%)	Sedim. volume (ml)	Pigment content (ppm)
Blocks	2	166.29	0.226	0.453*	0.63	3.250
Parents	3	663.70**	1.140**	2.364**	262.77**	2.284
Error	6	52.22	0.099	0.066	2.62	0.306
C.V.(%)		21.6	3.8	5.0	3.7	9.6

*, ** Significant at the 0.05, 0.01 probability levels, respectively.

Table 2. Mean values for grain yield, two hundred kernel weight, protein content, SDS-sedimentation volume and pigment content of four parental lines from a 4x4 diallel experiment grown under space planted conditions in Pendleton, Oregon, 1989-90.

Parents	Means				
	Grain Yield (gms)	Kernel Weight (gms)	Protein Content (%)	Sedim. volume (ml)	Pigment Content (ppm)
WD4	55.02 a	8.867 c	14.878 e	53.500 j	5.518 k
WD6	25.17 b	7.867 d	16.729 g	47.430 i	5.523 k
Altar 84	22.18 b	7.567 d	15.855 f	44.733 i	7.031 l
Uc606	31.67 b	8.633 c	16.907 g	31.333 h	5.015 k

* LSD test; means with a letter in common are not significantly different for the trait at the 0.05 probability level.

For grain yield, the winter line WD4 was the highest yielding parent. Two kernel weight groups were identified. The low kernel weight group contained Altar 84 and WD6 while the high kernel weight group consisted of WD4 and UC606.

For protein content, line WD4 was the lowest, while selection UC606 had the highest value. The opposite was true for sedimentation volume, as WD4 had the highest sedimentation volume while UC606 was the lowest. WD6 could not be distinguished from UC606 for protein content nor was it different from Altar 84 for sedimentation volume. With protein content ranging from 14.8% to 16.9%, all the four parental lines can be considered as high protein lines under the conditions of the experiment.

Altar 84 had significantly higher pigment content, while no significant differences in pigment content were found between WD4, WD6 and UC606.

Analysis of variance for the whole experiment

Observed mean squares for all traits involving parents, F1 and F2 generations are presented in Table 3. The F-test revealed differences between crosses (main plot effects) for all traits. Differences were also found between blocks for grain yield, protein content and pigment content. Differences between generations were significant for all traits. This was true for the interactions between crosses and generations as well. Coefficients of variation were low (<8%), with the exception of grain yield and pigment content for which the coefficients of variation were 22.1% and 17.4%, respectively.

Table 3. Observed mean squares for all traits for parental lines, F1 and F2 generations from a 4x4 diallel experiment grown under space planted conditions in Pendleton, Oregon, 1989-90.

Source of variation	df	Mean Squares				
		Grain Yield (gms)	Kernel Weight (gms)	Protein content (%)	Sedim. Volume (ml)	Pigment Content (ppm)
Replications	2	1916.51**	3.02**	5.92**	4.23	8.41**
Crosses	11	890.95**	3.51**	5.70**	462.93**	3.90**
Error (a)	22	155.02	0.84	0.89	7.51	1.12
Generations	3	6262.14**	38.75**	3.39**	85.31**	32.33**
Cross x Generations	33	501.61**	1.51**	1.65**	92.66**	2.78**
Error (b)	68	92.623	0.45	0.31	6.00	0.90
C.V.(%)		22.1	7.5	3.5	5.6	17.4

** Significant at the 0.01 probability level.

Magnitude of heterotic effects

Observed means squares for heterotic effects, as measured by the deviation from the mid-parental value, are presented in Table 4. Differences existed between hybrid combinations in terms of heterosis for kernel weight, protein content and sedimentation volume. Differences in heterotic effects were not observed for grain yield and pigment content. Heterotic effects for sedimentation volume and pigment content were deviations of F2 samples from mid-parental samples.

Results of the LSD test performed on heterotic effects for kernel weight, sedimentation volume and protein content can be found in Table 5. Heterosis for kernel weight was generally important in combinations involving at least one high kernel weight parent, either WD4 or Uc606. The highest heterotic effect was observed when WD4 was used as female with Uc606 as male. This effect was higher than that of the reciprocal combination of the same cross. All crosses had a negative heterotic effect for protein content with the exception of the cross Altar84 x Uc606 and its reciprocal. None of the crosses differed in their heterotic effect from that of its reciprocal. This was also the case for sedimentation volume. The cross WD4 x WD6 and its reciprocal showed the highest positive heterosis for sedimentation volume. Crosses involving the weak gluten parent Uc606 were characterized by having the highest negative heterotic values for this trait.

Table 4. Mean squares for grain yield, kernel weight and protein content for heterotic effects in F1 plants and for sedimentation volume and pigment content for heterotic effects in F2 seeds from a 4x4 diallel cross grown under space planted conditions in Pendleton, Oregon, 1989-90.

Source of variation	df	Mean Squares				
		Grain Yield (gms)	Kernel Weight (gms)	Protein Content (%)	Sedim. volume (ml)	Pigment content (ppm)
Blocks	2	246.02	0.08	0.53	1.41	14.65
Crosses	11	277.78	2.22**	2.48**	29.21**	7.97
Error	18	126.32	0.39	0.53	6.07	4.89

** Significant at the 0.01 level.

Table 5. Magnitude and differences in heterotic effects in twelve hybrid generations from a 4x4 diallel cross grown under space planted conditions in Pendleton, Oregon, 1989-90.

Cross	Deviation from the mid-parent		
	Kernel weight (gms)	Protein Content (%)	Sedim. Volume (ml)
WD4xWD6	1.09 a	-1.03 fg	7.67 l
WD4xAltar	2.03 abc	-1.10 fg	1.5 jk
WD4xUc606	4.09 e	-1.07 fg	-1.5 ij
WD6xWD4	1.68 abc	-1.91 f	4.75 kl
WD6xAltar	1.10 ab	-1.41 fg	0.38 jk
Wd6xUc606	2.53 c	-0.64 fg	0.50 jk
AltarxWD4	2.11 abc	-0.45 fg	1.00 jk
AltarxWD6	2.20 bc	-1.79 f	1.00 jk
AltarxUc606	3.69 de	1.04 h	-1.33 ij
Uc606xWD4	2.48 c	-0.24 g	-1.67 ij
Uc606xWD6	2.73 cd	-0.14 gh	-2.00 ij
Uc606xAltar	2.79 cd	1.04 h	-5.00 i

LSD test; effects with a letter in common do not differ significantly at the 0.05 level.

Combining ability analysis

Differences between genotypes are a prerequisite for combining ability analysis. The observed mean squares for parental lines and F1 plants are shown in Table 6. Significant mean squares were observed for crosses for all traits. The coefficients of variation were low (<10%) for all traits with the exception of grain yield(15.9%) and pigment content (23.5%). Average plot means for all traits involving parents and F1 plants used in the diallel are shown in Appendix Table 6. No differences in mean values were observed between a cross and its reciprocal for any of the traits with the exceptions of the combination involving Uc606 and Altar84 for kernel weight and pigment content. Another exception was noted for the combination involving Uc606 and WD4 for pigment content.

Means squares for GCA, SCA and reciprocal effects were computed and are presented in Table 7. For sedimentation volume these represented means squares computed on F2 material. Significant GCA effects were detected for all traits indicating that additive gene action was involved. The same was true for SCA effects with the exception of pigment content where SCA effects were significant at a lower probability level. This indicates that non additive type of gene action was also present. No reciprocal effects were found for any trait except for pigment content.

General Combining Ability effects contributed by each parental line are presented in Table 8 along with the corresponding critical differences used for comparison.

Table 6. Mean squares for five traits for parental lines and F1s from a 4x4 diallel cross grown under space planted conditions in Pendleton, Oregon, 1989-90.

Source of variation	df	Mean Squares				
		Grain Yield (gms)	Kernel Weight (gms)	Protein Content (%)	Sedimentation volume (ml)	Pigment content (ppm)
Blocks	2	1192.3**	1.30*	1.39*	4.15	5.86
Crosses	15	1095.4**	6.01**	3.29**	202.29**	7.92**
Error	30	76.88	0.37	0.26	1.50	2.15
C.V.(%)		15.9	6.1	3.2	2.8	23.5

*, ** Significant at the 0.05, 0.01 levels respectively.

Table 7. Observed mean squares for general combining ability (GCA), specific combining ability (SCA) and reciprocal effects (REC) from a 4x4 diallel cross involving parental lines and F1 plants planted in Pendleton, Oregon, 1989-90.

Source	df	Mean Square				
		Grain Yield (gms)	Kernel Weight (gms)	Protein Content (%)	Sedim. Volume (ml)	Pigment content (ppm)
GCA	3	783.8**	2.85**	3.46**	317.34**	4.37**
SCA	6	507.4**	3.38**	0.93**	14.03**	1.79*
REC	6	12.8	0.21	0.08	0.70	2.62**
GCA/SCA		1.5	0.84	3.72	22.62	2.44
Error	30	25.6	0.12	0.09	0.50	0.72

*, ** Significant at the 0.05, 0.01 levels respectively.

Table 8. Estimates of general combining ability (GCA) effects for all traits from a 4x4 diallel cross grown in Pendleton, Oregon,1989-90.

Parents	General Combining Ability Effects				
	Grain Yield (gms)	Kernel weight (gms)	Protein Content (%)	Sedim. volume (ml)	Pigment Content (ppm)
WD4	14.60 b	0.19 d	-0.85 f	5.80 l	0.06 n
WD6	-6.93 a	-0.61 c	0.10 g	2.93 k	-0.98 m
Altar84	-5.15 a	-0.33 c	-0.004 g	0.03 j	0.81 n
UC606	-2.52 a	0.75 e	0.75 h	-8.76 i	-1.44 m
C.D.	4.96	0.35	0.28	0.69	0.83

C.D.: Critical difference to determine significance of a difference in GCA effects of two parental lines.
Parental lines with a same letter for a trait do not differ significantly in their GCA effect on the trait.

Winter line WD4 had a significantly higher GCA effect for grain yield and sedimentation volume, however it contributed the lowest GCA effect for protein content. WD4's GCA effect for kernel weight was positive and intermediate in magnitude. WD6 had negative GCA effect for kernel weight, grain yield and pigment content while it ranked second for sedimentation volume and protein content. Altar84 had a low GCA effect for grain yield, kernel weight, while its GCA effect on sedimentation volume and protein content was close to zero. However, it showed the highest GCA effect for pigment content. Selection Uc606 contributed the highest GCA effect for kernel weight and protein content, an intermediate value for grain yield and the lowest for sedimentation volume and pigment content.

Specific combining ability estimates are presented in Table 9. Greater SCA effect for sedimentation volume was found in the cross involving WD4 and WD6. Altar84 x Uc606 had the highest SCA effect for pigment content and for protein content. Cross combination involving the two high kernel weight lines, WD4 and Uc606 had the greatest SCA effects for kernel weight.

Reciprocal effects are shown in Table 10 for pigment content which was the only trait where such effects were significant. Differences existed for reciprocal effects among the different combinations.

Components of variation were computed and are presented in Table 11. They include a) the variation due to the experimental error, b) variation due to general combining ability effects, c) variation due to specific combining ability effects, and

Table 9. Estimates for specific combining ability effects for grain yield, kernel weight and protein content in the F1 generation, for sedimentation volume and pigment content in the F2 generation of a 4x4 diallel cross grown in Pendleton, Oregon, 1989-90.

		Parents		
Parents	Trait	WD6	Altar84	UC606
WD4	Grain Yield (gms)	1.46	13.34	14.69
	Kernel Wt. (gms)	-0.10	0.47	1.10
	Protein (%)	-0.08	-0.36	-0.59
	Sed.vol. (ml)	4.15	-0.11	-1.49
	Pigment (ppm)	-0.13	0.15	0.83
WD6	Grain Yield		10.20	4.62
	Kernel Wt.		0.29	0.74
	Protein		-0.70	-0.05
	Sed.vol.		0.76	-2.03
	Pigment		-0.52	-0.59
Altar84	Grain Yield			-0.70
	Kernel Wt.			0.99
	Protein			0.89
	Sed.Vol.			-0.88
	Pigment			1.21

Critical Difference to compare:	Grain Yield	Protein content	Sedim. volume	Pigment content
SCA(ij/ik)	8.59	0.50	1.20	1.44
SCA(ij/kl)	7.02	0.41	0.98	1.17

Female parents figure in the first column.

Table 10. Estimates of reciprocal effects for pigment content (ppm) in the F2 generation seeds from a 4x4 diallel cross grown in Pendleton, Oregon, 1989-90.

	Reciprocal effects		
Parents	WD4	WD6	Altar84
WD6	0.10		
Altar84	-0.23	0.68	
Uc606	-2.29	-0.13	-1.44

Critical difference to compare effects: 1.66

Table 11. Estimates of the components of variation for all traits using the analysis of a 4x4 diallel cross grown in Pendleton, Oregon, 1989-90.

	Estimates				
Component of variation	Grain yield (gms)	Kernel Weight (gms)	Protein Content (%)	Sedim. Volume (ml)	Pigment Content (ppm)
σ^2_{error} = MSError	25.629	0.124	0.087	0.501	0.718
$\sigma^2_{recip.}$	-6.415	0.043	-0.003	0.098	0.950
σ^2_{sca}	296.451	2.002	0.520	8.327	0.622
σ^2_{gca}	39.183	-0.034	0.324	38.044	0.333
$\sigma^2_{gca}/\sigma^2_{sca}$	0.132	0.017	1.246	4.569	0.535
$\sigma^2_{dominance} = \sigma^2_{sca}$	296.451	2.002	0.520	8.327	
$\sigma^2_{additive} = 2x\sigma^2_{gca}$	78.367	-0.069	0.648	76.088	

d) variation due to reciprocal effects. Estimates of the variation due to non additive gene action (SCA) were higher then those due to additive gene action (GCA) for grain yield and kernel weight. The opposite was true for sedimentation volume. These two components of variation were similar for protein content. Non additive and additive components of variation could not be derived for pigment content because reciprocal effects were detected suggesting the existence of maternal effects.

Variability generated in the F2 plants populations

Genetic variances for the traits measured for each F2 plants population resulting from the diallel cross are presented in Table 12. For sedimentation volume and pigment content these represent genetic variances among F3 seed samples. The greatest variability for grain yield was generally generated in crosses involving the two highest yielding lines, WD4 and Uc606. For kernel weight, lowest genetic variances were a characteristic of the crosses where Uc606 (high kernel weight) was used as parent. The greatest variability for kernel weight was observed in the cross WD4 x WD6, the two winter lines and in the cross WD4 x Altar84. In terms of protein content, the greatest genetic variability was found in the F2 resulting from crosses involving WD6 and Altar84 and WD4 and WD6. These populations were also characterized by notable differences in the variability for sedimentation volume. Genetic variances were similar between reciprocal crosses, except for the combination involving Altar84 and WD4.

Table 12. Magnitude of the genetic variance generated in 12 F2 plants populations from a 4x4 diallel cross grown in Pendleton, Oregon, 1989-90.

Cross	Genetic Variance				
	Grain Yield (gms)	Kernel weight (gms)	Protein Content (%)	Sedim. Volume (ml)	Pigment Content (ppm)
WD4xWD6	-.-	0.723	1.064	9.111	-.-
WD4xAltar	242.10	0.447	0.604	49.248	-.-
WD4xUc606	549.43	0.134	0.197	56.385	-.-
WD6xWD4	80.39	0.156	0.574	12.178	2.795
WD6xAltar	102.11	0.077	1.064	2.722	-.-
WD6xUc606	272.95	0.032	0.340	25.480	0.341
AltarxWD4	113.91	0.272	0.475	11.669	-.-
AltarxWD6	168.88	0.237	0.626	0.532	-.-
AltarxUc606	214.80	0.174	0.472	37.758	0.509
Uc606xWD4	268.10	0.145	-.-	63.009	-.-
Uc606xWD6	198.98	-.-	0.447	18.015	-.-
Uc606xAltar	319.64	-.-	0.535	23.419	-.-

-.- : Undetected genetic variance.

The largest variability was generated by the cross involving the lines with the largest difference in sedimentation volume (WD4 and Uc606). The lowest variability was associated with the cross involving lines with similar sedimentation volume (Altar84 and WD6). With the exception of three crosses, no genetic variability was detected for pigment content. The exceptions were, WD4 x WD6, WD6 x Uc606 and Altar x Uc606. The first two crosses did not involved parents that differed in pigment content.

Potential transgressive segregation

Frequencies of F2 plants whose performance exceeded the best parent for a given trait are presented in Table 13. Unusually high frequencies of such F2 progenies were found for kernel weight. The lowest frequencies were found in the cross WD4 x WD6 and its reciprocal. However, when winter line WD4 was crossed with either of the spring parents, a greater frequency was observed. This was the case even when WD4 was crossed with Altar 84 that was similar to WD6 for kernel weight. High frequencies of F2 plants exceeding the best parent for kernel weight were observed in all crosses were the spring line Uc606 was used. F2 plants that exceeded the best line in the study (WD4) were found in crosses where this line was not a parent. Such plants were particularly numerous in cross Altar 84 and Uc606 and its reciprocal.

For protein content, an unusually high frequency of F2 plants exceeding the best parent was observed in the cross WD4 x WD6.

Table 13. Frequency of F2 plants showing better performance than the best parent for kernel weight, protein content, sedimentation volume and pigment content in 12 populations generated by a 4x4 diallel cross grown in Pendleton, Oregon, 1989-90.

Cross	Frequency (%)			
	Kernel weight	Protein Content	Sedim. Volume	Pigment Content
WD4xWD6	5	37	14	0
WD4xAltar	20	4	0	0
WD4xUc606	31	0	0	0
WD6xWD4	0	10	10	0
WD6xAltar	33	15	0	0
WD6xUc606	33	6	2	2
AltarxWD4	11	11	4	0
AltarxWD6	31	2	0	0
AltarxUc606	42	8	7	2
Uc606xWD4	46	0	0	2
Uc606xWD6	20	7	2	0
Uc606xAltar	42	7	0	0

Spring line Uc606 and winter line WD6 had similar maximum protein content (17.5%), but the former failed to generate any progeny that had a protein content greater than 17.5%. Plants with protein content that exceeded that of Uc606 (line with the highest protein content in the study) were found even in crosses not involving either of the lines with higher maximum protein content (WD6 or Uc606).

Transgressive segregation for sedimentation volume was observed particularly in crosses involving the two winter lines which had the highest sedimentation volume. Combinations involving Altar 84 as female and either of spring parent Uc606 or winter line WD4 yielded few transgressive segregants for sedimentation volume.

F3 Seed samples that outperformed the best parent for pigment content were rare. Two F2 plants, from cross Altar 84 x Uc606 exceeded the maximum pigment content of Altar 84 (8.7 ppm).

Correlations between traits:

Simple correlation coefficients between traits are shown in Table 14. No significant correlation was found between sedimentation volume and grain yield in any of the crosses. A correlation between sedimentation volume and kernel weight was detected in only one F2 population (Altar84 x WD4) which cannot be considered as substantial ($R^2 = 0.13$). Only four of twelve crosses showed significant correlations between sedimentation volume and protein content. However, the corresponding coefficients were low and again cannot be considered

as indicator of an effective relationship.

In general, pigment content was found to be independent from all other traits. A positive association between pigment content and sedimentation volume was however detected in the winter x winter populations, while a negative association between the same traits was found in one of the spring x spring population.

For protein content, a highly significant negative correlation with grain yield was detected. The coefficients ranged from low to moderately high (0.36-0.61) with 10 of the 12 populations exhibiting negative values. Protein content was found to be negatively correlated with kernel weight in three of twelve crosses and only two crosses showed a moderate to high correlation between the two traits.

Table 14. Correlation coefficients between traits within F2 populations generated from a 4x4 diallel grown under space planted conditions in Pendleton, Oregon, 1989-90.

	Correlation coefficients								
Variable 1	Sedimentation Volume				Pigment Content			Protein Content	
Variable 2 Crosses	Grain Yield	Kernel Weight	Protein content	Pigment content	Grain Yield	Kernel Weight	Protein content	Grain Yield	Kernel Weight
WD4xWD6	-0.12	0.25	-0.40*	0.34*	-0.15	-0.20	0.15	-0.44**	-0.76**
WD4xAlt	0.05	-0.18	-0.36*	0.28	0.26	-0.17	-0.16	-0.41**	-0.31*
WD4xUc606	0.02	-0.21	-0.24	0.12	0.06	-0.18	0.12	-0.41**	-0.23
WD6xWD4	0.22	-0.19	-0.54*	0.51*	0.06	-0.33	-0.22	-0.45*	-0.31
WD6xAlt	-0.07	-0.16	-0.27	-0.09	-0.31*	-0.27	0.17	-0.45**	-0.20
WD6xUc606	0.01	0.11	-0.38*	-0.14	0.11	-0.18	-0.02	-0.43**	-0.27
AltxWD4	0.17	-0.36*	-0.06	0.05	-0.01	-0.09	0.09	-0.36*	-0.47**
AltxWD6	0.02	-0.05	-0.11	0.11	-0.08	-0.31*	-0.08	-0.17	-0.30*
AltxUc606	-0.06	0.05	-0.08	-0.37*	0.09	0.10	-0.12	-0.58**	-0.12
Uc606xWD4	0.08	-0.17	-0.05	-0.03	-0.13	-0.4	-0.15	-0.11	0.23
Uc606xWD6	0.02	-0.06	-0.26	-0.16	0.12	-0.17	-0.17	-0.61**	-0.26
Uc606xAlt	0.24	0.06	-0.26	-0.20	-0.18	-0.28	0.31	-0.51**	-0.05
Overall	-0.21**	-0.39**	-0.14**	0.16**	-0.12**	-0.25**	0.04	-0.49**	-0.30**

*, ** Significant at the 0.05, 0.01 probability levels respectively. (N=45)

DISCUSSION

Durum wheat breeders are faced with the challenge of producing cultivars that meet strict quality requirements of the milling and pasta manufacturing industries. This is a major concern, particularly when additional genetic variation for yield and related traits is sought by combining two different gene pools through the systematic hybridization of winter and spring wheat lines. When such a strategy is used, it is critical to be able to efficiently evaluate the quality characteristics of the spring x winter breeding populations as early as possible. Undesirable lines or families are likely to exist in spring x winter breeding populations because of the often undesirable quality characteristics contributed by the winter parent. It is well established that a complete evaluation of the quality characteristics of a breeding line can only be achieved at the latest stages of the breeding process, when near homozygosity is attained and environmental effects can be estimated. Nevertheless, breeders can capitalize on the tests performed on low amounts of seeds to screen their early segregating material for promising lines. Consequently, the probability of producing good quality advanced lines can be maximized.

Quality is mainly the result of complex interactions between different protein entities synthesized in the durum wheat endosperm. This interaction is responsible for the milling, processing and cooking properties of a durum cultivar. One very important aspect of quality is gluten strength which influences both

rheological (processing) properties and cooking characteristics. In the present study, the nature of the gene action was investigated involving the inheritance of gluten strength as measured by the SDS sedimentation test (Dick and Quick, 1983) along with that of other grain characteristics which might be related or influence gluten strength. These traits are grain yield, kernel weight and total protein content of the grain. The SDS sedimentation test is widely used in the evaluation of gluten strength. However, little information exists on the nature of gene action involving the expression of gluten strength. Most of the genetic studies deal with mixogram scores as a measure of gluten strength. The other important quality trait of durum wheat is color as determined by the grain carotenoid pigment content. A study of the gene action involved in the inheritance of this trait was also undertaken.

Results from this study and the populations employed suggested that substantial genetic variability existed among the parental lines used, justifying an analysis of the type of gene action controlling the expression of each trait studied. This was accomplished by obtaining combining ability estimates for the traits of interest. Those traits that responded to additive gene action were identified in term of significant mean squares values associated with GCA. It is only this additive portion of the total genetic variation that is available for making effective progress through early generation selection in self pollinating species like durum wheat. Deviation from the additive scheme are reflected by significant means squares values for SCA. Under the experimental conditions of this study, all traits were

found to be controlled in part by additive type of gene action as shown by the highly significant mean squares for GCA. Highly significant SCA mean squares also were found suggesting the involvement of non additive type of gene action in all the traits as well.

Grain yield and kernel weight:

The relative magnitudes of GCA and SCA mean squares suggests a moderate predominance of the additive gene action in the control of grain yield. These results are in agreement with those reported by Rehman (1978) for spring wheat, by Schmidt et al. (1978) for winter wheat and by Quick (1978) for spring durum wheat. The two latter studies did not report any significant mean squares for SCA. Very little genetic variability, if any, could be detected, in the present study, in the winter x winter crosses. However, substantial genetic variability for grain yield was observed in the winter x spring crosses. Although the two spring lines did not significantly differ from line WD6 for grain yield, they did result in considerable genetic variability when crossed with the high yielding winter parent WD4. This illustrates the suitability of combining spring and winter germplasm for yield enhancement. Important variation for yield was also observed in the spring x spring populations.

Under the experimental conditions, an unusually high SCA means square was found for kernel weight suggesting the importance of non additive type gene action controlling the expression of this trait. Highly significant SCA mean squares for kernel weight were reported in spring wheat by Sayed (1978) and by

Schmidt et al. (1978) in hard red winter wheat. Quick (1978) found that SCA effects were not significant in F1s from a diallel involving an international array of spring durum wheats. In the present study, non additive gene action differentially influenced the F1 progenies toward higher kernel weights as suggested by the positive heterotic effects found in all crosses. These heterotic effects might have been somewhat inflated by the space planting in the fall of spring lines that resulted in a unusually profuse tillering. Due to a compensating effect of the major components of yield, the parental lines, devoid of hybrid vigor, were characterized by a low kernel weight. This environmental effect on the parental lines and residual non additive type of gene action are likely to be the causes of the high frequencies of F2 plants exceeding the best parent for kernel weight. These effects are confounded with transgressive segregation that is due to additive type gene action. Consequently, transgressive segregation for kernel weight can be assessed more accurately in subsequent generations when non additive gene action is reduced. The predominance of non additive gene action is in agreement with the fact that kernel weight is largely dependent on the environment and on other yield components, especially kernels per spike (Haugerud and Cantrell, 1983), tiller number (Quick, 1978) or number of heads per plant (Joppa and Williams, 1988). These results suggest that selection for high kernel weight in the populations studied should be delayed to the later generations as one half on the non additive gene action will be lost each generation of selfing.

Protein content:

Protein content appeared to be controlled largely by additive type gene action although the mean squares for SCA were highly significant. No reciprocal effects were detected in the expression of the trait. The non additive effect was generally directed in favor of the lowest protein parent as indicated by the negative heterotic effect in most crosses. These results are in agreement with most of those reviewed by Porceddu et al. (1983) and particularly with those reported by Mihaljev et al. (1978) from a 8x8 diallel cross in bread wheat. From the results of this study, we can suggest that segregates with highest protein content are most likely to occur from crosses involving high protein parents. However, because the expression of protein content is largely affected by the environment (Porceddu et al., 1983), a reliable identification of the high protein segregates in early generation, when the environmental effect cannot be assessed, is not possible. For this reason the high frequency of F2 plants exceeding the best parent in protein content should be considered with caution when making inferences concerning potential transgressive segregation. The latter is likely to be confounded with non additive type gene action and with environmental effects.

Differences in the genetic variance in the 12 F2 populations were not striking and no conclusion could be safely drawn as to which cross generated the maximum genetic variability for protein content. This could be explained by the fact that the parental lines were relatively similar in protein content. The results of this study could justify a program of selection for high protein content in the late generations (F4, F5) when the non additive type gene action is no longer an

issue.

Particular attention should be given to the negative correlation between total protein content and grain yield. This correlation was highly significant in most of the F2 populations screened in this study and was substantial in several populations. This association adds to the difficulty of selecting simultaneously for these two complex traits if they were to be considered as the only priority in a breeding program.

Sedimentation volume:

Sedimentation volume is a reliable, repeatable and widely used estimator of Gluten strength (Quick and Donnelly, 1980. Dexter et al., 1980. Dick and Quick, 1983. McDonald, 1985). The results from this study strongly suggest that this trait is controlled mainly by genes functioning in an additive manner. Mean squares associated with SCA (in F2 seeds) were highly significant but much smaller in magnitude than the mean squares associated with GCA. Heterotic effects (in F2 seeds) were of importance only in the winter x winter crosses and in the spring x spring cross Uc606 x Altar84. In other crosses they did not differ significantly from the mid parental values. It was also found that the best combiners in crosses for sedimentation volume, ie WD4 and WD6, were the two parental lines that had the highest sedimentation volumes. Also, the highest value of SCA effect was for the cross involving these same lines. Consequently, the evidence suggests that additive gene action prevailed in the expression of gluten strength as estimated by the SDS sedimentation test. This test should thus

provide durum wheat breeders with a reliable tool to screen for strong gluten lines in the early generations (F2, F3). Because of its effectiveness in weeding out weak gluten types from breeding populations, this test would allow breeders to work within a gene pool with acceptable gluten strength. These results are in agreement with those of Dick and Quick (1983) and Dexter and Matsuo (1980) where it was suggested that the SDS sedimentation test could be adopted to efficiently screen early generation material for gluten strength using a limited amount of seed.

The genetic variances for sedimentation volume among F3 seed samples obtained from single F2 plants were highly variable. The lowest variability was found within populations from crosses between parents that had similar sedimentation volume, ie WD6 x Altar84 or WD4 x WD6 and their reciprocals. Consequently, genetic variability appears to be dependent more on the difference in sedimentation volumes of the parents than on the type of cross considered. Nevertheless, it can be expected that crossing spring and winter durum wheats is likely to result in more genetic variability for sedimentation volume as spring durums usually differ markedly from winter durums in their gluten strength. In this study, the winter lines had higher sedimentation volumes than the spring lines. This is an exception as spring durums usually have stronger gluten than winter durums.

Because non additive type gene action was not important for gluten strength which is not strongly affected by the environment, the frequency of samples

exhibiting a higher sedimentation volume than the best parent can be seen as an indication of transgressive segregation. As expected from a trait that is largely under the control of additive type gene action, most of the transgressive segregation was observed in crosses involving lines with the highest sedimentation volume. Nevertheless, Altar 84 (intermediate sedimentation volume) contributed to the achievement of transgressive segregation when crossed with WD4. This illustrates another advantage of crossing spring durums with winter durums, that is to accumulate favorable alleles or genes for gluten strength and possibly for quality in general. Although gluten strength is a property of the protein complex of the durum wheat endosperm, it does not appear to be correlated to total protein content. This lack of substantial association between the two traits suggested by the results of this investigation agrees with the conclusions of several authors (Quick and Donnelly,1980. Dick and Quick, 1983. Autran et al., 1986). The absence of a correlation between these two traits is further supported by the fact that, despite of the parental lines and the environmental conditions resulting in a narrow range of protein content (14.9% to 16.9%), F2 individuals produced seed samples that were highly variable in their sedimentation volumes. Similar lines of evidence were reported by Fertini (1988) who found that semolina samples in the same protein range could have cooking quality varying from excellent to very poor. Sedimentation test values were not correlated with grain yield nor with kernel weight. These results suggest that selection on the basis of sedimentation volume per se should not result in selecting agronomically

unsuitable types or vice versa.

Reciprocal effects were not significant thereby excluding any maternal effect in the present material despite the fact that gluten strength is the result of interaction between endospermic proteins. Traits expressed in the endosperm tissue can be expected to show some maternal effects involved in their inheritance. Under the present experimental conditions F2 seed samples from different crosses did not differ in their mean sedimentation volumes from their reciprocals. Comparing crosses and their reciprocals in the F1 generation was not possible, using sedimentation tests, as it would have required running test on F1 seeds (from crossed heads). Theoretically, F1 seeds would have been a choice material for combining ability analysis. However, these are usually limited in number and size, often shrivelled as they do not grow in normal conditions.

The endospermic nature of this trait puts it under a triploid genetic control. Consequently, two doses of the female genes are involved in the expression of the trait. This is supported by the fact that dosage effect were found in the inheritance of gliadin bands 42 and 45 (Ducros and Hare, 1983) which expression is tightly linked to gluten properties. Dosage effects could not be demonstrated in this study as the number of genes or alleles contributed by each parent was not known.

Carotenoid pigment content:

Semolina color characterization requires a relatively large amount of seeds. An alternative method was used in this study and consisted in measuring the

absorbance of a pigment extract from wheat wholemeal. This experimental method resulted in relatively high coefficients of variation in the analysis of variance suggesting that some variability could not be accounted for. This was probably due to the presence of practically invisible suspensions in some extracts. These impurities could not be removed completely and could have affected the spectrophotometer readings. Despite this randomly occurring artifact, the method used permitted the identification of general trends related to the gene action involved in the inheritance of pigment content. Such results are in agreement with the findings of several other authors working on semolina color. Combining ability analysis in the F2 generation (seeds from F1 plants) revealed that additive and non additive gene action were present which influenced the expression of pigment content with the additive gene action prevailing. However, non additive type gene action can be considered as important in this case as the observed mean square for SCA was obtained from F2 tissue that is less heterozygous than F1 tissue material. The parental line with the highest pigment content had the highest GCA effect and the cross between the two spring lines resulted in the greatest SCA effect. Lee et al. (1976) reported the coexistence of both types of gene action influencing the expression of pigment content. From a diallel analysis for semolina color, Lee et al.(1976) reported that the expression of semolina color was influenced by the environment. Similar results were reported by Johnston et al.(1983). No genetic variation could be detected in the F2 population with the exception of populations from crosses WD6 x Uc606, Altar 84 x Uc606 and Uc606

x WD4. No logical pattern existed to explain these exceptions. Pigment extracts from F2 seed samples having greater absorbance than the best parent were identified mainly in the winter x winter populations despite the fact that the two winter parents were similar in terms of their pigment content.

The results suggest that some maternal effect was involved in the genetic control of pigment content in the material used. This was revealed by the highly significant mean square associated with reciprocal effects. It is reasonable to expect the existence of some maternal effect as carotenoids are synthesized in the endosperm. The endospermic nature of pigment content (triploid genetic control coupled with the existence of maternal effects) makes the nature of its inheritance difficult to investigate through conventional (in the F1 generation) combining ability analysis. Such analysis implies the determination of pigment content from seeds developed on crossed heads that are limited in number. Furthermore, combining ability analysis in the F2 generation seeds would be more accurate if population means were computed from data obtained on a single seed basis. Technical limitations (minimum of 3 grams of seed needed) do not allow for such evaluation of pigment content. No maternal effect was reported for semolina color and more investigation is needed with lines covering a wider range of pigment content in order to confirm the existence of maternal effect associated with the inheritance of the trait.

CONCLUSIONS

The following conclusions are drawn from results obtained through a combining ability analysis of a 4x4 diallel cross involving two winter lines and two spring lines. Data collected on F2 populations from these matings allowed for the estimation of the genetic variability generated in each cross and for the investigation of the possible association between the different traits.

1- Early generation selection for high kernel weight appears to be difficult as it is largely under the control of non additive type gene action and the influence of the environment. Selection for kernel weight should be addressed considering other yield components, especially tiller number and kernels per spike.

2- Although protein content is an important characteristics of durum wheat, it can not be used alone as a selection criteria for quality. As protein content is controlled by both additive and non additive gene action, it appears as a difficult trait to select for in the early generations, especially when the environmental effect is not assessable. Furthermore, selection for high protein content could substantially decrease the chances of breeding high yielding lines as the two traits are negatively correlated.

3- Gluten strength, as measured by the SDS sedimentation test is largely controlled by additive gene action. Sedimentation volume is a highly

heritable trait that can be used to efficiently select for strong gluten lines in the early stages of a breeding program. It should allow the breeder to maximize the chances of producing good quality advanced lines before an extensive quality testing is possible. As it allows for the discrimination between lines with similar protein content, it can be considered as an indicator of protein quality.

4- Selection for carotenoid pigment content as measured by spectrophotometer readings of pigment extracts should be effective among lines in late generations. It also appeared that more work is needed to perfect the method used and to assess its reliability as predictor of semolina color. Suggested maternal effect, if confirmed, should be considered when choosing parents in crossing program.

5- The use of spring x winter crosses to improve quality characteristics of a winter durum line is justified by the important genetic variability generated for gluten strength. This enhanced variability provide the breeder with material from which to select genotypes with superior quality characteristics. This is valid in selecting for either spring or winter types.

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APPENDIX

Appendix Table 1. Description of the parental lines used in the diallel cross.

WD4:
A winter durum line introduced from Turkey also designated as H9072-12. It is white awned line with large spikes. It has yielded 3.49 tons per hectare in yield trials conducted in Pendleton in 1989-90. It is characterized by high test weight and thousand kernel weight. It has a strong gluten as estimated by its sedimentation volume and an intermediate pigment content.

WD6:
A winter durum breeding line introduced from Turkey also designated as H9072-10. It is black awned with small spikes. It has not been evaluated for yield capacity. It is characterized by a low kernel weight, an intermediate sedimentation volume and pigment content.

Altar 84:
A spring durum cultivar developed at CIMMYT. and widely grown in Mexico. It is a high yielding, black awned variety. It has a yield potential above 4 tons per hectare in the Pendleton area. It has large spikes and kernels of intermediate size. It produces strong gluten as estimated by the SDS sedimentation test and has a high carotenoid pigment content.

Uc606:
A black awned spring durum breeding line from California that has a 3.8 tons per hectare yield potential in the Pendleton area. It has an intermediate size spike, a high kernel weight. It produces a weak gluten and intermediate pigment content.

Appendix Table 2. Summary of the climatic conditions for the Pendleton, Oregon experimental site during the growing season of 1989-90.

Month	Precipitation (mm)	Temperature (F)	
		Maximum	Minimum
September	6.10	79.5	41.4
October	25.40	64.5	35.0
November	41.91	53.9	33.6
December	12.45	39.8	25.9
January	36.32	44.5	31.1
February	16.00	45.9	25.7
March	48.01	56.7	31.3
April	44.96	67.6	37.5
May	54.36	68.0	42.0
June	17.78	77.8	49.2
July	9.40	92.0	53.4
August	19.30	87.5	53.4

Appendix Table 3. Procedure and calibration of the apparatus for NIR determination of total grain protein content in durum wheat.

1- Preparation of the samples: cleaned seeds from each sample were ground in a UDY-cyclone sample mill equipped with a 1 millimeter sieve. Samples were loaded into the apparatus according to the operating instructions provided by the manufacturer.

2- Calibration of the apparatus: the Technicon InfraAlyzer 400 was used in the Near Infrared Reflectance analysis of the samples. To obtain protein content in percent, the calibration equation used was that adopted by the Federal Grain Inspection Service (FGIS) and is based on the reflectance measured with three filters :

$$\% \text{ protein} = K_0 + K_1 x (ABS_{f20}) + K_2 x (ABS_{f14}) + K_3 x (ABS_{f10})$$

where:
* K1,..., K3 are the coefficient determined for each filter.
* ABS are the absorbance of the sample measured by reflectance (absorbance = Log (1/reflectance)).

The values were the following:

Filter number:	20	14	10
Coefficient:	-137.1	-298.6	404.6

* K_0 represent the bias and was determined and adjusted for by comparing technicon readings to known values from 18 samples collected from durum lines varying from 9 % to 18 % in protein content, as determined by the Kjeldahl method. The value of K_0 was 11.90.

Appendix Table 4. Procedure used to evaluate gluten strength by the SDS sedimentation test (Dick and Quick, 1983).

- Stock solutions of 85% lactic acid:distilled water (1:8 v/v) and of 2% SDS were prepared every day during the testing period.

- Samples were ground in a UDY-cyclone sample mill equipped with a 1 millimeter sieve.

- Six grams of whole meal were weighted and placed in 100 ml graduated glass cylinders. The wholemeal was suspended in 50 ml of distilled water by shaking vigorously for 15 seconds. Similar shaking was repeated twice at 2 and at 4 minutes.

- 50 ml of SDS solution and 1 ml of lactic acid solution were added and the cylinders were inverted 4 times. Inverting was repeated 3 more times at 2, 4 and 6 minutes.

- The content of the cylinder was allowed to settle for 10 minutes after which the volume of the sediments was recorded.

Appendix Table 5. Procedure for pigment content determination. (Modification of the AACC method 14-50).

- 3 grams of wholemeal were placed into 50 ml Nalgene centrifuge tubes with 15 ml of water saturated N-Butanol solution.

- Tubes content was vortexed at maximum speed for 10 seconds.

- Extraction was carried out for 2 hours. Tubes were vortexed every half hour during the extraction.

- The tubes were centrifuged for 15 minutes at 3500 rpm.

- Clear extract (supernatant) was filtered through a whatman fiberglass filter paper, grade GF/A, into small clean test tubes.

- Pigment extracts were immediately scored for their absorbance at a wavelength of 440 nm using a spectronic 1001 split-beam spectrophotometer against a water saturated solution of N-Butanol as blank.

_ Absorbance was multiplied by 30.1 and results were reported in p.p.m.

Appendix Table 6. Plot Means values for five traits measured on parental lines and F1s from a 4x4 diallel cross planted in Pendleton, Oregon, 1989-90.

		Means			
Parents	Traits	WD4	WD6	Altar 84	Uc606
WD4	Grain Yield	55.016 cde	62.235 cd	77.263 ab	82.450 a
	T.H.K.Wght.	8.865 fg	9.220 fg	10.307 de	12.453 a
	Protein	14.978 e	14.948 e	14.050 f	14.880 ef
	Sed.Vol.	53.503 b	58.333 a	50.333 c	40.000 f
	Pigment	5.518 bc	5.298 bc	7.054 bc	4.966 c
WD6	Grain Yield	66.620 bc	25.172 g	48.160 de	48.630 de
	T.H.K.Wght.	9.677 ef	7.818 hi	9.037 fg	10.753 cd
	Protein	14.704 ef	16.729 ab	15.242 ed	16.550 abc
	Sed.Vol.	56.333 a	47.427 d	47.667 d	37.333 gh
	Pigment	5.107 bc	5.523 bc	6.231 bc	4.665 c
Altar 84	Grain Yield	78.920 ab	58.690 cde	22.183 g	45.410 ef
	T.H.K.Wght.	10.273 de	9.593 efg	7.556 i	11.903 ab
	Protein	14.824 ef	14.765 ef	15.855 cd	17.208 a
	Sed.Vol.	50.000 c	48.667 cd	44.733 e	35.333 hi
	Pigment	7.505 ab	4.876 c	7.031 bc	6.953 bc
Uc606	Grain Yield	81.700 a	52.325 cde	48.233 de	31.674 fg
	T.H.K.Wght.	11.553 abc	10.947 bcd	10.830 cd	8.621 gh
	Protein	15.047 ed	16.352 bc	17.372 a	16.907 ab
	Sed.Vol.	40.000 f	38.000 fg	34.333 i	31.183 j
	Pigment	9.551 a	4.921 c	9.823 a	5.015 c

LSD test; means with a letter in common for a trait are not significantly different at the 0.05 level.

Appendix Table 7. Means and standard deviations for grain yield for parents, F1 and F2 generations from a complete 4x4 diallel experiment grown in Pendleton, 1989-90.

		CROSS					
GEN		WD4xWD6	WD4xALT	WD4x606	WD6xWD4	WD6xALT	WD6x606
P1	Mean	54.77	54.58	53.00	13.64	24.64	28.50
	Std.	19.21	20.62	20.88	2.17	11.59	10.24
P2	Mean	25.49	21.59	26.90	57.86	24.21	30.33
	Std.	12.11	8.23	18.44	5.09	7.25	8.28
F1	Mean	62.25	77.26	82.45	66.62	48.16	48.63
	Std.	13.39	16.99	9.44	17.15	21.37	11.38
F2	Mean	17.90	55.54	58.37	29.46	31.77	45.09
	Std.	3.97	7.12	14.76	3.51	1.76	4.72
GEN		ALTxWD4	ALTxWD6	ALTx606	606xWD4	606xWD6	606xALT
P1	Mean	14.02	20.22	23.97	32.51	41.77	32.62
	Std.	8.99	3.53	7.33	9.27	5.93	9.37
P2	Mean	54.59	25.19	25.91	55.30	29.47	25.53
	Std.	14.03	7.03	6.49	15.08	11.05	15.69
F1	Mean	78.92	58.69	45.65	81.70	37.55	48.23
	Std.	5.80	5.36	11.63	18.18	25.90	6.35
F2	Mean	45.41	42.05	48.78	64.57	39.92	51.19
	Std.	7.30	5.91	3.02	6.49	7.60	6.98

Appendix Table 8. Means and standard deviations for two hundred kernel weight for parents, F1 and F2 generations from a complete 4x4 diallel experiment grown in Pendleton, 1989-90.

		CROSS					
GEN		WD4xWD6	WD4xWD6	WD4x606	WD6xWD4	WD6xALT	WD6x606
P1	Mean	8.75	9.17	8.87	7.66	8.19	8.26
	Std.	0.38	0.34	0.23	0.23	0.34	1.59
P2	Mean	7.51	7.38	7.86	8.65	9.08	8.19
	Std.	0.21	0.34	1.81	1.26	1.24	0.74
F1	Mean	9.22	10.31	12.45	9.68	9.04	10.75
	Std.	0.74	0.69	0.94	1.08	1.14	0.50
F2	Mean	7.43	8.86	9.43	8.28	8.23	9.03
	Std.	1.01	0.37	0.40	0.27	0.16	0.44
GEN		AltxWD4	ALTxWD6	ALTx606	606xWD4	606xWD6	606xALT
P1	Mean	6.94	7.18	7.89	9.01	9.29	8.84
	Std.	0.07	0.51	0.51	0.68	0.86	0.49
P2	Mean	8.60	7.60	8.54	9.14	7.62	7.24
	Std.	0.59	0.48	0.23	0.12	0.36	0.36
F1	Mean	10.27	9.59	11.90	11.55	9.46	10.83
	Std.	0.89	0.45	0.48	0.26	2.60	0.57
F2	Mean	8.82	8.38	9.72	9.84	9.17	9.49
	Std.	0.50	0.28	0.36	0.11	0.49	0.05

Appendix Table 9. Means and standard deviations for protein content for parents, F1 and F2 generations from a complete 4x4 diallel experiment grown in Pendleton, 1989-90.

		CROSS					
GEN		WD4xWD6	WD4xALT	WD4x606	WD6xWD4	WD6xALT	WD6x606
P1	Mean	15.38	14.73	14.89	17.26	16.47	16.81
	Std.	0.11	0.62	0.43	0.01	0.83	1.46
P2	Mean	16.58	15.56	17.02	15.34	15.98	17.56
	Std.	0.60	0.30	1.14	0.99	0.27	0.80
F1	Mean	14.95	14.04	14.88	14.70	15.24	16.55
	Std.	0.45	0.34	0.11	1.03	1.07	0.66
F2	Mean	17.45	15.34	15.73	16.77	16.49	17.15
	Std.	1.14	0.43	0.53	0.50	0.61	0.35
GEN		ALTxWD4	ALTxWD6	ALTx606	606xWD4	606xWD6	606xALT
P1	Mean	16.03	16.04	15.55	15.93	17.33	16.80
	Std.	0.37	0.18	0.97	0.76	0.99	0.19
P2	Mean	14.88	17.06	16.79	14.65	16.18	15.85
	Std.	0.84	0.25	1.16	0.17	0.27	0.58
F1	Mean	14.82	14.76	17.20	15.05	17.62	17.37
	Std.	0.88	0.19	0.34	0.42	2.27	0.51
F2	Mean	15.58	15.80	16.53	15.24	16.83	16.40
	Std.	0.60	0.31	0.49	0.27	0.63	0.53

Appendix Table 10. Means and standard deviations for sedimentation volume for parents, F1 and F2 generations from a complete 4x4 diallel experiment grown in Pendleton, 1989-90.

		CROSS					
GEN		WD4xWD6	WD4xALT	WD4x606	WD6xWD4	WD6xALT	WD6x606
P1	Mean	54.00	53.00	52.00	49.50	47.50	43.00
	Std.	2.00	4.00	3.00	0.71	3.12	6.00
P2	Mean	47.33	44.66	31.00	55.00	44.50	30.67
	Std.	4.62	1.53	1.00	1.00	0.71	1.15
F1	Mean	58.33	50.33	40.00	56.33	47.67	37.33
	Std.	2.52	1.53	0.0	1.53	1.15	0.58
F2	Mean	51.54	42.54	36.85	50.20	43.25	36.13
	Std.	2.48	1.10	3.66	4.48	1.55	2.87
GEN		ALTxWD4	ALTxWD6	ALTx606	606xWD4	606xWD6	606xALT
P1	Mean	44.00	46.67	43.67	30.00	32.00	34.67
	Std.	2.83	2.89	1.15	2.00	3.46	6.43
P2	Mean	54.67	48.67	29.67	52.33	50.00	44.00
	Std.	1.15	1.15	0.58	2.52	1.41	1.73
F1	Mean	50.00	48.67	35.33	40.00	35.83	34.33
	Std.	1.00	1.15	1.53	0.00	3.88	0.58
F2	Mean	48.07	44.96	34.49	37.82	36.54	32.98
	Std.	2.80	0.41	2.60	1.80	0.94	1.14

Appendix Table 11. Means and standard deviations for pigment content for parents, F1 and F2 generations from a complete 4x4 diallel experiment grown in Pendleton, 1989-90.

		CROSS					
GEN		WD4xWD6	WD4xALT	WD4x606	WD6xWD4	WD6xALT	WD6x606
P1	Mean	5.43	5.58	5.24	5.61	5.81	5.90
	Std.	0.28	0.57	0.76	0.19	1.45	0.90
P2	Mean	4.96	7.81	4.86	6.21	6.56	4.99
	Std.	0.29	1.52	1.01	1.27	1.19	1.01
F1	Mean	5.30	7.05	4.97	5.11	6.23	4.66
	Std.	0.29	2.35	1.64	0.15	1.87	0.50
F2	Mean	4.57	4.16	3.83	4.49	4.17	3.93
	Std.	0.18	0.42	0.24	0.48	0.08	0.22
GEN		ALTxWD4	ALTxWD6	ALTx606	606xWD4	606xWD6	606xALT
P1	Mean	9.62	6.50	7.23	4.65	4.90	4.91
	Std.	0.02	1.36	1.92	0.96	1.32	1.11
P2	Mean	5.34	5.46	5.31	5.32	5.39	6.95
	Std.	0.37	0.79	0.98	0.30	0.47	1.53
F1	Mean	7.50	4.88	6.95	8.05	5.46	8.85
	Std.	2.06	0.25	1.96	2.32	1.07	1.57
F2	Mean	4.19	4.41	4.21	3.72	3.99	3.69
	Std.	0.19	0.11	0.58	0.18	0.03	0.13