Chromosome 7D of *Triticum aestivum* (cv. Canthatch): Effects on milling and baking quality and degree of differentiation from chromosome 7D of *Triticum tauschii*.

by

GREGORY A. PENNER

A thesis
presented to the University of Manitoba
in partial fulfillment of the
requirements for the degree of
Master's of Science
in
Department of Plant Science

Winnipeg, Manitoba

CHROMOSOME 7D OF *TRITICUM AESTIVUM* (CV. CANTHATCH): EFFECTS ON MILLING AND BAKING QUALITY AND DEGREE OF DIFFERENTIATION FROM CHROMOSOME 7D OF *TRITICUM TAUSCHII*

BY

GREGORY A. PENNER

A thesis submitted to the Faculty of Graduate Studies of the University of Manitoba in partial fulfillment of the requirements of the degree of

MASTER OF SCIENCE

ACKNOWLEDGMENTS

I would like to thank Dr. Erich Kerber for his supervision, support, constructive criticisms and friendship. The suggestions made by Drs. E. N. Larter, O. M. Lukow, W. Tai and M. Owen were greatly appreciated. I would also like to thank Rufus Oree, M. Rourke, R. Campbell, R. Zillman, D. Kozakevich and L. Tremblay for their technical assistance and patience. The friendship and support of Ariane Plourde, Brad Gabor, Bert Siemans, Meran Owen, Bill Legge, Alison Baillie, Pat McMullan and Conrad Black is gratefully appreciated. The financial support provided by the Natural Sciences and Engineering Research Council of Canada is also acknowledged. Finally, this thesis would not have been possible without the unwavering love, support, constructive criticisms and patience which I received from my wife, Pat.

FOREWORD

This thesis is written in the paper style, specified in the 1976 Plant Science Thesis Preparation Guide. It contains two manuscripts. The first entitled 'The differention between chromosome 7D of Triticum aestivum (cv. Canthatch) and Triticum tauschii as measured by chromosome pairing.' will be submitted to the Canadian Journal of Genetics and Cytology. The second entitled 'The effects of chromosome 7D of Triticum aestivum (cv. Canthatch) and of four varieties of Triticum tauschii on milling and baking quality.' will be submitted to the Canadian Journal of Plant Science.

GENERAL ABSTRACT

Chromosome 7D of Triticum aestivum cv. Canthatch was assayed for its effects on milling and baking quality and for its ability to pair with the corresponding homologous chromosome from each of four varieties of Triticum tauschii (2n = 14 = DD), typica, RL5003, anathera and strangulata. In addition, disomic substitutions in which chromosome 7D of Canthatch was replaced by chromosome 7D from each of these same varieties of Triticum tauschii were assayed to determine how well tauschii 7D compensated for Canthatch 7D in regards to milling and baking quality. Synthetic hexaploids (2n = 42 = AABBDD) produced by combining Tetra-Canthatch (2n = 28 = AABB) with these same varieties of Triticum tauschii were also tested for milling and baking quality.

To analyze the effect of Canthatch chromosome 7D on milling and baking quality, three aneuploid lines were used; one ditelosomic for 7DS, one ditelosomic for 7DL and one nullisomic for 7D. The long arm of Canthatch 7D was shown to affect seed size and density. Seed size had a significant negative regression on flour protein ($r = -0.62$). In addition, the long arm of chromosome 7D suppressed a w-gliadin protein. The long arm of 7D was also shown to have a positive effect on dough mixing time which was independent of flour protein content. In regards to milling and baking

quality, chromosome 7D of Triticum tauschii compensated fully for 7D of Canthatch. However, the D genome of Triticum tauschii did not fully compensate for the positive effects of the D genome of Canthatch in this regard.

The same disomic substitution lines used in the milling and baking analysis were crossed with Canthatch to investigate to what degree Canthatch 7D had differentiated from Triticum tauschii 7D in regards to pairing. These disomic substitutions were also crossed with a Canthatch plant doublemonotelosomic for chromosome 7D. Three doubletelotrisomics were produced in which the complete chromosome 7D was derived from two of the Triticum tauschii varieties (typica and strangulata) and from Canthatch. Analysis of chromosome pairing demonstrated that chromosome 7D from typica formed fewer chiasmata with Canthatch 7D than the corresponding chromosome from the other three tauschii varieties. The reduction in pairing between chromosome 7D of typica and 7D of Canthatch was greater than that previously reported in intraspecific D-genome chromosome pairing studies within Triticum aestivum. It is suggested that intraspecific divergence for at least chromosome 7D occurred between typica and the other three tauschii varieties tested before common hexaploid wheat evolved. It is also suggested that Canthatch chromosome 7D had not differentiated significantly in regards to pairing with chromosome 7D of the Triticum tauschii varieties anathera, RL5003 and strangulata.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Chapter I

GENERAL INTRODUCTION

Common hexaploid wheat is one of the most important cultivated plant species in the world in regards to human nutrition. The Canada Grains Council (1984) estimated that worldwide in 1984, 231,548,000 hectares of wheat were grown producing 491,762,000 tonnes of grain. Of this grain, most is used directly for human consumption and of this a significant portion is in the form of leavened products. The history of leavened products is a long one. Shellenberger (1971) noted that the first written references to bread date back to about 2600 B.C.. Thus a selection pressure within common wheat for functional quality has been applied for at least 5,000 years. Kerber and Tipples (1969) demonstrated that the removal of the D genome from Triticum aestivum drastically reduced baking quality. This substantiates previous evidence (See Harlan, 1981 for a review) that hexaploid wheat (2n = 42 = AABBDD) has gained prominence over tetraploid wheat (2n = 28 = AABB) because of the baking quality characteristics imparted to it by the addition of the D genome.

Chromosomes from the wild diploid species Triticum tauschii (2n = 14 = DD) have been shown to be homologous with

the D genome of hexaploid wheat (Kihara, 1982 cites Kihara, 1944; McFadden and Sears, 1944; Riley and Chapman, 1960). This discovery has uncovered a vast unexploited gene pool of potential significance in the improvement of hexaploid wheat. A great deal of variability in regard to baking quality within Triticum tauschii has been reported (Mettin, 1964; Yamashita et al., 1957; Kerber and Tipples, 1969).

Aneuploids, interspecific crosses and substitution lines have been used very effectively in common wheat in three ways. One, these techniques have been used to determine chromosomal control of qualitative and quantitative traits (Law, 1982). Two, both aneuploids and interspecific substitution lines have been used to elucidate the nature of the interaction within duplicate and triplicate sets of genes in common wheat (Hart, 1979). Three, interspecific crosses between common wheat and wild Triticum relatives have been used to transfer potentially useful genes into common wheat. An example of the successful use of this technique was the transfer of rust resistance genes from Triticum tauschii into Triticum aestivum (Kerber and Dyck, 1969, 1978 Dyck and Kerber, 1970).

The scope of this investigation was limited to chromosome 7D of Triticum aestivum cv. Canthatch and of four varieties of Triticum tauschii. However, several previous reports have indicated that within Triticum aestivum a number of grain and flour characteristics which impinge on functional quality could be attributed to this chromosome (Garcia-Olmedo and

Carbonero, 1970; Jha et al., 1971; Kosmolak et al., 1980; Doekes and Belderok, 1976; Morris et al., 1966).

By using aneuploids and interspecific substitution lines we attempted to answer three questions: first, whether Canthatch chromosome 7D has differentiated significantly from chromosome 7D of Triticum tauschii in regards to pairing. Second, whether chromosome 7D of Canthatch has an effect on milling and baking quality and third, to ascertain how well chromosome 7D of Canthatch is compensated for in regards to milling and baking quality by the corresponding homologue from Triticum tauschii.

Chapter II

LITERATURE REVIEW: A) PAIRING STUDY

2.1

Origin of the D genome of *Triticum aestivum*

Hexaploid wheat is made up of three genomes A, B and D each containing seven pairs of chomosomes. Sax and Sax (1924) demonstrated that *Triticum cylindricum* (2n = 28 = CCDD) contained the D genome of *Triticum aestivum*. In 1939 Kihara suggested that *Triticum tauschii* (2n = 14 = DD) had the D genome in common with *Triticum cylindricum* (Kihara, 1982). This was substantiated on the basis of meiotic pairing in hybrids produced from crosses of *cylindricum* and *tauschii* (Sears, 1941; Kondo, 1941). In 1944 McFadden and Sears, and Kihara produced synthetic hexaploids (2n = 42 = AABBDD) from crosses between *Triticum turgidum* (2n = 28 = AABB) and *Triticum tauschii* (Kihara, 1982). Chromosome pairing in the hybrids produced from crosses of these synthetics with *Triticum aestivum* indicated that *Triticum tauschii* was the source of the D genome of *Triticum aestivum* (Kihara, 1982). This was further confirmed by Riley and Chapman (1960) through the observation of chromosome pairing in a hybrid (2n = 28 = ABDD) produced from a *Triticum tauschii* by *Triticum aestivum* cross.

Eig (1929) classified Triticum tauschii on the basis of morphology into two subspecies, namely, ssp. eu-squarrosa and ssp. strangulata. Subspecies eu-squarrosa contains three varieties, typica, meyeri and anathera whereas subspecies strangulata contains only the variety strangulata. Types intermediate between these varieties also exist. Variety typica is the most common, with the widest distribution. Several studies have indicated the occurrence of intraspecific genetic variation within Triticum tauschii (Kihara et al., 1965; Kerber and Dyck, 1969; Johnson, 1972; Furata et al., 1975). Chennaveeraiah (1960) found differences in karyotypes among varieties. Typica had the most characteristics in common with other varieties. Meyeri and strangulata appeared to be specialized forms of typica. This correlates well with the geographical distribution of these varieties (Nakai, 1979).

2.2
Intraspecific chromosome pairing.

Hollingshead (1932) provided one of the first reports of differences in chromosome pairing between varieties in Triticum aestivum. She found that the percentage of cells containing univalents within the varieties Red Fife, Marquis, Garnet, H-44-24 and Marquillo ranged from 2.9 to 9.7%. In hybrids between these varieties the percentage of cells containing univalents ranged from 5.2 to 39.1%. Multivalent

associations were seen only rarely. Also, crosses which resulted in high univalent frequencies contained more open bivalents than those with fewer univalents. She concluded that the frequency of univalents was linearly related to chiasma frequency. Watanabe (1962) reported that in eight Japanese common wheat varieties the percentage of cells with at least one univalent ranged from 0.80 to 11.25%. However, the percentage of cells with univalents in hybrids produced from crosses between these varieties ranged from 4.40 to 72.80. Person (1956) observed univalent frequency over a number of generations in an intervarietal backcross program. He found that a high percentage of cells contained univalents in the F_1 hybrids and in the BC1 generation. Return to normal pairing was very slow and linear over subsequent backcross generations. He concluded that chromosome pairing was genetically determined in a quantitative manner.

Dvorak and McGuire (1981) crossed Chinese Spring with the varieties; Hope, Cheyenne and Timstein and found that the F1 hybrids had a higher frequency of univalents than that found in the parental lines. Since they found no multivalent associations they concluded that chromosome translocations were not implicated. Dvorak and Appels (1982) suggested that the amount of chromosome heterochromatin was not responsible for the reduction in pairing in interspecific hybrids. They referred to Kihara's (1963) work which indicated that the D-genome chromosomes of Triticum ventricosum (2n

= 28 = DDMvMv) pair well with those of Triticum tauschii and Triticum aestivum. On the other hand the Mv-genome chromosomes of Triticum ventricosum pair poorly with those of Triticum crassum (2n = 28 = DDMcrMcr) and with those of Triticum ovatum (2n = 28 = CuCuMoMo) (Kihara, 1954). All chromosomes in Triticum ventricosum are extensively heterochromatic. The D genome in Triticum tauschii and in Triticum aestivum has very little heterochromatin. Kihara (1954) also showed that in Triticum variabilis (2n = 28 = CuCuSvSv) the Cu genome pairs well with the Cu genome of Triticum ovatum (2n =28 = CuCuMoMo) but the Sv genome pairs poorly with the S genome of Triticum speltoides (2n = 14 = SS) (Kihara, 1963). Similar amounts of heterochromatin were found in both of these genomes in Triticum variabilis (Dvorak and Appels, 1982). Diploid S-genome species have prominent terminal C-bands. These particular bands are not found in Triticum variabilis or Triticum aestivum (Gill and Kimber, 1974). Nevertheless, S-genome chromosomes of variabilis pair no better with aestivum than they do with diploid species.

Dvorak and Appels (1982) also state that the reduction in pairing in intraspecific hybrids can not be adequately explained by structural differences. The two parental genotypes of Triticum araraticum that they used differed in the number of chromosome translocations and inversions. Both genotypes paired well with A-genome chromosomes of Chinese Spring and poorly with B-genome chromosomes. However, the number of translocation and inversion differences between

the Triticum araraticum genotypes and Chinese Spring did not differ significantly. Similar results were obtained by Feldman (1966) for Triticum timopheevi ssp. timopheevi and Chinese Spring.

More recently Crossway and Dvorak (1984) investigated the distribution of nonstructural variation along three chromosome arms of the common wheat cultivars Chinese Spring and Cheyenne. They also measured the mean pairing frequencies of Chinese Spring telosomes in Chinese Spring (2n = 20" + t') and as monotelosomic lines (2n = 20" + t1') substituted into Cheyenne. Pairing in the monotelosomic substitution lines was significantly lower than telosome pairing in Chinese Spring. Further, they produced recombinant monosomic lines (2n = 20" + 1') from these monotelosomic substitution lines. Subsequent pairing of the Chinese Spring telosomes with the recombinant monosomics varied between the extremes exhibited by the pairing frequencies of these telosomes with the original Chinese Spring and Cheyenne chromosomes. From this work they concluded that the pairing variation exhibited was of a quantitative nature.

Kihara et al. (1965) produced 24 different hybrids from eight varieties of Triticum tauschii representing eight geographic regions. They reported that in both the parental varieties and in the hybrids seven bivalents were normally found. Pollen fertility was reduced in the hybrids relative to the parents. They attributed this to genetic differences rather than to meiotic iregularities. Riley and Kimber

(1961) analyzed chromosome pairing in five diploid Triticum species including Triticum tauschii. They reported that an average of 1.7% of the pollen mother cells contained univalents over all five varieties; however, no univalents were observed in Triticum tauschii.

2.3

The use of telosomes in chromosome pairing studies.

Telocentric chromosomes of wheat have been used extensively in aneuploid and cytogenetic analysis. Feldman (1966) investigated the relationship between wheat telocentric chromosomes and the chromosomes of Triticum timopheevi. Linde-Laursen and Larsen (1974) used telosomes to identify translocations in wheat varieties. Chapman et al.(1976) investigated the relationship between the genome of Triticum urartu and the A genome of common wheat using telocentric and ditelocentric lines. Dvorak (1976) performed the same type of analysis on both the A and B genomes of Triticum urartu. Chapman and Riley (1966) crossed ditelocentric lines of Triticum aestivum with Triticum thaoudar in order to allocate chromosomes to either the A or the B genome. These studies are based on the fundamental assumption that telocentric chromosome arms pair as well with homologous complete chromosomes as do two homologous complete chromosomes.

Sears (1972) demonstrated that crossing over between the centromere and a closely linked locus is reduced in the association of a telosome and the corresponding complete homologous chromosome. Sallee and Kimber (1978) attempted a comprehensive analysis of telocentric pairing in Triticum aestivum. They recorded chiasma formation in 41 of the 42 possible chromosome arms in monotelodisomics of Chinese Spring, and found that there was no significant difference between the mean chiasma frequency of normal disomic Triticum aestivum and the sum of the chiasma frequencies of each of the telocentric lines. Moreover, there were no significant differences between the genomes in telocentric chiasma frequency. The D-genome telocentrics are shorter than the telocentrics of the other genomes. Consequently, the D-genome chromosomes had a significantly higher frequency of chiasma formation per unit length. They concluded that it was entirely valid to use telocentric lines to investigate chromosome relationships between Triticum aestivum and related species.

Chapter III

B) BAKING QUALITY AND ENDOSPERM STORAGE PROTEINS.

3.1

Structure of functional components

Wheat as a typical cereal grain produces a one-seeded fruit which consists of an embryo and an endosperm, enclosed by a nucellar epidermis, pericarp and a seed coat (Esau, 1977). Botanically this type of fruit, generally called a kernel or grain, is a caryopsis. After sieving, milled flour consists almost entirely of pulverised endosperm tissue. Thus it is chiefly the endosperm which concerns us as it alone determines the functional properties of flour.

The starchy endosperm is composed of two major regions. The sub-aleurone is the outermost layer and is characterized on a cellular level by containing relatively few small starch granules and large quantities of protein (McMasters et al., 1971). The central endosperm is the other region and on a cellular level it is characterized by large amounts of large starch granules and relatively small amounts of protein. The ability of a wheat dough to produce a leavened product is due to the presence of these proteins (Bushuk et al., 1969).

3.2

Proteins

Osborne (1907) classified wheat proteins into four groups based on solubility in various solvents. One group is made up of the albumins and globlins which are soluble in 10% NaCl solution; a second group, the gliadins, are soluble in 70% ethanol; glutenins, the third group, are soluble in acid solutions and the fourth group consists of the residual non-soluble proteins.

Albumins are relatively small proteins with molecular weights ranging from 10,000 to 20,000 daltons (Kasarda et al., 1971). The albumin purified by Ewart (1969) and by Fish and Abbott (1969) did not have free sulfhydral groups. Ewart (1969) suggested that albumin was stabilized by a hydrophobic core with the surface carrying the polar and ionic groups. The relatively high content of the basic amino acids lysine and arginine in globulins and to some degree in albumins could account for their relatively high electophoretic mobility compared with gliadins (Bushuk and Wrigley, 1974). Another class within the albumins and globulins are the chloroform-methanol (CM) proteins. Meredith (1965) classified this group of proteins as albumin contaminants in the extraction of gliadins, as they are soluble in 70% ethanol and occur in the same gel-filtration peak as the albumins and globulins (Bietz and Wall, 1972). However, Rodriguez-Loperena et al. (1975) indicated that these CM proteins

had properties identical to proteolipid proteins identified by Folch and Lees (1951) in brain tissue.

Gliadins have been classified into four groups on the basis of their electophoretic mobility in polyacrylamide gel electrophoresis (PAGE) by Bushuk and Zillman (1978). In order of ascending mobility these classes are w, γ, β and α. The w-gliadins range in molecular weight from 60,000 to 80,000 daltons, while the γ, β and α-gliadins range from 30,000 to 40,000 daltons (Bietz and Wall, 1972). Autran et al. (1979) sequenced the N-terminal amino acids of gliadins and found two major groups, one contained the α and β-gliadins and the other the γ-gliadins. Bietz et al. (1977) demonstrated that the w-gliadins fall into a third group as they are distinctly different in their N-terminal amino acid sequence from the γ-gliadins.

Payne and Corfield (1979) fractionated glutenin into twelve major subunits. They classified these subunits in order of descending molecular weight into groups A, B and C. Group A contains subunits ranging in molecular weight from 140,000 to 95,000 daltons, group B between 51,000 and 40,000 daltons and group C between 36,000 and 31,000 daltons. Group A has been classified as high molecular weight (HMW) glutenins whereas groups B and C have been labelled as low molecular weight (LMW) glutenins. Glutenin occurs naturally as an aggregation of these subunits which are primarily bonded by disulfide linkages. Ewart (1979) hypothesized a linear model for glutenin with only one disulfide bond be-

tween chains, based on observations of the drop in viscosity after addition of β-mercaptoethanol.

Residue protein can be dissolved by reducing agents such a β-mercaptoethanol in 1M SDS (Bietz and Wall, 1975). The resulting subunits are similar to those of glutenin. Bietz and Wall (1975) obtained both quantitative and qualitative differences between extractions with acetic acid, mercuric chloride and mercaptoethanol. Wall (1979) noted that since mercuric chloride is a mild reducing agent for disulfide bonds (Danno et al., 1975) these differences could be accounted for by differences in the number of disulfide cross linkages between subunits in the glutenin and residue fractions. Wall (1979) suggested that perhaps the residue protein is more like a three-dimensional matrix than a linear chain.

3.3
Dough formation

Dough consists of three major component groups (Bloksma, 1971). The most important group is that derived from the flour. This group contains the proteins mentioned above as well carbohydrates, lipids and many miscellaneous minor components. Another group includes water, which is essential for dough development, and air, which is necessary for the formation of gas cells. The final group consists of substances which are added to the dough, including yeast, malt, enzyme preparations, yeast nutrients, sugar, salt, dough

conditioners, improvers, fats, emulsifiers, milk solids and mold inhibitors.

The first step in dough formation involves mixing these ingredients together. The function of mixing is twofold: First, it serves to evenly distribute the ingredients and second, it induces the development of gluten structure. Protein must be hydrated before gluten structure can develop (Pomeranz, 1971). This development depends on the formation of a network of protein molecules with occasional cross-linkages. When this network is adsorbed at an air-water interface it forms a stable and highly compressible film with viscoelastic properties (Tschoegal and Alexander, 1960a,b). This film appears mostly as a sheet, but when exposed to lateral tension it ruptures and parallel fibres with lateral connections can be observed (Bernadin and Kasarda, 1973). These fibrils provide evidence that the gluten network is made up of aggregated elongated proteins (Wall, 1979). Seckinger and Wolf (1970) with the use of a transmission electron microscope, observed the spreading of wheat proteins on a liquid surface. Gliadins dispersed into discrete particles, whereas glutenin remained together with fibril extensions. Freeze dried glutenin appeared fibrous when examined by scanning electron microscopy (Orth et al., 1973; Khan and Bushuk, 1978). Disulfide bonds are probably preeminently responsible for this aggregation of wheat proteins. Within the wheat proteins the amino acid cysteine is responsible for these linkages.

Pence and Olcott (1952) found that by adding reducing agents such as sulfite to glutenin the viscoelastic properties of the dough were destroyed. Neilsen et al. (1962) demonstrated that after sulfite reduction the molecular weight of glutenin dropped markedly. Ewart (1972) attempted to measure the relative proportions of intra and intermolecular disulfide bonding in glutenin. He found that less than half of these bonds were intermolecular. The amino acid sequences of gliadin and glutenin differ in that the sequence of the gliadins favours intramolecular disulfide bond formation, whereas the sequence of glutenins favours intermolecular disulfide bonds (Wall, 1979).

Freshly mixed doughs contain up to 20% air by volume. These air cells form pockets in the dough in which the carbon dioxide produced by the yeast accumulates (Baker and Mize, 1946). The ability of common wheat dough to retain gas much better than dough from other cereals is the key to the development of a leavened product from wheat flour. This retention of gas is primarily due to the characteristics of the gluten network.

3.4

Components of functional quality.

3.4.1

Kernel characteristics

Functional quality is a complex characteristic made up of many components. One of the simplest parameters is that of test weight. This is simply the weight of the kernels per unit volume. This character is a function of not only the individual weight of each kernel but also the uniformity in size and shape (Hylinka and Bushuk, 1959). Hylinka and Bushuk (1959) also indicated that kernel size has very little effect on test weight. The manner in which the kernels pack into the container used is of greater importance. Mangels and Sanderson (1925) and Shuey (1960) found correlations of +0.762 and +0.744, respectively,between test weight and flour yield. Shrivelling of wheat kernels reduces test weight.

Kernel weight, usually expressed as weight per thousand kernels, is a function of kernel density and seed size (Schellenberger, 1971). The range in thousand kernel weight for U.S. hard red spring wheats is from about 20 to 32g (Schellenberger, 1971). Baker and Golumbic (1970) demonstrated that in hard red spring wheat kernel weight was superior to test weight in predicting flour yield.

Symes (1969) indicated that seed density and kernel hardness were equivalent. Baker and Dyck (1975) found that kernel hardness was positively related to flour yield and several baking quality tests. Symes (1969) reported that among lines which differed by a single gene for kernel hardness, those that were hard had superior flour yields, loaf texture and loaf volumes to those that were soft. Marshall et al. (1984) indicated on the basis of a theoretical analysis that both seed size and shape affect the ratio of interior volume to surface area of the wheat kernel and therefore flour yield. Seed size was shown to be the most important parameter in optimizing flour yield.

3.4.2

Protein content

It is generally accepted that protein content is related to baking quality (Pomeranz, 1971). Strong wheat flours are usually high in protein content and form tenacious, elastic gluten that produces high volume loaves with good texture. Weak wheat flours usually are low in protein, and form soft, weak gluten which results in doughs that are more prone to failure in baking. Finney and Barmore (1948) carried out a comprehensive analysis of the relationship between protein content and loaf volume. They found that the major factor accounting for variation in loaf volume was protein content. The relationship between the two was essentially linear for

a range of protein contents between 8 and 18%. This linear relationship was also reported by Fifield et al. (1950).

3.4.3

Protein quality

The kinds of proteins and the amounts of various types present are also important in determining baking quality. Bushuk et al. (1969) demonstrated that bread making quality varied among common wheat varieties of equal protein content. He concluded that this was due to variation in protein quality. Both Finney and Barmore (1948) and Fifield et al. (1950) found that the linear regressions which they had worked out between protein content and loaf volume were variety-dependent. The level of the regression line for any variety was dependent on its inherent protein quality.

3.4.3.1

Albumins and globulins.

Pence et al. (1951) reported that of the various endosperm protein fractions tested in reconstituted flours, the crude albumin fraction had the largest effect on loaf volume. The globulin fraction resulted in a slight decrease in loaf volume. Pence et al. (1954) attempted a more comprehensive analysis of these proteins and found that neither albumin nor the globulin quantity was correlated significantly with loaf volume. Also, the proportion of globulins

and albumins to glutenins and gliadins was not correlated with loaf volume. However, the ratio of albumins to globulins was correlated with baking quality. The authors suggested that perhaps this could be explained on the assumption that albumins had a beneficial effect on baking quality while globulins were deleterious.

3.4.3.2

Gliadins

Polyacrylamide gel electrophoresis is the most generally accepted method for separating gliadin proteins on a one-dimensional level. In this system proteins are separated on the basis of molecular size and electric charge. Using a computer-based grouping system of analysis, Wrigley et al. (1981) demonstrated that certain patterns of gliadin bands were significantly linked to varying dough strengths. In addition, they identified 11 bands that were individually associated with dough strength characteristics. However, the authors were unable to separate possible pedigree effects from gliadin group differences. Finney et al. (1982) fractionated wheat gluten with ultra-centrifugation and then reconstituted synthetic flours by adding fractions from various common wheat varieties. They found a strong relationship between gliadin composition and loaf volume. It is also of interest to note that a specific gliadin, band '45', has been positively correlated with dough properties in durum wheat (Damidaux et al., 1978; Kosmolak et al., 1980).

Subsequent analysis by duCros et al. (1980) has shown that this association appears to involve more than one gliadin protein.

3.4.3.3

Glutenins

Glutenin is the fraction of wheat gluten that contributes elasticity to the mixing properties of dough (Bushuk, 1977). Tanaka and Bushuk (1973) demonstrated that wheats with longer dough development times contained glutenin subunits of higher average molecular weight than wheats with shorter dough development times. Payne et al. (1979) identified a high molecular weight (145,000 daltons) glutenin subunit that was positively correlated with baking quality. They labelled this subunit '1' on the basis of its position in SDS-polyacrylamide electrophoregrams. A more comprehensive study by Payne et al. (1981a) substantiated the importance of this subunit. Plants containing subunit '1' had higher mean sedimentation values than those which did not. In addition, they discovered that subunits '5' and '10' were also strongly correlated with baking quality in the progeny of three crosses. They also discovered that the effects of subunits 1,5 and 10 were additive.

Burnouf and Bouriquet (1980) indicated that European wheat varieties with good baking quality contained glutenin subunits 3 and 5. They also suggested that subunits 9 and

10 had a definite but less important role in determining baking quality. Moonen et al. (1983) noted that wheat cultivars that contained subunits 3 and 10 had a higher average baking quality than cultivars which contained the allelic counterparts 2 and 11. In addition, they reported that the subunit 2*, which had been identified as being distinct from subunit 2 by Payne et al. (1981b), also was positively correlated at a significant level with baking quality. Baking quality in the Moonen et al. (1983) study was measured by loaf volume. These results appear to countradict those of Finney et al. (1982) who concluded that glutenin had a primary effect on mixing properties and that gliadin composition was more directly related to loaf volume. It would appear that these relationships are, to some extent, dependent on the baking procedure used. Hamada et al. (1982) indicated that with stronger doughs the AACC straight dough method resulted in lower than expected volumes ,whereas the remix procedure optimized loaf volumes.

3.4.3.4

Residue protein

Booth and Melvin (1979) investigated the factors responsible for the poor baking ability of the high yielding cultivar Maris Huntsman. They found that the amount of residue protein (protein insoluble in lactic acid) was much lower in this cultivar than in Canadian Western hard red spring wheat(CWRS). Reconstitution studies which involved increas-

ing the amount of residue protein in Maris Huntsman to the level found in CWRS wheats did not result in any change in quality. Thus they concluded that the composition of the residue proteins of CWRS wheats is instrumental in their superior baking quality. Orth and Bushuk (1972) demonstrated that the amount of residue protein (insoluble in dilute acetic acid) was positively associated with mixing strength. Also, Hamada et al. (1982) reported that this protein was positively related to loaf volume in tests where the remix baking procedure was used.

3.5 Chromosomal control of functional components

3.5.1 Albumins, globulins and chloroform methanol extract (CM) proteins

Garcia-Olmedo and Carbonero (1970) demonstrated that components of the chloroform-methanol (CM proteins) extract were controlled by chromosomes 7D and 7B. Bozzini et al. (1971) reported that chromosomes 3D and 4D each controlled the synthesis of an albumin protein. Aragoncillo et al. (1975) investigated the chromosomal control of the so called non-gliadin components extracted by 70% ethanol. They found that component 5 was controlled by the β-arm of chromosome 3D while several components were controlled by the short arm of chromosome 3B. Components 12, 13 and 16 were found by

these authors to be controlled by the β-arm of 4A and several other components were associated with chromosomes 4D, 5D, 6B, 7DS and 7BS. Components 12 and 13 correspond in electrophoretic mobility to the CM3 protein for which chromosomal control by 4A was also implicated (Aragoncillo, 1973). Chromosome arms 7DS and 7BS had previously been linked to the synthesis of CM1 and CM2, respectively (Garcia-Olmedo and Carbonero, 1970). Thus it is possible that these two reports refer to the same proteins. Aragoncillo et al. (1975) also noted that the component controlled by chromosome 6B is inhibited by 7B when 7D is absent.

3.5.2

Gliadins

It has become generally recognized that genes for the synthesis of all gliadin proteins are associated with six wheat chromosomes: 1A,1B,1D,6A,6B and 6D (Payne et al., 1982). Shepherd (1968), using one-dimensional PAGE, assigned 9 of the 17 major gliadin bands of the common wheat variety Chinese Spring to the nonstandard arms of chromosomes 1A,1B and 1D and the standard arms of chromosomes 6A and 6D. Standard arms being, those which are identified first. He also indicated that of the remaining eight bands, five were controlled by chromosomes 1A,1B,1D and 6B. With the improved resolution of two-dimensional gel electrophoresis Wrigley and Shepherd (1973) substantiated and added to these findings. They demonstrated that of 46 gliadin spots

of Chinese Spring, 33 could be assigned to chromosomes of homoeologous groups 1 and 6. Twelve of the remaining thirteen spots were faint to the extent that the verification of their presence varied. This chromosomal assignment of gliadin genes was also substantiated by Kasarda et al. (1976).

Brown and Flavell (1981) reported that all gliadin proteins of Chinese Spring were synthezised by the short arms of chromosomes of homoeologous groups 1 and 6. They also demonstrated that chromosome 2A had a regulatory effect on the synthesis of ∝-gliadin bands 17 and 18 which are synthesized by chromosome 6D. It was also suggested that chromosome 2B and 2D contained regulatory alleles as well. Lafiandra et al. (1984) indicated that the gliadin proteins of the American wheat variety Cheyenne are coded for by the same chromosomes as in Chinese Spring. Galili and Feldman, (1983) using a high resolution SDS-PAGE system, were able to attribute faint bands, previously poorly resolved, to the short arms of group 1 homoeologous chromosomes.

More recently Galili and Feldman (1984) provided evidence that genes in the D-genome of the common wheat cultivar 'Prelude" suppress the activity of gliadin synthesis genes in the A and B genomes. They reported the presence of two new bands in Tetra-Prelude, the tetraploid AABB component extracted from Prelude. These bands were not present in hexaploid Prelude nor in the Triticum turgidum ssp. durum

cv. Stewart used in the production of the extracted tetraploid. They also reported that at least six gliadins of hexaploid Canthatch (2n = 42 = AABBDD) were expressed in Tetra-Canthatch (2n = 28 = AABB) with increased staining intensity. In addition, two gliadins of hexaploid Canthatch were present with reduced staining intensity in Tetra-Canthatch.

3.5.3

Glutenins

Among cultivars of common wheat up to 20 different glutenin subunits have been identified electrophoretically (Lawrence and Shepherd, 1980; Payne et al., 1980). Orth and Bushuk (1974) indicated that several of these subunits are coded for by chromosome 1D. Payne et al. (1980) demonstrated that all of the HMW glutenin subunits of the seven varieties they investigated were controlled by either chromosome 1A,1B or 1D. Bietz et al. (1975) reported that four of the HMW glutenin subunits were coded for by the long arms of chromosomes 1B and 1D. They also attributed a presumed LMW glutenin subunit to the long arm of chromosome 4D. Subsequent work by Brown and Flavell (1981) indicated that this was most probably a HMW globulin. Lawrence and Shepherd (1980) demonstrated that a HMW glutenin subunit in the variety 'Hope' was controlled by a gene on the long arm of chromosome 1A. The location of genes for glutenin subunit

synthesis on the long arms of the chromosomes of the homoeologous group 1 has been confirmed by the inheritance studies of Lawrence and Shepherd (1981), Payne et al. (1982) and Poperelya and Babayants (1978).

Jackson et al. (1983) investigated the chromosomal localization of the genes coding for the LMW glutenins (groups B and C of Payne and Corfield (1979)). They indicated that genes controlling the synthesis of these subunits are on the short arms of the chromosomes of homoeologous group 1. This raises the question of whether these subunits are identical to the HMW gliadins that are controlled by genes on the same chromosome arms. Jackson et al. (1983) found that the two-dimensional electrophoresis patterns of these subunits are different from the patterns for the HMW gliadins. Bietz and Wall (1973) showed that the sulfur content and amino acid composition of the major LMW glutenin subunits and w-gliadins are different. However, these properties as well as electrophoretic mobility after reduction and alkylation (Charbonnier, 1973) are common to the LMW glutenins and γ-gliadins. Payne et al. (1984) found no recombination between LMW glutenin subunits and gliadins known to be controlled by the same chromosome arm. However, this is far from conclusive evidence that these two groups are in fact encoded by the same cistrons since the gliadin genes are believed to be very complex. Kasarda (1980) has speculated that the gene family on chromosome 6A coding for A-gliadin may be made up of as many as 100 structural cistrons.

3.5.4

Protein content

A number of researchers have investigated chromosomal control of protein content, but no consensus has been reached. There are two reasons for this; first, different groups of researchers have studied different varieties and second, the relationship between phenotype and gene action is not always clear for this trait. Genes can affect this characteristic in many ways and at many stages of development. For example, Law and Payne (1983) discovered that dwarfing genes Rht1 and Rht2, which are thought to desensitize the plant to gibberelic acid, also have a deleterious effect on protein content.

However, there have been studies that have identified specific chromosomes of some varieties as having a major effect in determining protein content. Morris et al. (1978) indicated that chromosome 5D of the variety 'Atlas 66' carried a major gene for protein content and that chromosome 5A carried a minor gene for this trait. Giorgi et al. (1978) noted that when 'Cheyenne' and 'Hope' chromosomes were substituted into Chinese Spring, chromosomes 1B, 1D, 2D and 7A resulted in lower protein content in Chinese Spring. Only chromosomes 2A and 2B from Hope and 2A from Cheyenne improved the protein content significantly. Jha et al. (1970) implicated chromosomes 1D, 2A, 3A, 3B, 5A, 6B, 7A, 7B and 7D as having genes controlling protein content in two Indian varieties when crossed to Chinese Spring. Miazga and Tar-

kowski (1982) reported that in the Polish wheat variety Luna, chromosomes 5A and 6A were associated with high protein, whereas chromosomes 3D and 5B were associated with low protein content.

Kuspira and Unrau (1957) working with chromosome substitution lines from the Canadian variety Thatcher into Chinese Spring indicated that Thatcher chromosomes 3D, 4D, 5A, 5B and 7B produced higher protein content in Chinese Spring. Kosmolak et al. (1980) using Cadet-Rescue reciprocal substitution lines noticed that Rescue chromosomes 5B and 6A increased protein content, while chromosomes 7A,1B and 7D decreased protein content in Cadet. Cadet chromosomes 1B and 5B reduced protein content in Rescue. In summary, among cultivars of common wheat it would appear that chromosomes from homoeologous groups 5 and 7 are primarily involved in the control of protein content.

3.5.5

Baking quality

The results of investigations into chromosomal control of baking quality also have been noted to be highly contradictary. This probably should be expected since baking quality is a function of protein content and several other parameters. In addition, the methods of measuring baking quality have varied from one investigation to another. Morris et al. (1966), using substitution lines of Cheyenne chromosomes

into Chinese Spring, indicated that chromosomes 4B, 7B and 5D of Cheyenne contained genes for strong dough mixing properties. In addition, the control of loaf volume, crust appearance and texture characteristics were assigned to chromosomes 1B, 4B, 7B and 7D. In a subsequent study, Morris et al. (1978) pointed out that their 1D substitution line was in error (i.e. did not contain chromosome 1D of the donor). They developed a new substitution line which did contain this chromosome and discovered that it too contributed to strong dough mixing ability.

Welsh et al. (1968) using substitution lines in which chromosomes from the varieties Hope, Thatcher and Timstein were placed into Chinese Spring, found that only chromosome 2A of Thatcher had an effect on flour quality. Chromosome 2B of Hope was associated with major effects on quality while minor effects were ascribed to ten other chromosomes. Sixteen Timstein chromosomes altered flour properties, with chromosomes 3B and 6B being the most important. Kosmolak et al. (1980) using Cadet-Rescue reciprocal substitution lines noted that Rescue chromosomes 1B, 7A and 7D decreased loaf volume in Cadet, whereas chromosomes 2A, 2D, 5B and 6A increased loaf volume. In the reciprocal substitution series only chromosome 5D of Cadet had a significant effect by causing a decrease in loaf volume. Several chromosomes were implicated in dough development.

Kerber and Tipples (1969) demonstrated that the D-genome from Triticum tauschii is the main source of the desirable baking properties of common wheat. The AABB tetraploid extracted from Canthatch was much inferior in baking tests than either the normal hexaploid Canthatch or the synthetic hexaploids produced by the addition to the tetraploid of the D-genome from any of five varieties of Triticum tauschii.

3.6
Variation of endosperm storage proteins and baking quality

3.6.1
Endosperm storage proteins in Triticum aestivum.

In Triticum aestivum considerable unexplored and unexploited variation for endosperm storage proteins exists. Allelic differences for most of the identified protein genes have been discovered. Studies by Payne et al. (1981a) and Payne and Lawrence (1983) indicated that three different patterns of glutenin subunit variation were found for chromosome 1A, eleven for 1B and six for 1D. Similar allelic differences for gliadins has also been noted. Galili and Feldman (1983) reported 16 different band combinations for those gliadins controlled by chromosome 1B and four different combinations for those controlled by 1D. These results were only for HMW gliadins and thus reflect only a part of the total gliadin variation. Given this variation Law and

Payne (1983) concluded that the number of possible combinations is enormous and that only a small proportion of this variation has been investigated and exploited in breeding programs.

3.6.2

Endosperm storage proteins in Triticum tauschii

As noted previously, considerable variation exists within Triticum tauschii in regard to many traits. Rodriguez-Loperena et al. (1975) reported that all the CM proteins in the variety of Triticum tauschii they investigated were also contained in Triticum aestivum. Caldwell and Kasarda (1978) indicated that in their investigation of albumins and globulins in four accessions of Triticum tauschii all bands could be accounted for in Triticum aestivum. Konarev et al. (1974) demonstrated that Triticum tauschii falls into two groups, delineated by the subspecies, on the basis of electrophoregram patterns and antigenic composition of their gliadins. They concluded that the subspecies strangulata represents an enlarged version of the subspecies eu-squarrosa since the ssp. strangulata contains all the antigenically active gliadins of eu-squarrosa plus a few more.

Bushuk and Kerber (1978) investigated the variance in PAGE gliadin patterns for the Triticum tauschii varieties typica, strangulata and meyeri and in the synthetic hexaploids produced from these and Tetra-Canthatch. While there were differences among these varieties, especially for the

slowest moving of the w-gliadins, all the bands expressed are found in Triticum aestivum. However, there are some faint tauschii bands which are suppressed in the synthetic hexaploids as well as a few bands which appear in the hexaploid but not in either the diploid or in the tetraploid parent.

Orth and Bushuk (1973) investigated glutenin subunit composition of the Triticum tauschii varieties, typica, anathera, strangulata and meyeri. The patterns produced by the first three varieties were almost identical. However, in the remaining variety, meyeri, the two highest molecular weight subunits were smaller than the corresponding subunits in the other varieties. The highest molecular weight band was the same as the subunit '1' identified by Payne et al. (1979) as being related to baking quality. All bands present in the first three varieties were also present in Triticum aestivum. Dhaliwal (1977) concluded that all differences within the Aegilops-Triticum group for gluten proteins could be attributed to allelic differences rather than differences in structural genes. This does not rule out the possibility that alleles exist in the wild species of this group that are not found in Triticum aestivum.

3.6.3

Baking quality of Triticum tauschii

Mettin (1964) reported that intraspecific variability within Triticum tauschii existed for protein content (a range from 19.5 to 26.8%) and for gluten quality. Yamashita et al. (1957) investigated the baking potential of two varieties of Triticum tauschii. They found that both varieties produced loaves similar in volume but lower in quality of appearance than those produced from Triticum aestivum. Kerber and Tipples (1969) analyzed the baking quality of synthetic hexaploids produced by crossing Tetra-Canthatch (AABB) with five varieties of Triticum tauschii. They found differences between these lines for almost all the quality tests utilizied. Although none of the lines was equal in quality to Canthatch, all were considerably better than Tetra-Canthatch. They indicated that presumably this was only a small sample of the variation present in Triticum tauschii. Lines may exist which approach the baking quality of Canthatch more closely.

Chapter IV

THE DIFFERENTIATION BETWEEN CHROMOSOME 7D OF *TRITICUM AESTIVUM* (CV. CANTHATCH) AND *TRITICUM TAUSCHII* AS MEASURED BY CHROMOSOME PAIRING.

Greg A. Penner, E.R. Kerber and E.N. Larter

To be submitted to the Canadian Journal of Genetics and Cytology.

The differention between chromosome 7D of Triticum aestivum (cv. Canthatch) and Triticum tauschii as measured by chromosome pairing.

4.1

Abstract

Disomic substitution stocks in which chromosome 7D of Triticum aestivum cv. Canthatch was replaced by the corresponding chromosome of each of four varieties of Triticum tauschii were crossed with Canthatch to investigate the degree of differentiation for this chromosome between these two species. These disomic substitutions were also crossed with a Canthatch plant doublemonotelosomic for chromosome 7D. Three doubletelotrisomics were produced, one in which the complete 7D chromosome was derived from Canthatch and two in which the complete 7D chromosome was derived from the Triticum tauschii varieties typica and strangulata. Analysis of chromosome pairing demonstrated that chromosome 7D from typica formed fewer chiasmata with Canthatch than did the corresponding chromosome from the other three tauschii varieties. The reduction in pairing between chromosomes 7D of typica and Canthatch is greater than that previously reported from intraspecific D-genome chromosome pairing studies within Triticum aestivum. It is suggested that intraspecific divergence for at least chromosome 7D occurred

between *typica* and these other three *tauschii* varieties before the synthesis of common hexaploid wheat. It is also suggested that Canthatch chromosome 7D had not differentiated significantly in regards to pairing with chromosome 7D of the *Triticum tauschii* variety from which the D genome of common wheat was derived.

4.2

Introduction

Substitution of chromosomes of common wheat by chromosomes from wild relatives has been used to determine the chromosomal location of common wheat genes (Law 1982) and to investigate the interaction of duplicate and triplicate gene sets in wheat (Hart 1979). Interspecific crosses between common wheat and wild relatives have been used to transfer potentially useful genes into common wheat (Kerber and Dyck 1969, 1973, 1978; Dyck and Kerber 1970; The 1973). One wild relative of common wheat, Triticum tauschii (2n = 14 = DD syn. Aegilops squarrosa) has been shown to have been the source of the D genome of Triticum aestivum (McFadden and Sears 1944; Kihara 1982; Riley and Chapman 1960). Kimber et al. (1981) have demonstrated that the degree of similarity between Triticum tauschii and the D genome of Triticum aestivum is greater than that between either of the A or B genomes of aestivum and any of their putative diploid sources.

The objective of the present investigation was to determine whether Canthatch chromosome 7D has differentiated significantly from its corresponding homologue in Triticum tauschii on the basis of metaphase pairing. This investigation also enabled us to determine whether a significant degree of intraspecific differentiation in this regard had occurred for chromosome 7D within the four varieties of Triticum tauschii tested.

4.3

Materials and Methods

Synthetic hexaploids (2n = 42 = AABBDD) were previously produced (Kerber and Rowland 1974) by combining Tetra-Canthatch (2n = 28 = AABB) with each of four varieties of Triticum tauschii (Table 1). Chromosome substitution lines used in this investigation were produced in which chromosome 7D of the common wheat cultivar Canthatch was replaced by 7D of each of the four synthetic hexaploids listed in Table 1 (2n = 20" + 7D" Triticum tauschii (7D Triticum aestivum)). Each synthetic hexaploid was crossed with Canthatch nullisomic 7D (2n = 20" + 0"7D). F1 plants (2n = 41) were backcrossed to the nullisomic 7D parent. Progeny with 41 chromosomes were selected by cytological observation and successively backcrossed five more times to the nullisomic 7D parent. Monosomic progeny (2n = 41) from the last back-

TABLE 1

Accession numbers and pedigrees for synthetic hexaploids

Accession No.	Pedigree[1]
RL5401	Tetra-Canthatch X T. tauschii RL5003
RL5402	Tetra-Canthatch X T. tauschii var. typica RL5261
RL5403	Tetra-Canthatch X T. tauschii var. anathera RL5266
RL5405	Tetra-Canthatch X T. tauschii var. strangulata RL5288

[1] Kerber and Rowland (1974)

cross were selfed and disomic substitutions (2n = 42) were cytologically selected in the progenies. Two of these disomic substitutions and Canthatch-K were crossed with Canthatch doublemonotelosomic plants in which both telosomes for chromosome 7D were present (2n = 20" + t'7DS + t'7DL). Three doubletelotrisomic plants were produced, one in which the complete chromosome 7D was derived from Canthatch and two in which the complete chromosome 7D was derived from the tauschii varieties typica and stranqulata, respectively. All four disomic substitution lines were also crossed with Canthatch-K to produce substitution lines in which one chromosome 7D of Triticum tauschii was present together with its homologue 7D from Canthatch-K (2n = 20" + 1'(7D) Triticum aestivum + 1'(7D) Triticum tauschii), hereafter referred to as mono-wheat, mono-tauschii substitutions. Canthatch nullisomic 7D and ditelosomic 7DL were derived from the same monosomic plant selection. Ditelosomic 7DS was derived from a different single plant selection designated Canthatch-K.

The standard acetocarmine squash technique was used to analyze chromosome pairing in pollen mother cells (PMCs) of the doubletelotrisomic plants, mono-wheat, mono-tauschii substitution lines and in the monosomic substitution lines used to produce the disomic substitutions. At least 100 cells per plant were analyzed in the doubletelotrisomic plants with the exception of the line involving typica in which only 70 cells were examined. For the mono-wheat,

mono-tauschii substitution lines at least 50 cells per plant were observed from anthers from three different plants per line. In addition, at least 50 cells per plant were observed from anthers from two different plants for the monosomic substitutions with the exception of the line typica in which only 60 cells from anthers of one plant were analyzed. The data were analyzed first by an analysis of variance and second where significant F values were obtained, by Dunnet's t method (Steele and Torrie 1980).

4.4

Results

In the doubletelotrisomic lines chiasma formation involving chromosome 7D was amenable to direct observation as the heteromorphic trivalents and heteromorphic bivalents formed between the two telosomes and the substituted 7D chromosome could be readily distinguished from the other chromosome associations. A telosome paired with the complete substituted chromosome was considered to represent one chiasma. Table 2 presents a summary of the frequencies of all possible pairing configurations between the two telosomes and the complete 7D chromosome. Chromosome 7D from typica formed significantly fewer chiasmata (at the 99% level) with the corresponding Canthatch telosomes than chromosome 7D from either strangulata or Canthatch. The difference in chiasma frequency between strangulata and Canthatch is not significant.

TABLE 2

Frequencies of chiasmata and chromosome configurations involving chromosome 7D and the corresponding telosomes in doubletelotrisomic lines

Source of complete chromos. 7D	No. of cells with given heteromorphic configuration			Total no. cells	Mean xmta (f)
	tt1	t + t1	t + t + 1		
strangulata	102	4	0	106	1.96a[1]
typica	58	9	3	70	1.79b
Canthatch	109	4	0	113	1.96a

[1] Significant at the 99% level

Chiasma frequency was also evaluated in the remaining 20 chromosome pairs in the cell to determine whether the heteromorphic configuration had an effect on overall pairing (Table 3). A closed bivalent was assumed to represent two chiasmata and an open bivalent one chiasma. Cells containing univalents and quadrivalents were also included in this analysis. Closed quadrivalents were assumed to represent four chiasmata and open quadrivalents three chiasmata. The mean chiasma frequency among the three doubletelotrisomic lines, disregarding the heteromorphic configuration, did not vary significantly. An expected chiasma frequency for 20 bivalents for Canthatch may be calculated by dividing the mean chiasma frequency for this line (Table 5) by 21 and then multipling by 20. This value of 39.26 is not significantly different from the mean chiasma frequencies in Table 3. Thus, it would appear that the heteromorphic configura-

TABLE 3

Frequencies of chiasmata and chromosome configurations involving complete chromosomes other than 7D in the doubletelotrisomic lines

Source of complete chromos. 7D	No. of cells with given no. of xmta/cell					No. of cells with 1'	Total 1 no. cells	Mean xmta(f)
	40	39	38	37	36			
strangulata	57	30	13	4	2	2	1	106	39.28[1]
typica	39	23	17	4	1	4	0	70	39.34
Canthatch	50	32	21	8	2	6	9	113	39.31

[1]F = 1.25 (df. = 2, 286)

tions did not have an effect on the pairing of the other bivalents.

Data on chromosome pairing of the monosomic substitutions

TABLE 4

Frequencies of chiasmata and chromosome configurations involving chromosomes other than the substituted 7D in the monosomic substitution lines

Source of complete chromos. 7D	No. of cells with given no. of xmta/cell						Total no. cells	Mean xmta (f)
	40	39	38	37	36	35		
RL5003	49	42	20	7	1	1	120	39.07[1]
typica	27	18	12	3	0	0	60	39.15
anathera	57	37	13	5	1	0	113	39.27
strangulata	39	34	25	8	0	1	107	38.94

[1]F = 1.715

is summarized in Table 4. No significant variability in chromosome pairing was found. Moreover, the overall mean chiasma frequency for this analysis (39.11) was not significantly different from that calculated for Canthatch (39.26). In the mono-wheat, mono-tauschii substitution analysis it was neccesary to assume that variation in chiasma frequency was due solely to the substituted 7D chromosome. The monosomic substitution analysis substantiates this assumption. Table 5 provides a summary of the pairing data for the mono-

TABLE 5

Frequencies of chiasmata and chromosome configurations involving all chromosomes in the mono-wheat, mono-tauschii substitution lines

Source of substituted chromos. 7D	No. of cells with given no. of xmta/cell						Total no. cells with		Total no. cells	Mean xmta(f)
	42	41	40	39	38	37	1'	1"		
RL5003	56	66	38	11	3	0	8	9	174	40.93a
typica	28	71	49	19	6	1	15	13	174	40.53b
anathera	52	55	46	14	1	0	11	13	168	40.85a
strangulata	45	65	33	12	2	0	9	6	157	40.89a
Canthatch (Control)	84	69	24	9	0	0	8	9	186	41.23a

F = 9.9969** (df. = 4, 852)

wheat, mono-tauschii substitution lines. Chromosome 7D from typica formed significantly fewer chiasmata with Canthatch chromosome 7D than 7D from the other varieties. There were no significant differences among the other three tauschii varieties and Canthatch regarding chromosome 7D.

Quadrivalents were observed in most of the material analyzed, suggesting the presence of translocations. However, approximately the same frequency of quadrivalents was observed in the monosomic substitution and doubletelotrisomic material as in the mono-wheat, mono-tauschii substitution lines. In the doubletelotrisomic and monosomic substitution lines the substituted 7D chromosome did not appear to be involved in multivalent associations. Thus, these quadrivalents probably are the result of translocations involving chromosomes other than 7D.

4.5 Discussion

Chromosome 7D from all Triticum tauschii varieties used in the mono-wheat, mono-tauschii substitution analysis formed fewer chiasmata with Canthatch chromosome 7D than would be expected from the analysis of doubletelotrisomics (Table 6). Canthatch itself, however, does not exhibit reduced pairing from one analysis to another. There are at least three possible explanations for this difference. First, the values derived from the doubletelotrisomic plants may be inflated due to an inherent observational error. A second possibility is that the substituted chromosome inhibits chiasma formation in the other bivalents. Finally, a third potential explanation is that the substituted chromosomes pair more completely with the telosomes than they do

TABLE 6

Differences in chiasmata frequency between the doubletelotelotrisomic and the mono-wheat, mono-*tauschii* substitution lines

Source of substituted 7D	Mean xmta frequency in 7D configuration	
	Mono-wheat, mono-tauschii	Doubletelotrisomic
RL5003	1.66	-
typica	1.27	1.79
anathera	1.59	-
strangulata	1.62	1.96
Canthatch (control)	1.96	1.96

$t = 12.528^{**}$ (df. = 2)

with the complete 7D chromosome. Of these possibilities the first appears the most likely. When analyzing the heteromorphic configurations in the doubletelotrisomic plants, those cells in which the complete 7D chromosome and both telosomes were not positively identifiable were excluded from the data. In cells which contained heteromorphic trivalents it was easier to positively identify both telosomes than in those cells in which either one or both of the telosomes were unpaired with the complete 7D chromosome. In the latter case the likelihood of one of the telosomes being hidden by another chromosome association was increased. This would tend to inflate the estimates of chiasma frequencies given in Table 2. This error would not affect the end analysis as it should be of the same magnitude for all lines.

As for the second explanation, Dvorak and McGuire (1981) analysed a Chinese Spring monotelodisomic series in which the telosomes were of Chinese Spring origin and the corresponding complete chromosome had been replaced by a homologous chromosome from another Triticum aestivum variety. They found that in some cases the substituted chromosome appeared to affect the pairing of other Chinese Spring chromosomes. However, it would appear that this is not the case in our material as the substituted 7D chromosome did not appear to have an effect either on chiasma frequency of the remaining chromosomes in the doubletelotrisomic plants or in the monosomic substitution lines (Tables 3 and 4). As for the third possibility, Sallee and Kimber (1978) have indicated that within Triticum aestivum there is no significant difference between telocentric chromosome pairing and normal bivalent formation. This would seem to substantiate our assumption that variation in chiasma frequency in the mono-wheat, mono-tauschii substitution lines is attributable primarily to the bivalent involving the substituted 7D chromosome.

Results from the mono-wheat, mono-tauschii substitution analysis appear to substantiate those from the doubletelotrisomic analysis in indicating that for chromosome 7D the Triticum tauschii variety typica has diverged significantly in its ability to pair with chromosome 7D of Canthatch relative to chromosome 7D from the other three Triticum tauschii varieties tested. It has been suggested that the major

cause of variability in intraspecific chromosome pairing is nucleotide sequence divergence (Dvorak and Appels 1982; Dvorak and McGuire 1981). In light of this argument it is possible that the nucleotide sequence differences between chromosome 7D of typica and chromosome 7D of Canthatch are greater than the differences between 7D of Canthatch and 7D of the other three tauschii varieties. This supports the hypothesis that typica diverged from the other three tauschii varieties tested before the origin of Triticum aestivum. The possibility that typica is one of the more primitive varieties of Triticum tauschii, and may in fact have given rise to the other more specialized varieties, has been suggested by Chennaveeraiah (1960) on the basis of karyotypes and by Nakai (1979) in regards to geographical distribution. The qualification that this conclusion is based on the analysis of the pairing of a single chromosome is probably necessary. It is possible that the pairing of other typica chromosomes with corresponding homologous Canthatch chromosomes could be better than for the corresponding chromosomes from the other three tauschii varieties tested.

Is the variability expressed by chromosome 7D of typica greater than the intraspecific chromosome variability reported within Triticum aestivum? The differences in mean chiasma frequencies for the pairing between Chinese Spring telosomes and the corresponding Chinese Spring complete chromosomes and the same telosomes paired with the corre-

sponding substituted complete chromosomes from three other Triticum aestivum cultivars can be calculated using the data from Dvorak and McGuire (1981). This produces a range of 0.09 to 0.21 for the A-genome differences, 0.31 to 0.38 for the B-genome differences and 0.01 to 0.02 for the D-genome differences. In our data the difference in mean chiasma frequency between chromosome 7D of typica and Canthatch is 0.18 and 0.69 for the doubletelotrisomic and mono-wheat, mono-tauschii data, respectively. Thus, while the variance exhibited by typica chromosome 7D is not greater than that found within the A or B genomes of Triticum aestivum, it is greater than that found in the D genome. Sallee and Kimber (1978) found a significantly higher frequency of chiasmata per unit of relative length in D-genome chromosomes relative to A- and B-genome chromosomes. However, D-genome chromosomes are shorter than those of either the A or B genomes. The overall mean number of chiasmata per telocentric in the A, B and D genomes in their study was not significantly different from one another. Thus, the marked reduction in intraspecific variability within the D genome of Triticum aestivum is not completely explained by an increase in chiasma frequency. An alternative explanation is that the origin of hexaploid wheat is a relatively recent evolutionary event compared to the origin of tetraploid wheat. Thus the D genome of hexaploid wheat has had less time in which to diverge within aestivum than have the A or B genomes. Alternatively, perhaps the characteristics imparted by the D

genome to hexaploid wheat have been more stringently selected for than those of the other genomes,thereby maintaining less variability within the D genome.

LITERATURE CITED

CHENNAVEERAIAH, M. S. 1960. Karymorphological and cytotaxonomic studies in Aegilops. Acta. Hort. Gotob. 23:85-178.

DVORAK, J. and R. APPELS. 1982. Chromosome and nucleotide sequence differentiation in genomes of polyploid Triticum species. Theor. Appl. Genet. 63:349-360.

DVORAK, J. and P. E. McGUIRE. 1981. Nonstructural chromosome differentiation among wheat cultivars with special reference to differentiation of chromosomes in related species. Genetics. 97:391-414.

DYCK, P. L. and E. R. KERBER. 1970. Inheritance in hexaploid wheats of adult-plant leaf rust resistance derived from Aegilops squarrosa. Can. J. Genet. Cytol. 11:639-647.

HART, G. E. 1979. Genetical and chromosomal relationships among the wheats and their relatives. Stadler Symp. Vol. 11:9-29. University of Missouri.

KERBER, E. R. and P. L. DYCK. 1969. Inheritance in hexaploid wheat of leaf rust resistance and other characters derived from Aegilops squarrosa. Can. J. Genet. Cytol. 11:639-647.

KERBER, E. R. and P. L. DYCK. 1973. Inheritance of stem rust resistance transferred from diploid wheat (Triticum monococcum) to tetraploid and hexaploid wheat and chromosome location the gene involved. Can. J. Genet. Cytol. 15:397-409.

KERBER, E. R. and P. L. DYCK. 1978. Resistance to stem and leaf rust of wheat in Aegilops squarrosa and transfer of a gene for stem rust resistance to hexaploid wheat. 5th Int. Wheat Genet. Symp. New Dehli, India. 358-364.

KERBER, E. R. and G. G. ROWLAND. 1974. Origin of the free threshing character in hexaploid wheat. Can J. Genet. Cytol. 16:145-154.

KIHARA, H. 1982. Wheat studies, retrospect and prospects. pub. by Elsevier Scientific Publishing Co., Tokyo.

KIMBER, G., L. C. ALONSO and P. J. SALLEE. 1981. The analysis of meiosis in hybrids. I. Aneuploid hybrids. Can. J. Genet. Cytol. 23:209-219.

LAW, C.N. 1982. Aspects of the uses of aneuploid methods in wheat breeding. In, Induced variability in plant breeding, Eucarpia Symp., Wageningen, the Netherlands. August 31st - September 4th, 1981. 62-70.

McFADDEN, E. S. and E. R. SEARS. 1944. The artificial synthesis of Triticum spelta. Res. Genet. Soc. Amer. 13:26-27.

NAKAI, Y. 1979. Isozyme variations in Aegilops and Triticum. IV. On the origin of common wheat revealed by the study of esterase isozymes. Japan. J. Genet. 54:175-190.

RILEY, R. and V. CHAPMAN. 1960. The D genome of hexaploid wheat. Wheat Inform. Serv. 11:18-19.

SALLEE, P. J. and G. KIMBER. 1978. An analysis of the pairing of wheat telocentric chromosomes. 5th Int. Wheat Genet. Symp. New Dehli, India. 408-419.

STEEL, R. G. and D. J. H. TORRIE. 1980. Principles and Procedures of Statistics. McGraw-Hill Inc. U.S.A..

THE, T.T. 1973. Chromosome location of genes conditioning stem rust resistance transferred from diploid to hexaploid wheat. Nature, New Biol. 241:256.

Chapter V

THE EFFECTS OF CHROMOSOME 7D OF *TRITICUM AESTIVUM* (CV. CANTHATCH) AND OF FOUR VARIETIES OF *TRITICUM TAUSCHII* ON MILLING AND BAKING QUALITY.

Greg A. Penner, E. R. Kerber, E. N. Larter and O. M. Lukow

To be submitted to the Canadian Journal of Plant Science.

The effects of chromosome 7D of Triticum aestivum (cv. Canthatch) and of four varieties of Triticum tauschii on milling and baking quality.

5.1

Abstract

Chromosome 7D of Triticum aestivum cv. Canthatch was assayed for its effects on milling and baking quality by investigating three aneuploid lines -one ditelosomic for 7DS, one ditelosomic for 7DL and one nullisomic for 7D. Also, disomic substitutions in which chromosme 7D of Canthatch was replaced by the corresponding chromosome of the Triticum tauschii (2n = 14 = DD) varieties typica, anathera, RL5003 and stranqulata, were assayed to determine how well 7D of tauschii compensates for 7D of Canthatch in regard to milling and baking quality. Synthetic hexaploids (2n = 42 = AABBDD) produced by combining Tetra-Canthatch (2n = 28 = AABB) with these same varieties of Triticum tauschii were also tested for milling and baking quality. The long arm of Canthatch chromosome 7D was shown to affect seed size and density. Seed size had a significant negative regression on flour protein content (r = -0.62). In addition, the long arm of chromosome 7D suppressed a w-gliadin protein. Moreover, evidence was produced which suggested the presence of a factor(s) on the long arm of Canthatch chromosome 7D which

was related to longer dough development times. This effect appeared to be independent of flour protein content. In regard to milling and baking quality chromosome 7D of Triticum tauschii fully compensated for 7D of Canthatch. However, the complete D genome of Triticum tauschii did not fully compensate for the D genome of Canthatch in this regard.

5.2

Introduction

Kerber and Tipples (1969) demonstrated that the removal of the D genome from Triticum aestivum cv. Canthatch dramatically reduced baking quality. These authors also reported that the addition of the chromosomes of Triticum tauschii (2n = 14 = DD) to Tetra-Canthatch (2n = 28 = AABB) partially compensated for the D genome of Canthatch in regard to baking quality. Of the D genome chromosomes, 7D has been reported to have some control over loaf volume (Morris et al., 1966; Kosmolak et al., 1980), protein content (Jha et al., 1971; Kosmolak et al., 1980), protein quality (Aragoncillo et al., 1975) and kernel hardness (Doekes and Belderok, 1976).

The objectives of this study were to determine whether chromosome 7D of Canthatch has an effect on milling and baking quality and to determine how well chromosome 7D of Canthatch-K is compensated for by the corresponding chromosome from four varieties of Triticum tauschii. In addition, we analyzed the same synthetic hexaploids investigated by Ker-

ber and Tipples (1969) in order to determine whether a significant proportion of the reduction in quality exhibited by the synthetic hexaploids when compared with Canthatch-K could be attributed to chromosome 7D of Triticum tauschii.

5.3 Materials and Methods

5.3.1 Materials

Aneuploids used in this investigation included nullisomic 7D (2n = 20"), ditelosomic 7DS (2n = 20" + t"7DS) and ditelosomic 7DL (2n = 20" + t"7DL), all of the cultivar Canthatch. Ditelosomic 7DS was derived from a monosomic 7D plant (2n = 20" + 1'7D) which was derived from a single plant selection designated Canthatch-K. Nullisomic 7D and ditelosomic 7DL were derived from a monosomic 7D sib of the original Canthatch-K plant. Doublemonotelosomics (2n = 20" + t'7DS + t"7DL) derived from reciprocal crosses between the two ditelosomic lines were also included.

Synthetic hexaploids (2n = 42 = AABBDD) used in this investigation were produced by Kerber and Tipples (1969) by combining Tetra-Canthatch (2n = 28 = AABB) with each of four varieties of Triticum tauschii (2n = 14 = DD) (Table 7). Disomic substitution lines (2n = 20" + 1"Canthatch 7D/Triticum tauschii 7D) were produced in which chromosome

7D of Canthatch-K was replaced by the corresponding chromosome of Triticum tauschii by crossing Canthatch nullisomic 7D with each of the four synthetic hexaploids listed in Table 7. A series of successive backcrosses of F1 monosomic plants to Canthatch nullisomic 7D were made. On the completion of the final backcross F1 monosomic plants were selfed and disomic substitutions (2n = 42) were selected in the

TABLE 7

Accession numbers and pedigrees for synthetic hexaploids

Accession no.	Pedigree[1]
RL5401	Tetra-Canthatch X T. tauschii RL5003
RL5402	Tetra-Canthatch X T. tauschii var. typica RL5261
RL5403	Tetra-Canthatch X T. tauschii var. anathera RL5266
RL5405	Tetra-Canthatch X T. tauschii var. strangulata RL5288

[1] Kerber and Rowland (1974)

progeny. Seed of the disomic substitutions was increased, under controlled pollination to provide enough seed for the field plots. For electrophoretic analysis the disomic substitution lines were subjected to an additional backcross before they were selfed.

5.3.2

Methods

5.3.2.1

Electrophoresis

For gliadin analysis two kernels from which the embryos had been removed, were ground and the endosperm solubilized in 70% ethanol for each line. A ratio of 3mg of endosperm to 1ul of 70% ethanol was used. After centrifugation the supernatant was diluted by a ratio of 1:1 by the addition of sodium lactate buffer ph 3.1 (100ul), glycerol (10mg) and methyl-green tracking dye (5mg). Polyacrylamide gel electrophoresis (PAGE) was carried out according to the procedure of Bushuk and Zillman (1978) with some modifications. Sodium lactate was substituted for aluminum lactate and the amount of ferrous sulfate per gel was reduced to 0.0025mg. Gels were horizontal and 3mm thick. Gels were stained overnight in a 12% TCA/Commassie Brilliant Blue solution and destained in a 12% TCA solution. Triticum aestivum cv. Marquis-K was included as a standard reference in each gel.

Glutenin was extracted from two kernels per line according to the procedure of Bietz et al. (1975). The procedure was modified by dissolving the glutenin in 0.125 M Tris/HCl (pH 8.7) containing 0.1% SDS and 1% 2-mercaptoethanol instead of 0.125M Tris/Borate (pH 8.9). For SDS-PAGE, the O'-Farrell (1975) technique was followed with a 5% acrylamide stacking gel layered onto a 10% acrylamide separating gel.

Gels were run at 20mA until the tracking dye entered the separating gel then run for 3 hours at 35mA (constant current) at 20 C in an LKB 2001 Vertical Electrophoresis Unit. Gels were stained overnight in Coomassie Brilliant Blue followed by destaining in several changes of an acetic acid and methanol solution. For better resolution of low molecular weight glutenin subunits, gels were silver stained according to the procedure of Merril et al. (1981).

Whole protein was extracted according to the procedure of Brown et al. (1981). SDS-PAGE was performed according to the procedure of O'Farrell (1975) with a 5% acrylamide stacking gel layered onto a 14% acrylamide separating gel. Gels were run at 10mA until the tracking dye entered the separating gel and then run at 25mA (constant current) for 4 hours. Staining and destaining of the gels was performed as for glutenin.

5.3.2.2

Functional quality

Lines were grown at Glenlea in the summer of 1984 in a completely randomized block design in two replicates. In order to generate enough seed, two plots of the aneuploid lines were included in the first replicate. For the majority of the quality tests, lines were analyzed using the field plots as replicates and the extra aneuploid plots were not included. However, additional flour was required for the aneuploids for the farinograph and loaf volume tests. At

this point flour derived from the grain of extra aneuploid plots was added to the respective lines and two laboratory samples were analyzed per line. Flour from all other plots was bulked within lines and two samples similarily analyzed.

Measurement of grain characteristics was facilitiated by the use of an electronic seed counter. Seed size was determined by dividing the number of seeds in a 30ml beaker by the volume of the beaker (41ml). Seed density was derived by multiplying seed size by the weight of the seeds in the above beaker and adjusting to mg/cm^3.

Yield of flour was determined on grain from two replicates milled in the Brabender micro-mill. Samples were tempered to equal moisture content before milling (15.5%). Enough grain was available for two replications of milling in the Buhler mill for all lines except the aneuploids and the synthetic hexaploid RL5403 in which the D genome was derived from the Triticum tauschii variety anathera.

Protein content of flour (14% moisture) was determined with the Dickey-John near-infrared protein analyzer. The Zeleny sedimentation test was performed according to Approved Methods of the American Association of Cereal Chemists (AACC) (1983) procedure except that 50ml of lactic acid was used for a total volume of 100ml instead of 25ml and 75ml, respectively. Mixographs were produced according to AACC procedure on a 10g Electronic Recording Mixograph

(developed by the Engineering and Statistical Research Branch of the Canada Department of Agriculture, Ottawa). A constant absorption of 60% was used. Farinograms were produced on the 50g Brabender Farinograph according to AACC procedure. Baking was performed using the standard remix baking procedure (Kilborn and Tipples, 1981) with 50g of flour. Baking absorption was 2% lower than farinograph absorption. Loaf volumes were measured by the rapeseed displacement method. Data were first analyzed by an analysis of variance. Where there were significant F values, data were re-analyzed by the lsd multiple comparison method α = .05 (Steel and Torrie, 1980).

5.4 Results

5.4.1 Electrophoresis

PAGE analysis of gliadins revealed the presence of up to 25 distinct bands in Canthatch-K (Figure 1). Canthatch nullisomic 7D and ditelosomic 7DS exhibited a w-gliadin band with a relative mobility of 26.6 which was not found in either Canthatch-K, ditelosomic 7DL or either of the two doublemonotelosomic lines. This would seem to indicate that a gene suppressing the formation of this protein is present on the long arm of chromosome 7D, but its presence in nullisom-

ic 7D suggests that a chromosome other than 7D is responsible for its synthesis. Interestingly, this protein is also found in Marquis-K, indicating that Marquis-K does not contain this suppressor gene.

Figure 2 shows the gliadin pattern of the disomic substitutions and synthetic hexaploids. The synthetic hexaploid RL5403 in which the D genome came from anathera and the two Canthatch disomic substitutions in which chromosome 7D was derived from anathera and strangulata, exhibit the w-gliadin band which is suppressed in Canthatch-K. This indicates variability for this suppressor gene exists within Triticum tauschii. Other than the w-gliadin band all other bands produced by the disomic substitutions are in common with those found in Canthatch. In the synthetic hexaploids four bands of relative mobility 11.5, 14.6, 16.7 and 44.8 were absent when compared to Canthatch-K (indicated by arrows in Figure 2). The synthetic hexaploid in which the D genome was derived from typica exhibited a band not found in Canthatch-K (relative mobility of 20.8).

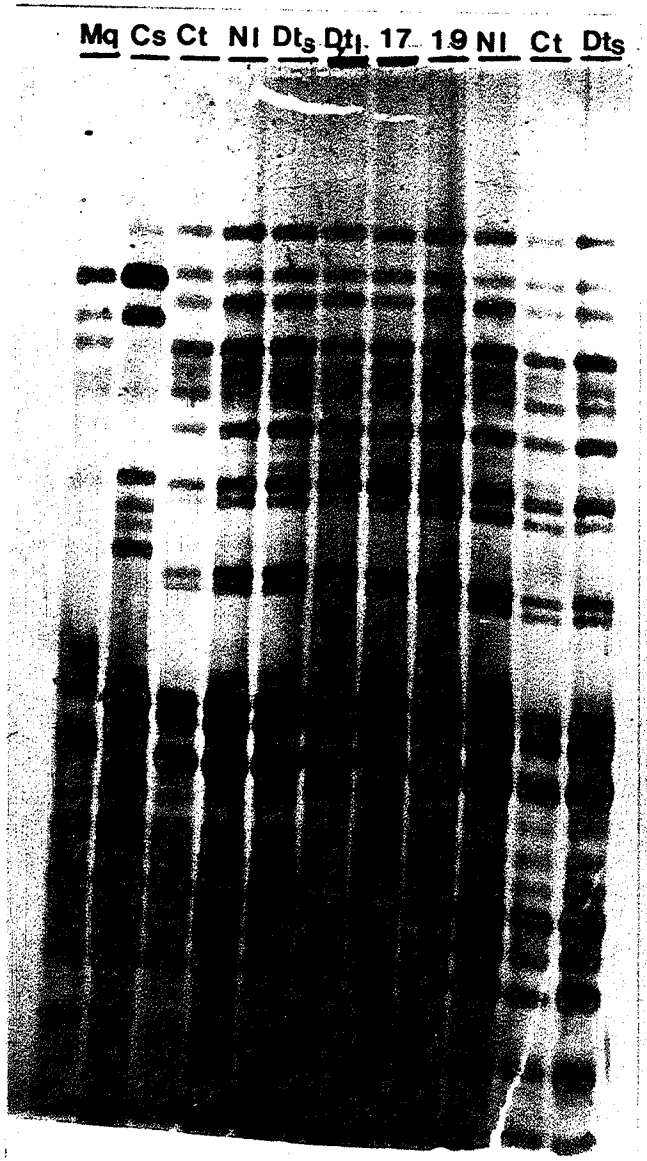
SDS-PAGE analysis was applied to Canthatch nullisomic 7D, ditelosomic 7DS, ditelosomic 7DL and Canthatch-K. No qualitative differences in glutenin subunit composition were found for any of these lines even when the extremely sensitive silver nitrate stain was used (Figure 3). The protein composition derived from the whole protein extraction of the aneuploids, Canthatch-K and the disomic substitutions is

FIGURE 1

PAGE of gliadins from Canthatch 7D aneuploids and from Canthatch (K)

Mq = Marquis (K); CS = Chinese Spring; Ct = Canthatch (K); Nl = Canthatch nullisomic 7D; Dts = Canthatch ditelosomic 7DS; Dtl = Canthatch ditelosomic 7DL; 17 and 19 are doublemonotelosomics derived from reciprocal crosses (2n = 20" + t'7DS + t'7DL)

Arrow indicates suppressed w-gliadin


Mq Cs Ct NI Dts Dtl 17 19 NI Ct Dts

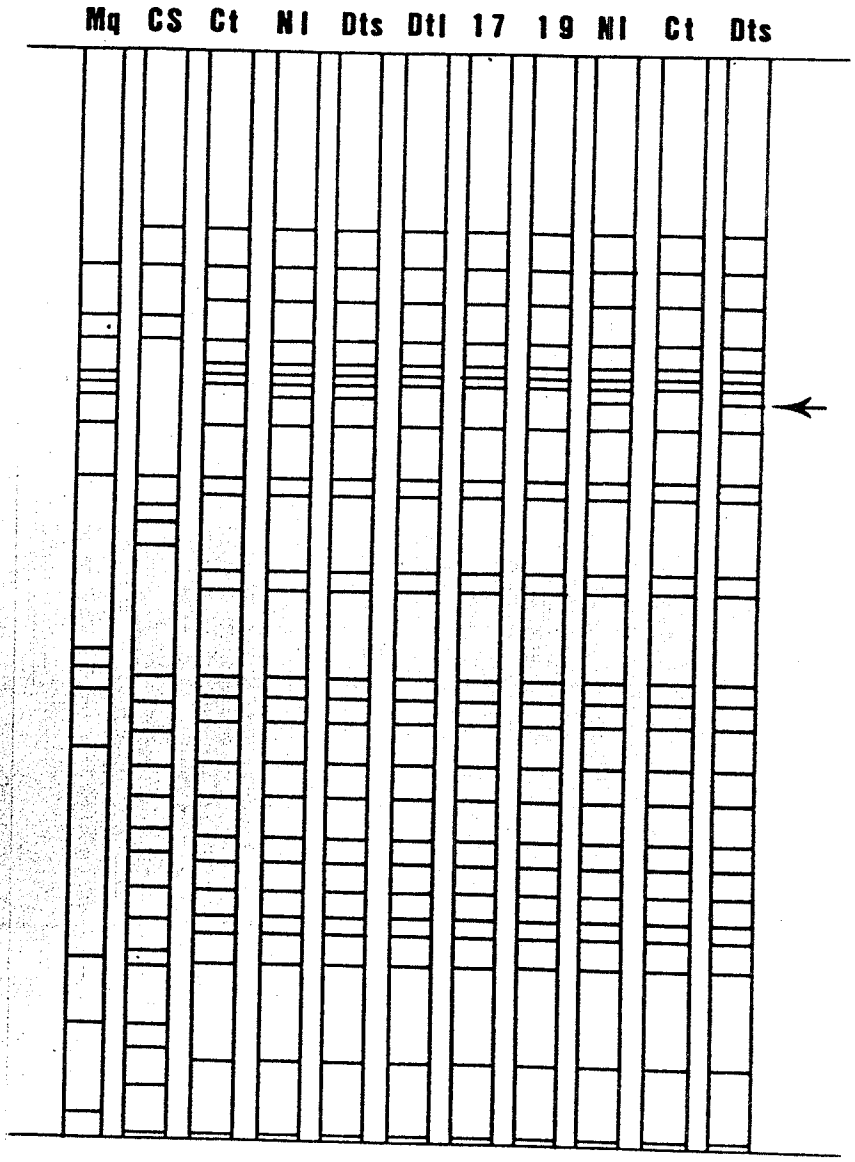
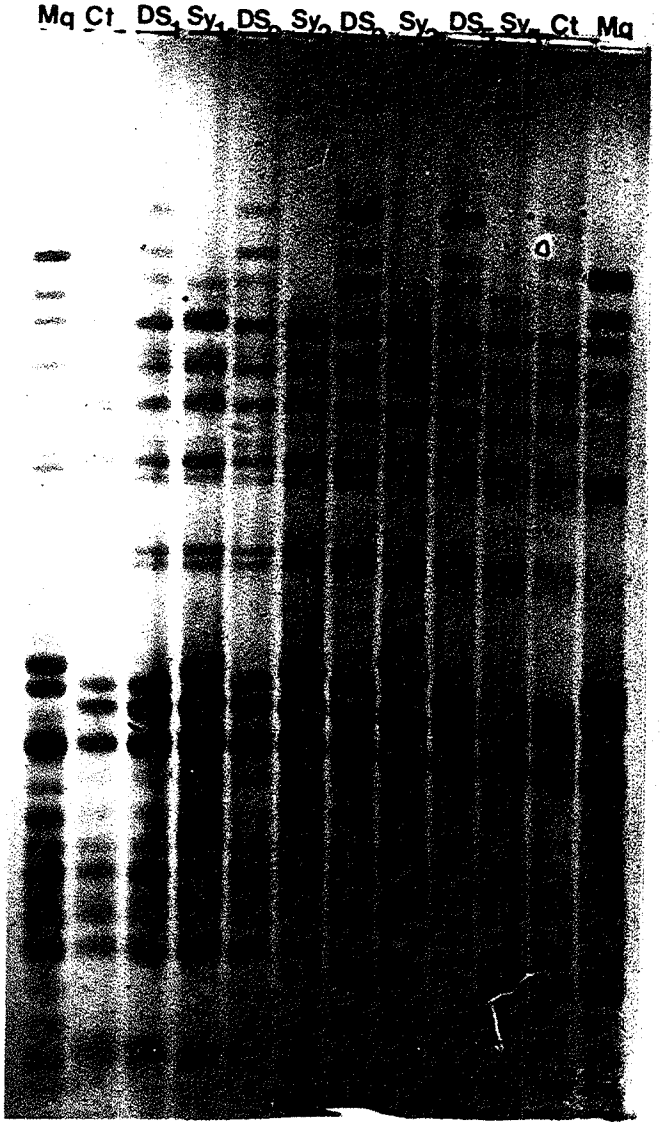

Mq CS Ct NI Dts Dtl 17 19 NI Ct Dts

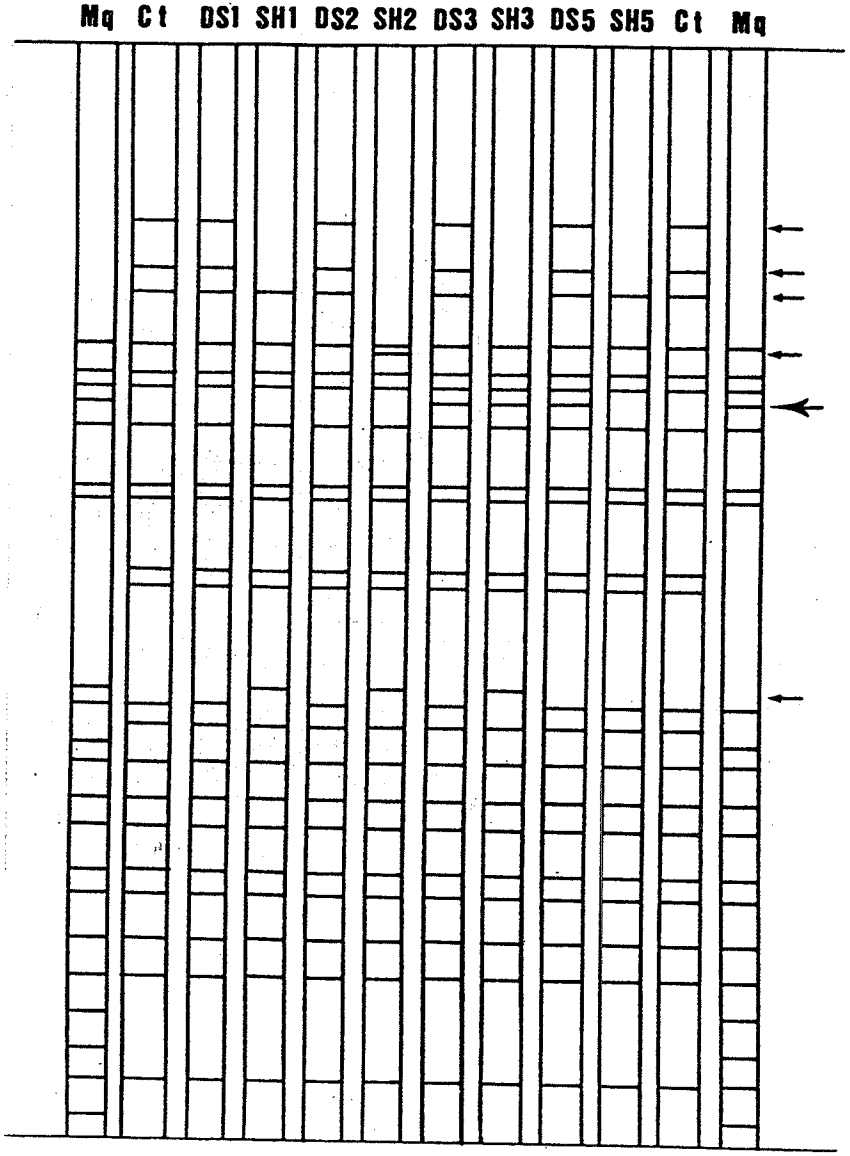
FIGURE 2

PAGE of gliadins of disomic substitutions and synthetic hexaploids

Mq = Marquis (K); Ct = Canthatch (K); DS1,2,3 and 5 are disomic substitutions in which chromosome 7D was derived from RL5003, *typica*, *anathera* and *strangulata*, respectively; SH1, 2, 3 and 5 are synthetic hexaploids in which the D genome was derived from RL5003, *typica*, *anathera* and *strangulata*, respectively

Arrows indicate bands whose presence varied among lines.


Mq Ct DS1 Sy1 DS2 Sy2 DS3 Sy3 DS5 Sy5 Ct Mq


Mq Ct DS1 SH1 DS2 SH2 DS3 SH3 DS5 SH5 Ct Mq

shown in Figure 4. Again no differences among lines could be detected. The protein extracted from the disomic substitutions did not resolve as well as the protein from the aneuploids presumably because of a less pure extraction. Thus the bands missing in the disomic substitutions may be present but cannot be distinguished.

FIGURE 3

SDS-PAGE of glutenin.

N1 = Canthatch nullisomic 7D, Dts = Canthatch ditelosomic 7DS, Dt1 = Canthatch ditelosomic 7DL, Ct = Canthatch (K).

Schematic composite for SDS_PAGE of glutenin.

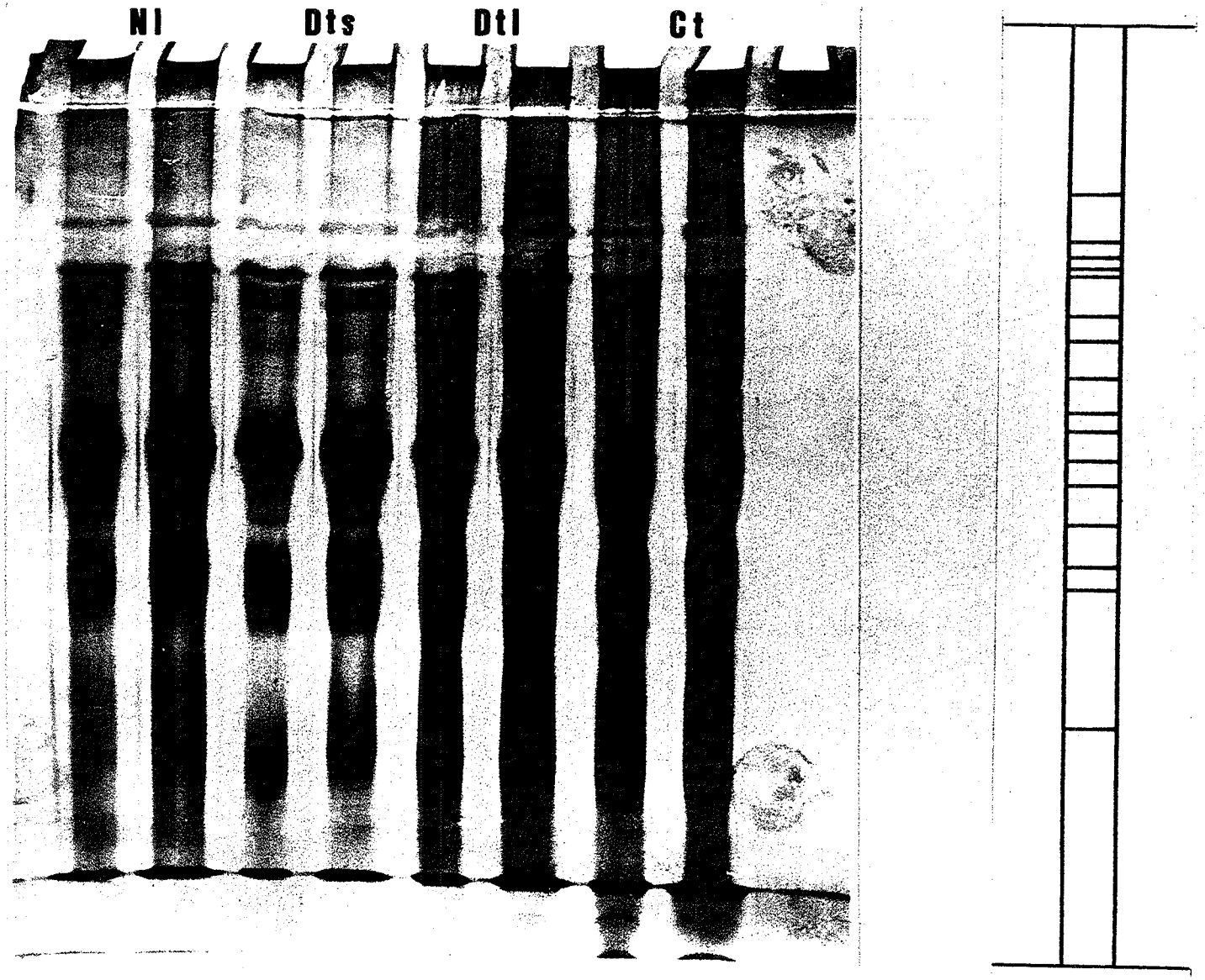

Nl
Dts
Dtl
Ct

FIGURE 4

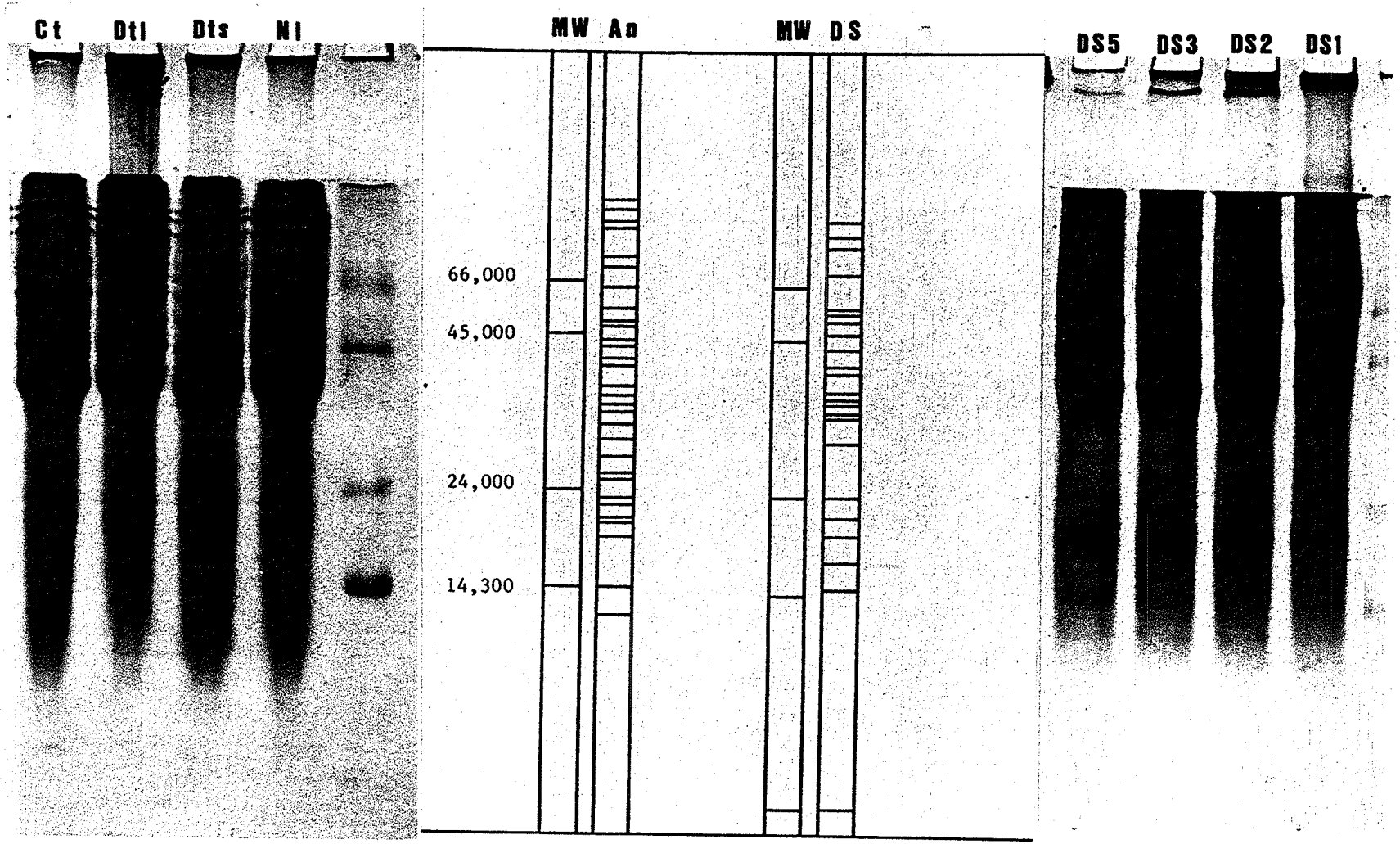
SDS-PAGE of whole protein

MW = molecular weight; Ct = Canthatch (K); Dt1 = Canthatch ditelosomic 7DL; Dts = Canthatch ditelosomic 7DS; N1 = Canthatch nullisomic 7D

Schematic composite for SDS-PAGE of whole protein

MW = molecular weight; An = Aneuploids; DS = Disomic substitutions

DS5 = Disomic substitution involving *strangulata*; DS3 = Disomic substitution involving *anathera*; DS2 = Disomic substitution involving *typica*; DS1 = Disomic substitution involving RL5003


Ct
Dtl
Dts
Nl
MW An
MW DS
DS5
DS3
DS2
DS1
66,000
45,000
24,000
14,300

5.4.2

Functional quality

Mean values for grain characteristics seed size, density

TABLE 8

Mean values for grain characteristics

Lines tested	Seed size(mm^3)	Thousand kernel wt.(g)	Seed density(mg/cm^3)
Canthatch-K	28.46a	20.94a	7.35a
Cth. Nulli 7D	24.06b	16.20b	6.73ef
Cth. Ditelo 7DS	19.80c	12.95c	6.54f
Cth. Ditelo 7DL	23.36b	17.20b	7.36a
D.S. RL5003	32.44d	21.89ad	6.75ef
D.S. typica	31.69d	21.94ad	6.92bcd
D.S. anathera	32.56d	22.15ad	6.80de
D.S. strangulata	32.25d	22.65ad	7.02bc
S.H. RL5003	35.49e	23.99d	6.76e
S.H. typica	35.46e	24.15d	6.81cde
S.H. anathera	41.46f	28.03e	6.74ef
S.H. strangulata	42.14f	29.46e	6.99bcd

[1] Disomic substitution (D.S.) in which chromosome 7D was derived from the variety of Triticum tauschii listed.
[2] Synthetic hexaploid (S.H.) in which the the D genome was derived from the variety of Triticum tauschii listed.
Values with the same letter are not significantly different at = .05

and thousand kernel weight are presented in Table 8. Canthatch chromosome 7D appears to have a significant positive

effect on all of these characteristics as evidenced by the reduced values in the absence of the entire chromosome or of either arm. Seed size is more profoundly affected in the absence of the long arm of chromosome 7D than in the absence of the entire chromosome. This result may indicate the presence of a factor(s) on the short arm of chromosome 7D which reduces seed size but is normally suppressed by a factor(s) on the long arm of 7D. Seed density appears to be controlled by the long arm of chromosome 7D as ditelosomic 7DL is not significantly different from Canthatch for this characteristic whereas ditelosomic 7DS and nullisomic 7D are significantly below Canthatch-K. A regression of seed size on seed density is nonsignificant, indicating that seed density is independent of seed size.

Variability for grain characteristics was expressed by the disomic substitutions and the synthetic hexaploids. All disomic substitutions produced larger seeds with lower densities than Canthatch-K. Seed of the synthetic hexaploids was significantly larger than that of the disomic substitutions, thus there must also be factors on chromosomes 1D to 6D of Triticum tauschii that affect this character.

Table 9 provides a summary of the milling data. The low flour yield of the aneuploids may be accounted for in part by small seed size. However, the slightly higher flour yield of Canthatch ditelosomic 7DL may be linked to the higher seed density of this line. There are no significant differences between any of the disomic substitutions and

TABLE 9

Mean values for milling properties

Lines tested	Brabender flour yield(%)	Buhler flour yield(%)
Canthatch-K	66.6a[3]	75.4a[3]
Cth. Nulli 7D	56.9d	-
Cth. Ditelo 7DL	59.3cd	-
Cth. Ditelo 7DS	61.6bc	-
D.S. RL5003[1]	63.5ab	75.2a
D. S. typica	64.3ab	75.5a
D.S. anathera	65.9a	75.3a
D.S. strangulata	63.5ab	75.6a
S.H. RL5003[2]	45.6e	72.5d
S.H. typica	47.7e	73.4c
S.H. anathera	49.1e	-
S.H. strangulata	56.2d	74.0b

[1] Disomic substitution (D.S.) in which chromosome 7D was derived from the variety of Triticum tauschii listed.
[2] Synthetic hexaploid (S.H.) in which the the D genome was derived from the variety of Triticum tauschii listed.
[3] Values with a letter in common are not significantly different at $\alpha = .05$

Canthatch-K for flour yield from either the Brabender or the Buhler milling tests.

A summary of the flour quality data is presented in Table 10 and the farinograms are represented in Figure 5. Although protein content is lower in ditelosomic 7DL than in nullisomic 7D, mean values for sedimentation, mixograph peak

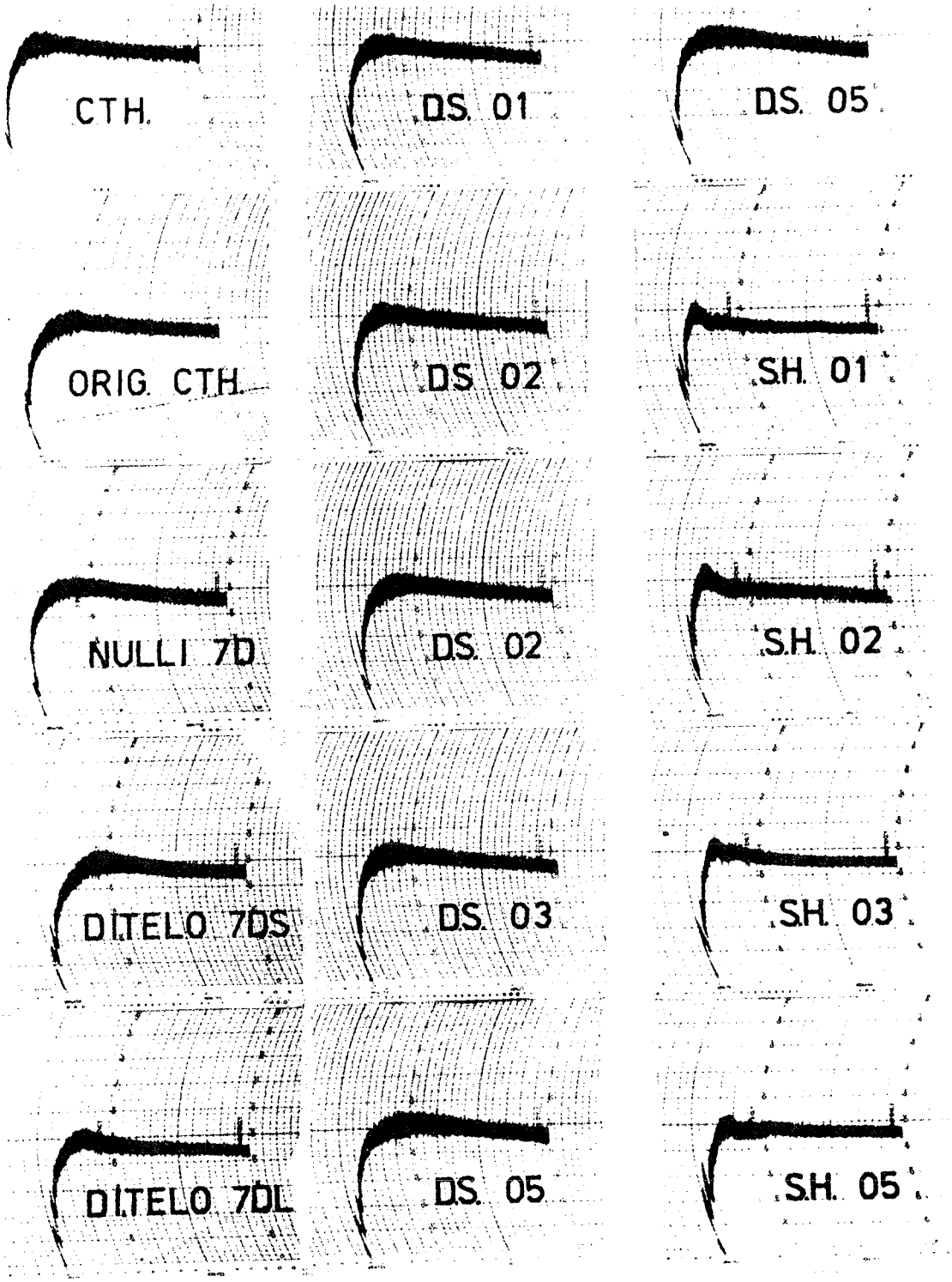
TABLE 10

Mean values for flour quality tests

sted	Flour protein(%)	Sedimentation value(ml)	Falling number(sec)	Mixograph(cm) Peak ht.	Mixograph(cm) Mixing time	Mixograph(cm) Peak area(cm^2)	Farinograph DDT (min)	Farinograph FAB (%)	Farinograph MTI (BU)	Loaf volume(cc)
h-K	15.2^{a}	57^{ab}	366	12.2^{a}	6.1^{ab}	37.0^{ab}	4.0	59.8	25	338^{abc}
li 7D	16.8^{b}	43^{de}	389	15.6^{bc}	4.5^{c}	35.3^{b}	4.0	56.7	30	333^{abc}
elo 7DS	18.3^{c}	58^{ab}	408	18.0^{c}	5.7^{abc}	50.9^{c}	4.5	63.6	30	343^{abc}
elo 7DL	16.1^{d}	52^{bc}	396	15.7^{bc}	5.8^{abc}	45.0^{ac}	3.3	62.6	40	303^{c}
5003	13.9^{ef}	56^{ab}	375	12.7^{ab}	5.9^{ab}	37.5^{ab}	3.0	59.5	30	375^{ab}
ica	14.2^{ef}	53^{bc}	398	12.9^{ab}	5.5^{bc}	35.4^{b}	3.5	59.6	30	371^{ab}
thera	13.8^{ef}	56^{ab}	390	11.9^{a}	6.3^{ab}	37.0^{ab}	3.5	59.6	25	328^{bc}
angulata	14.4^{e}	61^{a}	402	14.1^{ab}	6.8^{a}	47.6^{c}	4.3	59.5	25	379^{ab}
5003	14.4^{e}	38^{ef}	392	12.7^{ab}	1.8^{d}	11.0^{d}	2.0	55.6	50	213^{d}
ica	13.9^{f}	49^{cd}	441	14.3^{ab}	2.5^{d}	17.8^{d}	2.0	55.6	50	230^{d}
thera	14.2^{ef}	37^{f}	412	14.1^{ab}	1.8^{d}	12.3^{d}	2.0	55.6	40	207^{d}
angulata	14.3^{ef}	39^{ef}	378	13.2^{ab}	2.0^{d}	13.3^{d}	2.5	57.0	30	240^{d}

Disomic substitution with chromosome 7D of Canthatch substituted for by the corresponding chromosome of the variety of Triticum tauschii listed.
Synthetic hexaploid (2n = 42 = AABBDD) in which the D genome was derived from the Triticum tauschii listed.
with a letter in common are not significantly different at = 0.05.

Figure 5: Farinograms of all lines


CTH.
DS. 01
DS. 05
ORIG. CTH.
DS 02
SH. 01
NULLI 7D
DS. 02
SH. 02
DITELO 7DS
DS. 03
SH. 03
DITELO 7DL
DS. 05
SH. 05

area and farinograph absorption were significantly higher for ditelosomic 7DL. Ditelosomic 7DS had a higher flour protein content than ditelosomic 7DL but did not perform significantly better than 7DL on any of the flour quality tests. It would appear that the long arm of chromosome 7D has a positive effect on baking quality.

Flour protein content of all four disomic substitution lines was significantly lower than that of Canthatch-K. The mixograph peak area of the line in which chromosome 7D was derived from strangulata was significantly larger than that of Canthatch-K. There were no other significant differences between any of the disomic substitutions and Canthatch-K for any of the flour quality tests listed in Table 10. All four of the synthetic hexaploid lines produced significantly lower values than that produced by Canthatch-K for the flour quality parameters, sedimentation value, mixograph mixing time and peak area, farinograph mixing time, strength and absorption, (Figure 5) and loaf volume The lower sedimentation values, mixograph peak heights and farinograph stability values for the synthetic hexaploids when compared to Canthatch-K indicates a lower gluten strength. Lower gluten strength translates into poor gas retention, which in turn results in poorly formed loaves. The sedimentation value of the synthetic hexaploid produced from the Triticum tauschii variety typica was more similar to Canthatch-K than any of the other three synthetic hexaploids.

Analysis of variance of the values for falling number indicated that the means for all lines did not vary significantly. Loaf volume means for all the aneuploids and disomic substitutions were also not significantly different from that of Canthatch-K. The loaves produced from the synthetic hexaploids were significantly smaller and more dense than that of Canthatch-K.

Flour quality data were regressed on loaf volume to determine how well these parameters explained variation in

TABLE 11

Regression of baking quality data on loaf volume

X	Loaf volume
Flour protein	N.S.
Sedimentation	0.83**
Peak height (mixograph)	N.S.
Mixing time (mixograph)	0.78**
Peak area (mixograph)	0.83**
DDT (farinograph)	0.85**
MTI (farinograph)	N.S.
FAB (farinograph)	N.S.

** significant at $\alpha = 0.01$
N.S. Non-significant at $\alpha = 0.05$
DDT = Dough development time; MTI = Mixing tolerance index; FAB = Farinograph absorption

loaf volume (Table 11). Two parameters which exhibited significant variability among lines and high regression values

with loaf volume were mixograph peak area and sedimentation value (Table 11). Mixograph peak area is a function of both peak height and mixing time. Flour protein content regressed significantly on mixograph peak height (r = 0.82**) and on mixograph peak area (r = 0.44*) but not on mixing time as mixing time has been reported to be associated with protein quality. A significant negative regression of -0.62** is obtained when seed size is used to explain protein content. Presumably a dilution effect is responsible as larger seeds had lower flour protein content.

5.5 Discussion

The suppression of gliadin proteins synthesized by genes on chromosomes of the A and B genomes by D-genome chromosomes has been reported by Galili and Feldman (1984) in the Canadian wheat variety Prelude. They also indicated that some gliadins were less intensely stained in Tetra-Canthatch (2n = 28 = AABB) than in Canthatch (2n = 42 = AABBDD). Since their extraction differed from ours and because they used SDS-PAGE, it is difficult to establish whether the w-gliadin we report as suppressed by the long arm of chromosome 7D is the same as any of the proteins affected in their investigation. In our analysis, it seems that the the *Triticum tauschii* variety *anathera* does not contain this suppressor gene(s) as the affected w-gliadin is expressed in

both the corresponding disomic substitution and synthetic hexaploid. It also appears that the Triticum tauschii variety strangulata contains this suppressor gene(s) on a D-genome chromosome other than chromosome 7D as the affected w-gliadin is expressed in the corresponding disomic substitution but not in the synthetic hexaploid. The other two Triticum tauschii varieties tested, typica and RL5003, appear to have this suppressor on chromosome 7D.

All synthetic hexaploids performed poorly relative to Canthatch-K in the functional quality tests. The synthetic hexaploid in which typica was the D genome parent performed somewhat better than the other synthetic hexaploids. This conflicts with the conclusions of Kerber and Tipples (1969) who indicated that of these synthetic hexaploids the one in which the D genome was derived from strangulata approached Canthatch in quality more closely than the corresponding synthetic hexaploid in which typica was involved. This led them to speculate that strangulata could be the source of the high baking quality characteristics imparted by the D genome of common wheat. Baker and Kosmolak (1977) demonstrated that of the two characteristics, remix loaf volume and sedimentation value, the former exhibits a significant environmental interaction whereas the latter does not. Sedimentation values in the investigation by Kerber and Tipples (1969) were similar for all synthetic hexaploids tested. Thus the discrepancy between our findings and theirs may be due to differences in environment during the growing season.

These differences in environment are quantitated to some extent by the higher flour protein values obtained in our investigation. Speculation by Kerber and Tipples (1969) on the role of strangulata in the origin of the D genome of hexaploid wheat is substantiated by a comparison of gliadin patterns in the synthetic hexaploids and Canthatch-K (Fig. 2). The lack of certain Canthatch-K gliadin proteins in all four synthetic hexaploids may be at least partially responsible for their relatively poorer quality. The only band absent from all the synthetic hexaploids but present in Canthatch-K was the first w-gliadin band. The synthetic hexaploid in which the D genome was derived from typica contains an extra w-gliadin band not found in the others or in Canthatch-K.

It does not appear that differences in protein quality in regard to qualitative band differences are responsible for the variability in baking quality performance of the Canthatch aneuploids and disomic substitutions. The only protein difference detected for these lines is the aforementioned suppressed w-gliadin. The variation in expression of this protein may be due to variability in the amount present; insufficient quantities to be detected were produced by lines which did not exhibit this band.

However, chromosome 7D of Canthatch-K did appear to have an effect on the rheological properties of flour. In this analysis effects on sedimentation value, mixograph peak

height and farinograph strength are predominantly explained by flour protein content. Mixing time, however, has been linked in other varieties to the ratio between the relative amounts of residue protein and acetic acid soluble glutenin (Orth and Bushuk, 1972). They reported that larger relative amounts of residue protein were correlated with longer mixing times. Both Canthatch-K and ditelosomic 7DL had significantly longer mixing times than nullisomic 7D and both mixograph mixing time and farinograph dough development time exhibited high regression values when regressed on loaf volume. This would seem to strongly suggest that an investigation into the effect of chromosome of Canthatch on protein group ratios could prove interesting.

The Canthatch 7D aneuploids had significantly higher flour protein content than Canthatch-K but did not produce significantly larger loaves. This is not entirely unexpected as Tipples et al. (1977) and Bushuk et al. (1978) reported that raising the protein content within a cultivar above 16% results in a decrease in loaf volume. Strabac et al. (1974) demonstrated that an increase in protein content within a cultivar resulted in a disproportionate increase in the amount of gliadins relative to other storage proteins. Bushuk et al. (1978) indicated that this decrease in baking quality could be due to the relatively higher ratio of soluble glutenin to insoluble glutenin in the higher protein lines. Measurement of the relative proportions of different protein species was beyond the scope of this study.

Chromosome 7D from all four Triticum tauschii varieties tested appeared to compensate fully for chromosome 7D of Canthatch-K in regard to milling and baking quality. There are two possible reasons for this. First, this may indicate that chromosome 7D of Canthatch-K has not diverged significantly in regard to factors controlling functional quality from the corresponding chromosome of Triticum tauschii or secondly, that chromosome 7D of Canthatch-K does not affect functional quality in a significant way. These two explanations are not mutually exclusive and both are probably useful to some degree. Obviously the D genome of Canthatch-K has diverged significantly from Triticum tauschii in regard to baking quality as evidenced by the relatively poor performance of the synthetic hexaploids. It seems dubious that divergence would be found for tauschii chromosomes other than 7D, unless factors existed on tauschii 7D which have been conserved because of their crucial importance. As for the second explanation, chromosome 7D of Canthatch-K appeared to have a significant effect on both protein content and quality. Thus, neither of these explanations by themselves adequately explain our results, but taken together they provide a reasonable intrepretation.

Strangulata chromosome 7D appears to have a gene(s) for seed density in common with Canthatch-K. This is in contrast to the other three tauschii varieties tested which appear to lack this gene(s). Thus it would appear that strangulata chromosome 7D has diverged from Canthatch-K

chromosome 7D less than the corresponding chromosomes of the other three tauschii varieties tested. This substantiates other studies (Nishikawa et al., 1975 Jaaska, 1980; Konarev, et al., 1979) which have suggested that within Triticum tauschii the variety strangulata has diverged the least from the D genome of Triticum aestivum.

In summary, our data substantiates the conclusions of Jha et al. (1971) and Kosmolak et al. (1980) in that chromosome 7D of common wheat has an effect on protein content. However, this countradicts the conclusions of Morris et al. (1978); Giorgi et al. (1977); Miazga and Tarkowski (1982); and Kuspira and Unrau (1957). All previous reports of chromosomal control of any of the characteristic investigated in our study have utilized varieties other than Canthatch, thus these contradictions may not be real. We have also substantiated the conclusion of Doekes and Belderok (1976) that chromosome 7D has a positive effect on seed density. In addition we have shown that in regard to milling and baking quality chromosome 7D from Triticum tauschii compensates fully for chromosome 7D of Canthatch-K.

LITERATURE CITED

APPROVED METHODS COMMITTEE. 1983 Approved Methods of the American Association of Cereal Chemists. Eighth edition, St. Paul Minnesota

ARAGONCILLO, C., RODRIGUEZ-LOPERENA, M. A., CARBONERO, P. and GARCIA-OLMEDO, F. 1975. Chromosomal control of non-gliadin proteins from the 70% ethanol extract of wheat endosperm. Theor. Appl. Genet. 45:322-326.

BAKER, R. J. and DYCK, P. L. 1975. Relation of several quality characteristics to hardness in two spring wheat crosses. Can. J. Plant Sci. 55:625-627.

BAKER, R. J. and KOSMOLAK, F. G. 1977. Effect of genotype-environment inter-action on bread wheat quality in western Canada. Can. J. Plant Sci. 57:185-191

BIETZ, J. A., SHEPHERD, K. W. and WALL, J. S. 1975. Single kernel analysis of glutenin. Cereal Chem. 52:513-532.

BROWN, J. W. S., LAW, C. N., WORLAND, A. J. and FLAVELL, R. B. 1981. Genetic variation in wheat endosperm proteins: an analysis by two-dimensional electrophoresis using intervarietal chromosomal substitution lines. Theor. Appl. Genet. 59:361-371.

BUSHUK, W., RODRIGUEZ-BORES, F. J. and DUBETZ, S. 1978. Effects of high rates of nitrogen on Neepawa wheat grown under irrigation. III Protein quality for breadmaking as reflected by various tests. Can. J. Plant Sci. 58:923-927.

BUSHUK, W. and ZILLMAN, R. R. 1978. Wheat cultivar identification by gliadin electrophoregrams. 1.) Apparatus, method and nomenclature. Can. J. Plant Sci. 58:505-515.

DOEKES G. J. and BELDEROK B. 1976. Kernel hardness and baking quality of wheat - A genetic analysis using chromosome substitution lines. Euphytica 25:565-576.

GALILI, G. and FELDMAN, M. 1984. Intergenomic suppression of endosperm protein genes in common wheat. Can. J. Genet. Cytol. 26:651-656.

GIORGI, B., PALMIERI, E. and PALLA, L. 1978. Seed protein content in intervarietal chromosome substitution lines of bread wheat with Chinese Spring background. IAEA, Vienna. 569-577.

JAASKA, V. 1980. Electrophoretic survey of seedling esterases in wheats in relation to their phylogeny. Theor. Appl. Genet. 56:273-284.

JHA, M. P., KAAL, A. K., RAGHAVIAH, P. and SWAMINATHAN, M. S. 1971. Identification of chromosomes carrying factors for seed storage proteins. Wheat Inform. Serv. 32:9-13.

KERBER, E. R. and ROWLAND, G. G. 1974. Origin of the free threshing character in hexaploid wheat. Can J. Genet. Cytol. 16:145-154.

KERBER, E. R. and TIPPLES, K. H. 1969. Effects of the D genome on milling and baking properties of wheat. Can. J. Plant Sci. 49:255-263.

KILBORN, R. H. and TIPPLES, K. H. 1981. Canadian test baking procedures. I GRL. remix method and variations. Cereal Foods World. 26:624-628.

KONAREV, V. G., KHAKIMOVA, A. G., GAVRILUK, I. P. and MIGUSHOVA, E. F. 1974. Differentiation of genome D according to data of electrophoretic and immunological analysis of gliadin. Sel'skokhoziaistvennaia biologia. 9:358.

KOSMOLAK, F. G., LARSON, R. I., McKENZIE, H. 1980. Milling and baking quality of Rescue-Cadet reciprocal substitution lines. Can. J. Plant Sci. 60:1333-1341.

KUSPIRA, J. and UNRAU, J. 1957. Genetic analyses of certain characteristics in common wheat using whole chromosome substitution lines. Can. J. of Plant Sci. 37:300-326.

MERRIL, C. R., GOLDMAN, D., SEDMAN, S. A. and EBERT, M. H. 1981. Ultrasensitive stain for proteins in polyacrylamide gels shows regional variation in cerebrospinal fluid proteins. Science 211:1437-1438.

MIAZGA, D. and TARKOWSKI, C. 1982. The influence of chromosomes on protein and amino acid level in kernels of the substitution lines Chinese Spring/Cappelle Desprez. Cereal Res. Commun. 11:21-27.

MORRIS, R., MATTERN, P. J., SCHMIDT, J. W. and JOHNSON, V. A. 1978. Quality tests of 'Cheyenne' wheat chromosome 1D substitution in 'Chinese Spring'. Wheat Info. Serv. 45,46:12-17.

MORRIS, R., SCHMIDT, J. W., MATTERN, P. J. and JOHNSON, V. A. 1966. Chromosomal location of genes for flour quality in the wheat variety 'Cheyenne' using substitution lines. Crop Science 6:119-122.

NISHIKAWA, K., FURUTA, Y. and GOSHIMA, H. 1975. Genetic studies of ∝-amylase isozymes in wheat II. Reconstituted AABB tetraploid, Aegilops squarrosa and their synthetic AABBDD hexaploid. Japan J. Genet. 50:409-416.

O'FARRELL, P. H. 1975. High resolution two-dimensional electrophoresis of proteins. J. Biol. Chem. 250:4007-4021.

ORTH, R. A. and BUSHUK, W. 1972 A comparitive study of the proteins of wheats of diverse baking qualities. Cereal Chem. 49:268-275.

STEEL, R. G. D., TORRIE, J. H. 1980. Principles and Procedures of Statistics. McGraw-Hill Inc. U.S.A..

STRABAC, V. D., AYERS, G. S. and RIES, S. K. 1974. The protein fractions in chemically induced high-protein wheat seed. Cereal Chem. 51:316-323.

TIPPLES, K. H., DUBETZ, S. and IRVINE, G. N. 1977. Effects of high rates of nitrogen on Neepawa wheat grown under irrigation. II Milling and baking quality. Can. J. Plant Sci. 57:337-350.

Chapter VI

GENERAL DISCUSSION

Results from this investigation of intraspecific divergence within Triticum tauschii for the pairing of chromosome 7D with the corresponding chromosome from Triticum aestivum (cv. Canthatch) indicates that a significant degree of divergence has occurred. Chromosome 7D from the tauschii variety typica exhibited a lower chiasma frequency when paired with chromosome 7D of Canthatch than did the corresponding chromosomes from the three other tauschii varieties tested. Dvorak and Appels (1982); Dvorak and McGuire (1981) suggested that the major cause of the reduction in chiasmata in intraspecific chromosome pairing compared to intravarietal chromosome pairing is divergence in nucleotide sequence. However, Appels and Dvorak (1982) demonstrated that intraspecific nucleotide sequence divergence can be primarily explained by differences in regions of repetitive DNA. They suggested that in an evolutionary sense, modifications in base pair sequence could be tolerated much more easily within repetitive DNA elements than in unique DNA. Thus, although chromosome 7D from typica possibly exhibited a higher degree of nucleotide sequence divergence from 7D of Canthatch than did the corresponding chromosomes of the other tauschii varieties tested, this could be of little conse-

quence because the majority of the divergence is likely to be contained within non-transcribed DNA regions.

Dvorak and McGuire (1981) reported a low level of intraspecific divergence within D-genome chromosomes of Triticum aestivum. We have suggested that this could be due to the relative importance of D-genome genes and the subsequent conservation of the nucleotide sequences found therein. At first this appears to be at odds with the suggestion of Appels and Dvorak (1982) that repetitive DNA is predominantly the location of sequence divergence. However, two factors offset this: First, D-genome chromosomes are shorter (Sallee and Kimber, 1978) and contain fewer and less prominent C-bands (Gill and Kimber, 1974) than A or B-genome chromosomes. This suggests that these chromosomes contain relatively less repetitive DNA than do the other aestivum chromosomes. Second, Owen and Larter (1983) have demonstrated that rye heterochromatin can have an effect on the expression of gliadin synthesis on genes of the A and B genomes of Triticum turgidum ssp. durum within triticale. Galili and Feldman (1984) have demonstrated that the D genome of aestivum also affects gliadin synthesis on genes of the A and B genomes. It is possible that repetitive elements within the D genome are responsible for this effect. The very low level of intraspecific divergence for D-genome chromosomes reported by Dvorak and McGuire (1981) would seem to substantiate the importance of the repetitive DNA in the D-genome as evidenced by its sequence conservation. If this is the

case, then the variation found on chromosome 7D of typica may be of a useful nature. In fact, the frequency of chiasmata formed when chromosome 7D of Canthatch was paired with the corresponding 7D chromosome of the other three tauschii varieties tested was lower than that reported by Dvorak and McGuire (1981) for intraspecific pairing of D-genome chromosomes. This may signify that the degree of nucleotide sequence divergence for these tauschii chromosomes is also greater than that which is found intraspecifically within aestivum. The expression of a w-gliadin protein in the disomic substitution in which chromosome 7D was derived from the tauschii varieties anathera and stranqulata, which was not expressed in Canthatch may therefore be the result of differences in repetitive DNA within chromosome 7D. A banding study of the substituted 7D chromosomes and Canthatch 7D could prove interesting.

The aneuploid investigation into the effect of chromosome 7D of Canthatch-K on grain characteristics demonstrated that the long arm of this chromosome has a significant effect on protein content and seed density. However, these characteristics appeared to have little or no effect on either milling or baking quality in this analysis. Chromosome 7D from each of the Triticum tauschii varieties tested appeared to compensate fully for chromosome 7D of Canthatch-K in regard to milling and baking quality. The only disomic substitution which approached the kernel density of Canthatch-K

were those from the line in which chromosome 7D was derived from the tauschii variety strangulata. This substantiates the conclusion that chromosome 7D affects seed density suggested by the variance expressed for this character in the aneuploids lines. In addition, this agrees with the conclusions of others (Cheneevaraiah, 1960; Nakai, 1979; Jaaska, 1980) that Triticum tauschii ssp. strangulata could be the source of the D genome of Triticum aestivum.

The synthetic hexaploids exhibited additional variation in regard to baking quality which was not accounted for by Triticum tauschii 7D for the characters seed size, thousand kernel weight and baking quality. This suggests that a study of a disomic substitution series utilizing chromosomes 1-6 of the Triticum tauschii varieties tested in this analysis would be of considerable interest.

In conclusion, it would appear that variation exists within Triticum tauschii for baking quality which is undoubtly the most important characteristic of common wheat. Triticum tauschii chromosome 7D pairs fully with chromosome 7D of Canthatch-K. Therefore, the potential appears to be great for the discovery of useful baking quality characteristics in Triticum tauschii and for the transfer of these characteristics to Triticum aestivum even if they are of a quantitative genetic nature. The combination of tetraploid wheat with Triticum tauschii to form hexaploid wheat was a chance occurence yet it is an event which provided the world with one of its most important food sources. Still, evi-

dence indicates that the D genome of hexaploid wheat contains only a narrow selection of the total variation found within Triticum tauschii and thus it seems unlikely that the optimum hexaploid has yet been generated.

LITERATURE CITED

APPROVED METHODS COMMITTEE. 1983 Approved Methods of the American Association of Cereal Chemists. Eighth edition, St. Paul Minnesota

ARAGONCILLO, C. 1973. Proteinas CM en Triticum spp. Purificacion, caracterizacion y regulacion genetica. Dr. Ing. Agr. Thesis. Polytechnical University of Madrid.

ARAGONCILLO, C., RODRIGUEZ-LOPERENA, M. A., CARBONERO, P. and GARCIA-OLMEDO, F. 1975. Chromosomal control of non-gliadin proteins from the 70% ethanol extract of wheat endosperm. Theor. Appl. Genet. 45:322-326.

APPELS, R. and DVORAK, A.J. 1982. The wheat ribosomal DNA spacer region: Its structure and variation in populations and among species. Theor. Appl. Genet. 63:337-348.

AUTRAN, J. C., NIMMO, C. C., LAW, E. and KASARDA, D. D. 1979. Comparison of w-gliadin components by N-terminal amino acid sequencing. In "Seed protein improvement in cereals and grain legumes II. Proc. Int. Symp. Neuherberg, (1978) IAEA, Vienna.

BAKER, R. J. and DYCK, P. L. 1975. Relation of several quality characteristics to hardness in two spring wheat crosses. Can. J. Plant Sci. 55:625-627.

BAKER, D. and GOLUMBIC, C. 1970. Estimation of flour yielding capacity of wheat. Northwest Miller 277:8.

BAKER, R. J. and KOSMOLAK, F. G. 1977. Effect of genotype-environment inter-action on bread wheat quality in Western Canada. Can. J. Plant Sci. 57:185-191

BAKER, J. C. and MIZE, M. D. 1946. Gas occlusion during dough mixing. Cereal Chem. 23:39.

BERNARDIN, J. E. and KASARDA, D. D. 1973. The microstructure of wheat protein fibrils. Cereal Chem. 50:735-745.

BIETZ, J. A., HUEBNER, F. R., SANDERSON, J. E. and WALL, J. S. 1977. Wheat gliadin homology revealed through N-terminal amino acid sequence analysis. Cereal Chem. 54:1070-1083.

BIETZ, J. A., SHEPHERD, K. W. and WALL, J. S. 1975. Single kernel analysis of glutenin. Cereal Chem. 52:513-532.

BIETZ, J. A. and WALL, J. S. 1972. Wheat gluten subunits: Molecular weights determined by sodium dodecyl sulfate-polyacrylamide gel electrophoresis. Cereal Chem. 49:416-430.

BIETZ, J. A. and WALL, J. S. 1973. Isolation and characterization of gliadin-like subunits from glutenin. Cereal Chem. 50:537-547.

BIETZ, J. A. and WALL, J. S. 1975. The effect of various extractants on the subunit composition and associatiations of wheat glutenins. Cereal Chem. 52:145-155.

BOOTH, M. R. and MELVIN, M. A. 1979. Factors responsible for the poor breadmaking quality of high yielding European wheat. J. Sci. Food Agric. 30:1057-1064.

BLOKSMA, A. H. 1971. Rheology and chemistry of dough. In "Wheat - Chemistry and Technology." (Y. Pomeranz. ed). 2nd ed. pp. 523-584. Am. Assoc. Cereal Chem. St. Paul, Minnesota.

BOZZINI, A., CANTAGALLI, P., PIAZZI, S. E. 1971. Chromosomal location of the genetic control of two proteins specifically attributed to hexaploid wheat by immunochemical methods. E. W. A. C. Newsl. 3:16-17.

BROWN, J. W. S. and FLAVELL, R. B. 1981. Fractionation of wheat gliadin and glutenin subunits by two-dimensional electrophoresis and the role of group 6 and group 2 chromosomes in gliadin synthesis. Theor. Appl. Genet. 59:349-359.

BROWN, J. W. S., LAW, C. N., WORLAND, A. J. and FLAVELL, R. B. 1981. Genetic variation in wheat endosperm proteins: an analysis by two-dimensional electrophoresis using intervarietal chromosomal substitution lines. Theor. Appl. Genet. 59:361-371.

BURNOUF, T. and BOURIQUET, R. 1980. Glutenin subunits of genetically related European hexaploid wheat cultivars: Their relation to bread-making quality. Theor. Appl. Genet. 58:107-111.

BUSHUK, W. 1977. Glutenin: Key protein in breadmaking quality of wheat. University of Manitoba, Faculty of Agr. 23rd Ann. Prog. Rpt. Jan. 1977. 45-49.

BUSHUK, W. and KERBER, E. R. 1978. The role of Triticum carthlicum in the origin of bread wheat based on gliadin electrophoregrams. Can. J. Plant Sci. 58:1019-1024.

BUSHUK, W., BRIGGS, K. G. and SHEBESKI, L. H. 1969. Protein quantity and quality as factors in the evaluation of bread wheats. Can. J. Plant Sci. 49:113-122.

BUSHUK, W., RODRIGUEZ-BORES, F. J. and DUBETZ, S. 1978. Effects of high rates of nitrogen on Neepawa wheat grown under irrigation. III Protein quality for breadmaking as reflected by various tests. Can. J. Plant Sci. 58:923-927.

BUSHUK, W. and WRIGLEY, C. W. 1974. Proteins: Composition, structure and function. In "Wheat: Production and Utilization," (G. E. Inglett. ed). pp 119-145. Ari. Publ. Westport, Connecticut.

BUSHUK, W. and ZILLMAN, R. R. 1978. Wheat cultivar identification by gliadin electrophoregrams. 1.) Apparatus, method and nomenclature. Can. J. Plant Sci. 58:505-515.

CALDWELL, K. A. and KASARDA, D. D. 1978. Assessment of genomic and species relationships in Triticum and Aegilops by PAGE and by differential staining of seed albumins and globulins. Theor. Appl. Genet. 52:273-280.

CANADA GRAINS INDUSTRY. 1984. Canadian Grains Industry Stastical Handbook 84. Canada Grains Council pp 25.

CHAPMAN, V., MITTLER, T. E. and RILEY, R. 1976. Equivalence of the A genome of bread wheat and that of T. urartu. Genet. Res. 27:69-76.

CHAPMAN, V. and RILEY, R. 1966. The allocation of the chromosomes of Triticum aestivum to the A and B genomes and evidence on genome structure Can. J. Genet. Cytol. 8:57-63.

CHARBONNIER, L. 1973. Studies of the all soluble protein of wheat flour. Biochimie 55:1217-1225.

CHENNAVEERAIAH, M. S. 1960. Karyomorphological and cytotaxonomic studies in Aegilops. Acta. Hort. Gotob. 23:85-178.

CROSSWAY, A. and DVORAK, J. 1984. Distribution of nonstructural variation along three chromosome arms between wheat cultivars Chinese Spring and Cheyenne Genetics 106:309-324.

DAMIDAUX, R., AUTRAN, J. C., GRIGNAC, P. and FEILLET, P. 1978. Mise en evidence de relations applicables en selection entre l'electrophoregrams des gliadines et les proprietes viscoelastiques du gluten de Triticum durum. Desf. CR Acad. Sci. Paris {D}. 287:701-704.

DANNO, G., KANZAWA, K. and NATAKE, M. 1975. Cleavage of disulfide bonds of wheat glutenin by mercuric chloride. Agric. Biol. Chem. 39:1379.

DHALIWAL, H. S. 1977. Genetic control of seed proteins in wheat. Theor. Appl. Genet. 50:235-239.

DOEKES G. J. and BELDEROK B. 1976. Kernel hardness and baking quality of wheat - A genetic analysis using chromosome substitution lines. Euphytica 25:565-576.

duCROS, D. L., LAWRENCE, G. J., MISKELLY, D. and WRIGLEY, C. W. 1980. Systematic identification of Australian wheat varieties by laboratory methods. Tech. Publ. no. 7. North Ryde, Australia: CSIRO Wheat Research Unit.

DVORAK, J. 1976. The relationship between the genome of Triticum urartu and the A and B genomes of Triticum aestivum. Can. J. Genet. Cytol. 18:371-377.

DVORAK, J. and APPELS, R. 1982. Chromosome and nucleotide sequence differentiation in genomes of polyploid Triticum species. Theor. Appl. Genet. 63:349-360.

DVORAK, J. and McGUIRE, P. E. 1981. Nonstructural chromosome differentiation among wheat cultivars with special reference to differentiation of chromosmes in related species. Genetics 97:391-414.

DYCK, P. L. AND KERBER, E. R. 1970. Inheritance in hexaploid wheat of adult-plant leaf rust resistance derived from Aegilops squarrosa. Can. J. Genet. Cytol. 11:639-647.

EIG, A. 1929. Monograph-kritische Ubersicht der guttung Aegilops. Fedde Repert. Spec. Nov. 1st. 1929.

ESAU, K. 1977. Anatomy of Seed Plants. pp 435-437. John Wiley and Sons Inc. U.S.A..

EWART, J. A. D. 1969. Isolation and characterization of a wheat albumin. J. Sci. Food Agric. 20:730-73.

EWART, J. A. D. 1972. A modified hypothesis for the structure and rheology of glutelins J. Sci. Food Agric. 23:687-699.

EWART, J. A. D. 1979. Glutenin structure. J. Sci. Food Agric. 30:482-492.

FELDMAN, M. 1966. Identification of unpaired chromosomes in F1 hybrids involving T. aestivum and T. timopheevi. Can. J. Genet. Cytol. 8:144-151.

FIFIELD, C. C., WEAVER, R. AND HAYES, J. F. 1950. Bread loaf volume and protein content of hard red spring wheats. Cereal Chem. 27:383.

FINNEY, K. F. and BARMORE M. 1948. A. Loaf volume and protein content of hard winter and spring wheats. Cereal Chem. 25:291.

FINNEY, K. F., JONES, B. L. and SHOGREN, M. D. 1982. Functional (bread-making) properties of wheat protein fractions obtained by ultracentrifugation. Cereal Chem. 59:449-453.

FISH, W. W. and ABBOTT, D. C. 1969. Isolation and characterization of a water soluble wheat protein. J. Sci. Food Agric. 20:723-730.

FOLCH, J. and LEES, M. 1951. Proteolipids, a new type of tissue lipoproteins. J. Biol. Chem. 191:807-817.

FURUTA, Y., NISHIKAWA, K. and MAKINO, T. 1975. Interspecific variation of nuclear DNA content in Aegilops squarrosa L. Japan. J. Genet. 50:257-263.

GALILI, G. and FELDMAN, M. 1983. Genetic control of endosperm proteins in wheat. Theor. Appl. Genet. 64:97-101.

GALILI, G. and FELDMAN, M. 1984. Intergenomic suppression of endosperm protein genes in common wheat. Can. J. Genet. Cytol. 26:651-656.

GARCIA-OLMEDO, F. and CARBONERO, P. 1970. Homoeologous protein synthesis controlled by homoeologous chromosomes in wheat. Phytochemistry 9:1495-1497.

GILL, B. S. and KIMBER, G. 1974. Giesma C-banding and the evolution of wheat. Proc. Natl. Acad. Sci. USA. 71:4086-4090.

GIORGI, B., PALMIERI, E. and PALLA, L. 1978. Seed protein content in intervarietal chromosome substitution lines of bread wheat with Chinese Spring background. IAEA, Vienna. 569-577.

HAMADA, A. S., McDONALD, C. E. and SIBBITT, L. D. 1982. Relationship of protein fractions of spring wheat flour to baking quality. Cereal Chem. 59:296-301.

HARLAN, J. R. 1981. The early history of wheat: Earliest traces to the sack of Rome. In "Wheat Science - today and tomorrow. (Evans and Peacock ed) Cambridge University Press.

HART, G. E. 1979. Genetical and chromosomal relationships among the wheats and their relatives. Stadler Symp. 11:9-29. University of Missouri.

HOLLINGSHEAD, L. 1932. The occurrence of unpaired chromosomes in hybrids between varieties of Triticum vulgare. Cytologia 3:119-141.

HYLINKA, I. and BUSHUK, W. 1959. The weight per bushel. Cereal Sci. Today 4:239.

JAASKA, V. 1980. Electrophoretic survey of seedling esterases in wheats in relation to their phylogeny. Theor. Appl. Genet. 56:273-284.

JACKSON, E. A., HOLT, L. M. and PAYNE, P. I. 1983. Characterisation of high molecular weight gliadin and low-molecular-weight glutenin subunits of wheat endosperm by 2-dimensional electrophoresis and the chromosomal localisation of their controlling genes. Theor. Appl. Genet. 66:29-37.

JHA M. P., KAAL A. K., RAGHAVIAH P. and SWAMINATHAN M. S. 1971. Identification of chromosomes carrying factors for seed storage proteins. Wheat Inform. Serv. 32:9-13.

JOHNSON, B. L. 1972. Seed protein profiles and the origin of the hexaploid wheats. Amer. J. Bot. 59:952-960.

KASARDA, D. D. 1980. Structure and properties of -gliadins. Ann. Technol. Agric. 29:151-173.

KASARDA, D. D., BERNARDIN, J. E. and QUALSET, C. O. 1976. Relationship of gliadin protein components to chromosomes in hexaploid wheats. Proc. Natl. Acad. of Sci. USA. 73:3646-3650.

KASARDA, D. D., NIMMO, C. C. and KOHLER, G. O. 1971. Proteins and the amino acid composition of wheat fractions. In "Wheat - Chemistry and Technology". (Pomeranz Y. ed). pp 227-299. Am. Assoc. Cereal Chem., St. Paul, Minnesota.

KERBER, E. R. and DYCK, P. L. 1969. Inheritance in hexaploid wheat of leaf rust resistance and other characters derived from Aegilops squarrosa. Can. J. Genet. Cytol. 11:639-647.

KERBER, E. R. and DYCK, P. L. 1973. Inheritance of stem rust resistance transferred from diploid wheat (Triticum monococcum) to tetraploid and hexaploid wheat and chromosome location of the gene involved. Can. J. Genet. Cytol. 15:397-409.

KERBER, E. R. and DYCK, P. L. 1978. Resistance to stem and leaf rust of wheat in Aegilops squarrosa and transfer of a gene for stem rust resistance to hexaploid wheat. 5th Int. Wheat Genet. Symp. New Delhi. India, 358-364.

KERBER E. R. and ROWLAND G. G. 1974. Origin of the free threshing character in hexaploid wheat. Can J. Genet. Cytol. 16:145-154.

KERBER, E. R. and TIPPLES, K. H. 1969. Effects of the D genome on milling and baking properties of wheat. Can. J. Plant Sci. 49:255-263.

KHAN, K. and BUSHUK, W. 1978. Glutenin: Structure and functionality in breadmaking. Bakers Digest. April 14-20.

KIHARA, H. 1954. Considerations on the evolution and distribution of Aegilops species based on the analyser method. Cytologia 19:336-357.

KIHARA, H. 1963. Interspecific relationship in Triticum and Aegilops. Seiken Ziho 15:1-12.

KIHARA, H., YAMASHITA, K. and TANAKA, M. 1965, Morphological, physiological, genetical and cytological studies in Aegilops and Triticum collected from Pakistan, Afganistan and Iran. Results of the Kyota Univewrsity Scientific Expedition to the Karakorum and Hindukush, 1955 Vol. 1:1-118.

KIHARA, H. 1982. Wheat Studies - retrospect and prospects. Kondansha ltd., Tokyo.

KILBORN, R. H. and TIPPLES, K. H. 1981. Canadian test baking procedures. I GRL. remix method and variations. Cereal Foods World. 26:624-628.

KIMBER, G., ALONSO, L. C. and SALLEE, P. J. 1981. The analysis of meiosis in hybrids. I. Aneuploid hybrids. Can. J. Genet. Cytol. 23:209-219.

KONDO, N. 1941. Chromosome doubling in Secale, Haynaldia and Aegilops by colchichine treatment. Japan. J. Genet. 17:

KONAREV, V. G., KHAKIMOVA, A. G., GAVRILUK, I. P. and MIGUSHOVA, E. F. 1974. Differentiation of genome D according to data of electrophoretic and immunological analysis of gliadin. Sel'skokhoziaistvennaia biologia. 9:358.

KOSMOLAK, F. G., LARSON, R. I., McKENZIE, H. 1980. Milling and baking quality of Rescue-Cadet reciprocal substitution lines. Can. J. Plant Sci. 60:1333-1341.

KUSPIRA, J. and UNRAU, J. 1957. Genetic analysis of certain characters in common wheat using whole chromosome substitution lines. Can. J. Plant Sci. 37:300-326.

LAFIANDRA, D., KASARDA, D. D. and MORRIS, R. 1984. Chromosomal assignment of genes coding for the wheat gliadin protein components of the cultivars 'Cheyenne' and 'Chinese Spring' by two-dimensional (two-pH) electrophoresis. Theor. Appl. Genet. 68:531-539.

LAW, C. N. and PAYNE, P. I. 1983. Genetical aspects of breeding for improved grain protein content and type in wheat. J. of Cereal Science 1:79-93.

LAW, C. N. 1982. Aspects of the uses of aneuploid methods in wheat breeding. In "Induced variability in plant breeding." Eucarpia Symp. Wageningen, the Netherlands August 31st- September 4th, 1981 pp 62-70.

LAWRENCE, G. J. and SHEPERD K. W. 1980. Variation in glutenin protein subunits of wheat. Theor. Appl. Genet. 59:25-31.

LAWRENCE, G. J. and SHEPHERD, K. W. 1981. Inheritance of glutenin protein subunits of wheat. Theor. Appl. Genet. 60:333-337.

LINDE-LAURSEN, I. B. and LARSEN, J. 1974. The use of double-monotelodisomics to identify translocations in Triticum aestivum. Hereditias 78:245-250.

MacMASTERS, M. M., HINTON, J. J. C. and BRADBURY, D. 1971. Microscopic structure and composition of the wheat kernel. In " Wheat - Chemistry and Technology. (Pomeranz Y. ed). Am. Assoc. of Cereal Chem. Inc. St. Paul, Minnesota. pp 51-114.

MANGELS, C. E. and SANDERSON, T. 1925. Correlation of test weight per bushel with flour yield and other factors of quality. Cereal Chem. 2:365.

MARSHALL, D. R., ELLISON, F. W. and MORES, D. J. 1984. Effects of grain shape and size on milling yields in wheat. I. Theoretical analysis based on simple geometric models. Aust. J. Agric. Res. 35:619-630.

McFADDEN, E. S. and SEARS, E. R. 1944. The artificial synthesis of Triticum spelta. Res. Genet. Soc. Amer. 13:26-27.

MEREDITH, P. 1965. The oxidation of ascorbic acid and its improver effect in bread doughs. J. Sci. Food Agr. 16:474.

MERRIL, C. R., GOLDMAN, D., SEDMAN, S. A. and EBERT, M. H. 1981. Ultrasensitive stain for proteins in polyacrylamide gels shows regional variation in cerebrospinal fluid proteins. Science 211:1437-1438.

METTIN, D. 1964. On the intraspecific variability of baking quality components in einkorn-wheats, Aegilops speltoides and Aegilops squarrosa. Wheat Info. Serv.

MIAZGA, D. and TARKOWSKI, C. 1982. The influence of chromosomes on protein and amino acid level in kernels of the substitution lines Chinese Spring/Cappelle Desprez. Cereal Res. Commun. 11:21-27.

MOONEN, J. E., SCHEEPSTRA, A. and GRAVELAND, A. 1983. The positive effects of the high molecular weight subunits 3 + 10 and 2* of glutenin on the breadmaking quality of wheat cultivars. Euphytica 32:735-742.

MORRIS, R., SCHMIDT, J. W., MATTWERN,P. J. and JOHNSON, V. A. 1966. Chromosomal location of genes for flour quality in the wheat variety 'Cheyenne' using substitution lines. Crop Science 6:119-122.

MORRIS, R., MATTERN, P. J., SCHMIDT, J. W. and JOHNSON, V. A. 1978. Quality tests of 'Cheyenne' wheat chromosome 1D substitution in 'Chinese Spring'. Wheat Info. Serv. 45,46:12-17.

NAKAI, Y. 1979. Isozyme variations in Aegilops and Triticum, IV. On the origin of common wheat revealed by the study of esterase isozymes. Japan. J. Genet. 54:175-190.

NIELSEN, H. C., BABCOCK, B. E. and SENTI, F. R. 1962. Molecular weight studies on glutenin before and after disulfide-bond splitting. Arch. Biochem. Biophys. 96:252

NISHIKAWA, K., FURUTA, Y. and GOSHIMA, H. 1975. Genetic studies of -amylase isozymes in wheat II. Reconstituted AABB tetraploid, Aegilops squarrosa and their synthetic AABBDD hexaploid. Japan J. Genet. 50:409-416.

O'FARRELL, P. H. 1975. High resolution two-dimensional electrophoresis of proteins. J. Biol. Chem. 250:4007-4021.

ORTH, R. A. and BUSHUK, W. 1972. A comparitive study of the proteins of wheats of diverse baking qualities. Cereal Chem. 49:268-275.

ORTH, R. A. and BUSHUK, W. 1973. Studies of glutenin. III. Identification of subunits coded by the D-genome and their relation to breadmaking quality. Cereal Chem. 50:680-687.

ORTH, R. A., and BUSHUK, W. 1974. Studies of glutenin. VI. Chromosomal location of genes coding for subunits of glutenin of common wheat. Cereal Chem. 51:118-126.

ORTH, R. A., DRONZEK, B. L. and BUSHUK, W. 1973. Studies of glutenin. IV. Microscopic structure and its relation to breadmaking quality. Cereal Chem. 50:688-701.

OSBORNE, T. B. 1907. The proteins of the wheat kernel. Carnegie Inst. Washington Publ. 84:1-119.

OWEN, M. R. L. and LARTER, E. N. 1983. The effect of rye telomeric heterochomatin on prolamine and glutenin synthesis in isogenic lines of triticale (X Triticosecale Wittmack). Proc. 6th Int. Wheat Genet. Symp. Kyoto, Japan 1983 pp 871-880.

PAYNE, P. I. and CORFIELD, K. G. 1979. Subunit composition of wheat glutenin proteins, isolated by gel filtration in a dissociating medium. Planta 145:83-88.

PAYNE, P. I., CORFIELD, K. G. and BLACKMAN, J. 1979. Identification of a high molecular weight subunit of glutenin whose presence correlates with breadmaking quality in wheats of related pedigree. Theor. Appl. Genet. 55:153-159.

PAYNE, P. I., CORFIELD, K. G., HOLT, L. M. and BLACKMAN, J. A. 1981a. Correlations between the inheritance of certain high-molecular weight subunits of glutenin and breadmaking quality in progenies of six crosses of bread wheat. J. Sci. Food Agric. 32:51-60.

PAYNE, P. I., HOLT, L. M. and LAWRENCE, G. J. 1981b. Structural and genetical studies on the high-molecular weight subunits of wheat glutenin. Theor. Appl. Genet. 60:229-236.

PAYNE, P. I., HOLT, L. M., JACKSON, E. A. and LAW, C. N. 1984. Wheat storage proteins: their genetics and their potential for manipulation by plant breeding. Phil. Trans. R. Soc. Lond. B 304:359-371.

PAYNE, P. I., HOLT, L. M., LAWRENCE, G. J. and LAW, C. N. 1982. The genetics of gliadin and glutenin, the major storage proteins of the wheat endosperm. Qual. Plant Plant Foods Hum. Nutr. 31:229-241.

PAYNE, P. I., LAW, C. N. and MUDD, E. E. 1980. Control by homoeologous group 1 chromosomes of the high molecular weight subunits of glutenin, a major protein of wheat endosperm. Theor. Appl. Genet. 58:113-120.

PAYNE, P. I. and LAWRENCE, G. J. 1983. Catalogue of alleles for the complex gene loci Glu-A1, Glu-B1 and Glu-D1 which code for high-molecular-weight subunits of glutenin in hexaploid wheat. Cereal Res. Commun. 11:29-35.

PENCE, J. W., ELDER, A. H. and MECHAM, D. K. 1951. Some effects of soluble flour components on baking behavior. Cereal Chem. 28:94.

PENCE, J. W. and OLCOTT, H. S. 1952. Effect of reducing agents on gluten protein. Cereal Chem. 29:292.

PENCE, J. W., WEINSTEIN, N. E. and MECHAM, D. K. 1954. The albumin and globulin contents of wheat flour and their relationship to protein quality. Cereal Chem. 31:303.

PERSON, C. 1956. Some aspects of monosomic wheat breeding Can. J. Bot. 34:60-70.

POMERANZ, Y. 1971. Composition and functionality of wheat flour components. In "Wheat - Chemistry and Technology." (Pomeranz Y. ed). 2nd ed. pp 585-674. Am. Assoc. Cereal Chem. St. Paul, Minnesota.

POPERELYA, F. A. and BABAYANTS, L. T. 1978. The GLD 1B3 gliadin-component group as a marker for the gene responsible for the resistance of wheat plants to stem rust. Sov. Agric. Sci. 6:8-9.

RILEY, R. and CHAPMAN, V. 1960. The D genome of hexaploid wheat. Wheat Info. Serv. 11:18-19.

RILEY, R. and KIMBER, G. 1961. Aneuploids and the cytogenetic structure of wheat varietal populations. Heredity 16:275-290.

RODRIGUEZ-LOPERENA, M. A., ARAGONCILLO, C., CARBONERO, P. and GARCIA-OLMEDO, F. 1975. Heterogeneity of wheat endosperm proteolipids (CM proteins). Phytochemistry 14:1219-1223.

SALLEE, P. J. and KIMBER, G. 1978. An analysis of the pairing of wheat telocentric chromosomes. 5th Int. Wheat Genet. Symp. New Dehli, India pp 408-419.

SAX, K. and SAX, H. J. 1924. Chromosome behaviour in a genus cross. Genetics 9:454-464.

SEARS, E. R. 1941. Amphiploids in the 7-chromosome Triticinae. Missouri Agr. Exp. Sta. Res. Bull. 336:1-46.

SEARS, E. R. 1972. Reduced proximal crossing-over in telocentric chromosomes of wheat. Genet. Iber. 24:233-239.

SECKINGER, H. L. and WOLF, M. J. 1970. Electron microscopy of endosperm proteins from hard and soft wheats. Cereal Chem. 47:236-243.

SHEPHERD, K. W. 1968. Chromosomal control of endosperm proteins in wheat and rye. Proc. 3rd Int. Wheat Genet. Symp. pp 86-96.

SHELLENBERGER, J. A. 1971. Production and utilization of wheat. In "Wheat - Chemistry and Technology." (Pomeranz Y. ed) pp 1-18. Am. Assoc. Cereal Chem. St. Paul, Minnesota.

SHUEY, W. C. 1960. A wheat sizing technique for predicting flour milling yield. Cereal Sci. Today 5,71,72 and 75.

STEEL, R. G. and D., TORRIE, J. H. 1980. Principles and Procedures of Statistics. McGraw-Hill Inc. U.S.A..

STRABAC, V. D., AYERS, G. S. and RIES, S. K. 1974. The protein fractions in chemically induced high-protein wheat seed. Cereal Chem. 51:316-323.

SYMES, K. J. 1969. Influence of a gene causing hardness on milling and baking quality of two wheats. Aust. J. Agric. Res. 20:971-979.

TANAKA, K. and BUSHUK, W. 1973. Changes in flour proteins during dough mixing. II. Gel filtration and electrophoresis results. Cereal Chem. 50:597-605.

TIPPLES, K. H., DUBETZ, S. and IRVINE, G. N. 1977. Effects of high rates of nitrogen on Neepawa wheat grown under irrigation. II. Milling and baking quality. Can. J. Plant Sci. 57:337-350.

THE, T. T. 1973. Chromosome location of genes conditioning stem rust resistance transferred from diploid to hexaploid wheat. Nature, New Biol. 241:256.

TSCHOEGAL, N. W. and ALEXANDER A. E. 1960a. The surface chemistry of wheat gluten. I. Surface pressure measurements. J. Colloid Sci. 15:155.

TSCHOEGAL, N. W. and ALEXANDER, A. E. 1960b The surface chemistry of wheat gluten. II. Measurments of surface viscoelasticity. J. Colloid Sci. 15:168.

WALL, J. S. 1979. The role of wheat proteins in determining baking quality. In "Recent advances in the biochemistry of cereals." (LAIDMAN, D. L. and WYN JONES, R. G.ed). pp 275-311. New York:Academic Press.

WATANABE, Y. 1962. Meiotic irregularities in intervarietal hybrids of common wheat. Wheat Info. Serv. 14:5-7.

WELSH, J. R., WATSON, C. A. and GREEN, C. W. 1968. Chromosomal control of flour properties in three substitution sets of common wheat (Triticum aestivum L.) Crop Sci. 8:81-82.

WRIGLEY, C. W., ROBINSON, P. J. and WILLIAMS, W. T. 1981. Associations between electrophoretic patterns of gliadins proteins and quality characteristics of wheat cultivars. J. Sci. Food Agric. 32:433-442.

WRIGLEY, C. W. and SHEPHERD, K. W. 1973. Electrofocusing of grain proteins from wheat genotypes. Ann. N. Y. Acad. Sci. 209:154-162.

YAMASHITA, K., TANAKA, M. and KOYAMA, M. 1957. Studies on flour quality in Triticum and Aegilops. Seiken Ziho 8:20-26.