scientific knowledge needed for solving these problems. However, even at present, improved communications between pilots and meteorologists on the ground can improve the situation.

Conclusion

It has been shown that clear air turbulence is an important problem for both aviation and atmospheric science, and that the difficulties it raises can be attacked only when we have a thorough knowledge of the details of its formation and evolution.

The available empirical knowledge appears to be in agreement with the hypothesis that at least some of the clear air turbulence results from the hydrodynamic instability of internal fronts in accord with the Kelvin-Helmholtz model; the investigation of this hypothesis seems to provide an important new vista for research into the processes of the turbulence.

An important consequence of the establishment of a physical model of clear air turbulence would be the ability to determine what resolution and spacing of observations are necessary for accurate prediction of the likelihood of turbulence.

However, our main point is that clear air turbulence is neither capricious nor mysterious; it obeys the laws of physics, and careful measurements and intelligent data processing should reveal its secrets.

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22. We thank S. A. Thorpe (National Institute of Oceanography, Great Britain), J. D. Woods (Meteorological Office, Bracknell, Great Britain), and K. R. Hardy (U.S. Air Force Cambridge Research Laboratories) for permission to reproduce the figures taken from their publications. This article (contribution No. 68-57) draws to some extent on research being conducted under NSF grant GA 1959X to Pennsylvania State University.

Molecular Approach to Breadmaking

Biochemistry of components that control breadmaking is described.

Y. Pomeranz,, K. F. Finney, R. C. Hoseney

The functional (breadmaking) properties of wheat flour depend on several factors including wheat variety, environmental and soil conditions under which the wheat was grown, the process used to mill the wheat into flour, and the chemical composition of the flour. Wheat varies widely in chemical composition. Percentages of proteins, lipids, minerals, vitamins, pigments, and enzymes show up to a fivefold range among cargoes of wheat. Such differences in composition have far-reaching effects on processing and on the best way of use. The problem of relating the chemical composition and structure of wheat components to functional properties has kept more cereal chemists at work than any other single problem in the field.

Over 200 years ago (in 1745) Becari reported separating gluten from wheat flour, the first plant protein to be isolated. Approximately 150 years ago, it was found that about half of the gluten proteins is soluble in 70 percent ethanol. A century ago, Ritthausen laid the foundations of seed protein chemistry so ably expanded by Osborne half a century or so later (*1*). However, biochemical methods only recently have been applied to studying breadmaking quality of wheat. This article summarizes some studies on the relation between chemical composition and breadmaking potentialities of wheat flour.

Performance Test

Relating chemical composition and structure of wheat flour components to functional properties in breadmaking requires: (i) knowledge or analytical data of the components present; (ii) methods to extract, fractionate, and characterize flour components; (iii) techniques to reconstitute the isolated moieties; and (iv) tools to ascertain that neither the fractionation nor the reconstitution procedures impair functional properties of the components.

Historically, the last requirement was met first. Investigations of Finney and Barmore (*2*) led to an optimized baking test. In that test, five factors—mixing time, oxidation level, yeast activity, fer-

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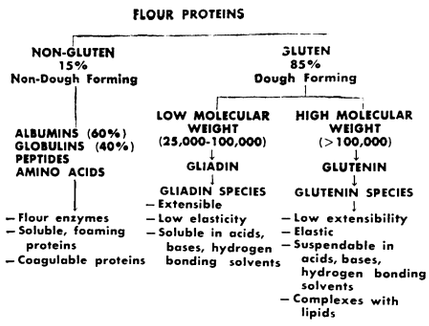

Fig. 1. A schematic presentation of the main protein fractions of wheat flour (from *4*).

mentation time, and water absorption—are optimized and balanced. In addition, added ingredients (shortening, sugar, salt, milk, and malt), essential to produce an optimum loaf of bread, are in excess, and none is permitted in a limiting capacity. Evaluating breadmaking potentialities in an optimized system (rather than determining performance of a wheat flour under a set of fixed and arbitrarily selected conditions) provided a meaningful and reproducible analytical tool for the determination of quality characteristics inherent in wheat and flour components. The original test involved baking 100-gram samples of flour; recently, the baking test was scaled down to 10 grams of flour for studies on fractions separated by physical, chemical, and physical-chemical techniques (*3*). The optimized baking test can be performed on white flour with the analytical precision of most generally accepted biological assays. Several parameters are determined in the test; the most important parameter is loaf volume. Loaf volume is highly correlated, over a relatively wide range, with consumer acceptance, technological versatility, rheological properties, and other important breadmaking characteristics including inherent protein quality, protein content, and oxidation requirement.

Proteins

Wheat flour used in breadmaking contains about 12 percent protein. The proteins include components that are soluble in dilute salt solutions (mainly albumins and globulins) and those insoluble in salt (gliadin, a mixture of prolamins soluble in 70 percent alcohol, and glutenin, a mixture of glutelins soluble in dilute acids and alkalis). The albumins and globulins each comprise about 6 percent, and the gliadin and glutenin each comprise about 45 percent of the total wheat proteins. A schematic outline of wheat proteins is given in Fig. 1 (*4*); starch-gel electrophoretic patterns of the main protein groups are given in Fig. 2 (*5*).

When wheat flour is wetted and mixed, the water-insoluble proteins hydrate and form gluten, a complex coherent mass. This unique gluten formation, rather than any distinctive nutritive property, gives wheat its prominence in the diet. It is generally agreed that the gluten is the skeleton or framework of wheat flour dough and that it is responsible for gas retention which is required in the production of light, yeast-leavened products (*4*, *6*). The percentage of dry gluten is closely related to the percentage of protein, and gluten determinations were widely used before being replaced by the more precise Kjeldahl method for determining nitrogen.

To study the significance of proteins in breadmaking, bread was baked by the optimized formula from flours milled from wheat varieties grown under a wide range of climatic and soil conditions and from commerical wheat samples (*7*). The major factor accounting for variation in loaf volume within a variety was protein content; the relation between loaf volume and protein content was essentially linear between 8 and 18 percent protein, the range encountered. The regression of loaf volume on protein content differed with wheat varieties. The loaf-volume-to-protein-content regression lines for different varieties represent differences in protein quality (Fig. 3).

The relation of protein content and loaf volume being linear within a variety greatly simplifies the determination of breadmaking quality of new wheat varieties. In practice, only two or three samples of a new variety, at different protein concentrations, establish with remarkable accuracy a new variety's protein-to-loaf-volume regression in relation to standard varieties.

The findings on the significance of proteins in breadmaking were confirmed by fractionation studies. Wheat flours representing a wide range in quality characteristics were fractionated into starch, gluten, and water-soluble fractions; fractions were recombined in their original and in different proportions; and various fractions of some varieties were interchanged (*8*). In each case, flours that were recombined in their original proportions gave bread equal to that made with the original unfractionated flour. Gluten fractions accounted for the recognized differences in bread quality of the varieties studied.

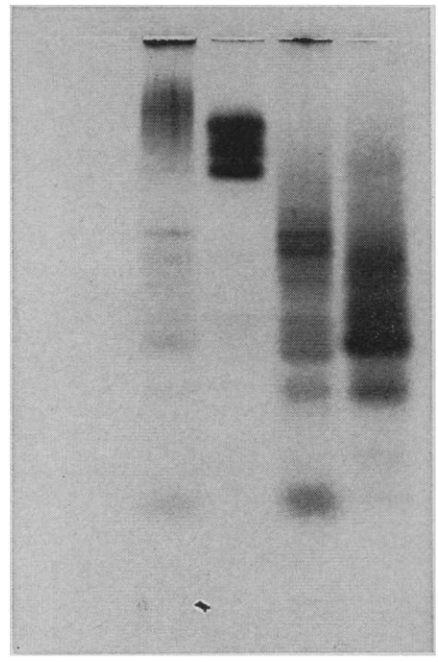

Fig. 2. Starch-gel electrophoretic patterns characterizing the four groups of wheat flour proteins including glutenins (pattern 1), gliadins (pattern 2), globulins (pattern 3), and water-soluble proteins (pattern 4) (from *5*).

While the above and other investigations prove that gluten governs differences in breadmaking potential of wheat varieties, it should be emphasized that an acceptable loaf of bread cannot

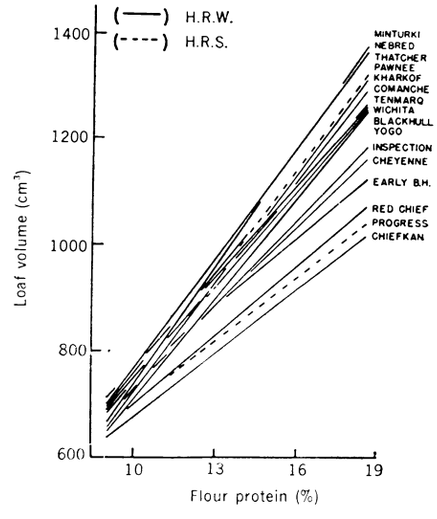

Fig. 3. Loaf volume-protein content regression lines for hard winter (HRW) and hard spring (HRS) wheat varieties. Each variety regression line represents many samples harvested throughout the Great Plains during several crop years (from *7*).

be produced unless the other wheat flour components also are present as in a normal, unfractionated flour (*9*).

Thus, for example, loaf volume of bread baked without the water-soluble fraction was about two-thirds that of bread baked with all wheat flour components reconstituted (*10*). Baking experiments showed that the role of the water-solubles in baking is twofold. First, a dialyzate (containing mainly soluble carbohydrates, minerals, amino acids, and peptides) contributed to gas production, a contribution that also could be obtained by replacing the dialyzate with synthetic yeast food, Second, a fraction that contained water-soluble pentosans and glycoproteins contributed to gas retention and gluten extensibility. Neither the globulins nor the albumins were required to produce a normal loaf.

Gluten proteins can be separated by ultracentrifugation (100,000*g* for 5 hours) into two major fractions, centrifugate (100-5C) and supernatant (100-5S) (*11*). When examined by starch-gel electrophoresis (Fig. 4), most proteins in the supernatant (mainly gliadins, soluble in 70 percent ethanol) migrate into the gel; most proteins in centrifugate (mainly glutenins, insoluble in 70 percent ethanol) are retained at the origin. Reconstitution studies with gluten proteins, separated by ultracentrifugation and by solubility, showed conclusively that the gliadin fraction is responsible for the differences in loaf volume of flours that differ in breadmaking potential. The factor responsible for mixing time and dough development is located in the glutenin fraction.

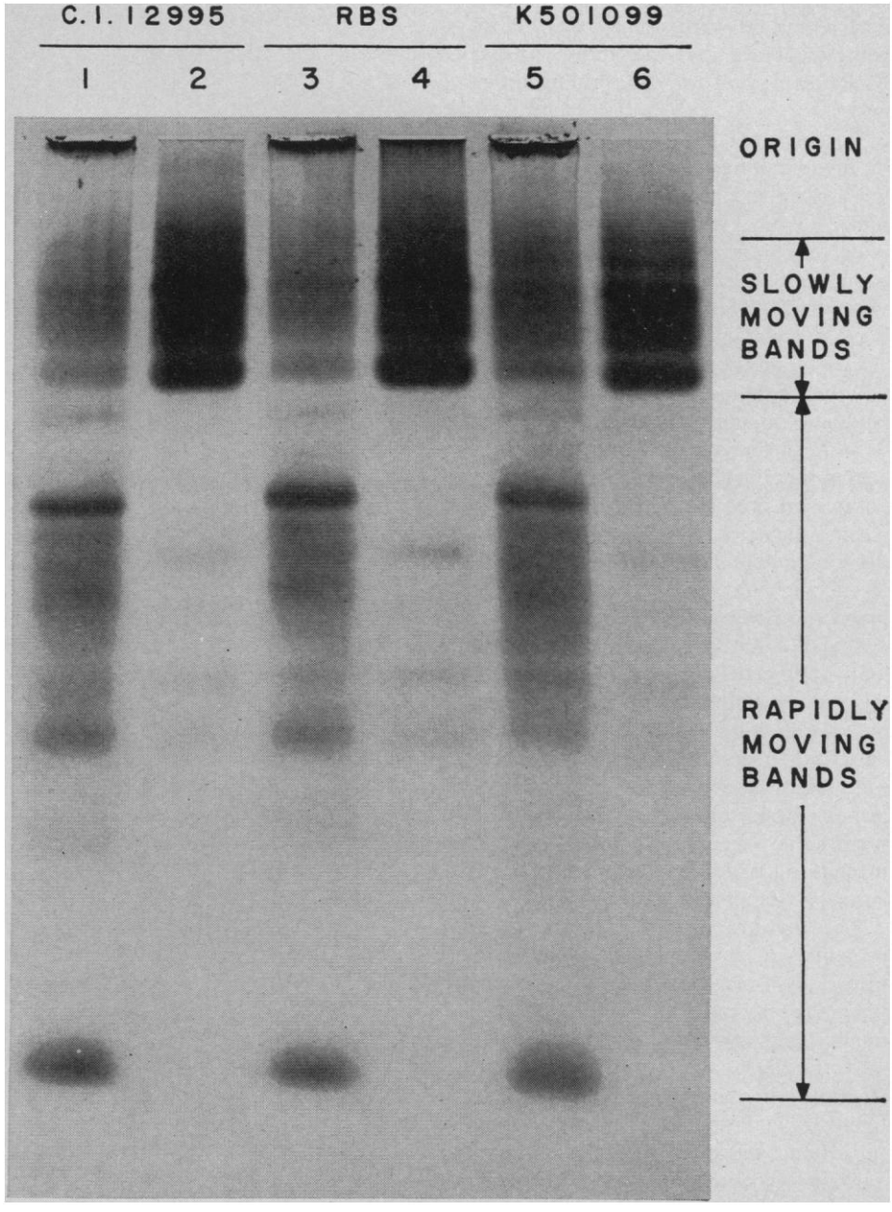

Fig. 4. Starch-gel electrophoretic patterns of centrifugate (patterns 1, 3, and 5) and supernatant fractions (patterns 2, 4, and 6) of C.I. 12995, RBS (regional baking standard) composite, and K501099 (from *5*).

The failure of glutenin to migrate into starch gel is attributable to their high molecular weights that vary into the millions (*12*). In these high-molecular-weight polymers, polypeptide chains with molecular weights that range from 20,000 to 50,000 are attached to each other by disulfide bridges. At the same time, some intraunit disulfide bonds hold each unit in a folded or looped conformation (*13*). Gliadin contains several components. The disulfide linkages are intramolecular because their reductive or oxidative cleavage causes little or no change in molecular weight (*14*). The molecular weights of the gliadins are relatively low and generally vary from 20,000 to 50,000 (*15*).

Amino Acids

Wheat gluten proteins are characterized by high concentrations of glutamic acid (35 percent) and proline (14 percent). About 40 percent of the acidic amino acid side chains occur as amides (*16*). According to Bigelow (*17*), hydrophobicities of proteins range from 440 to 2000 calories for an average amino acid residue. The hydrophobicities of gliadin and glutenin, calculated from data on amino acid composition (*18*) are 1109 and 1016 calories, respectively, for an average amino acid residue. The higher hydrophobicity of gliadin is experimentally confirmed by its α-helix content, which is about twice that of glutenin (*19*). α-Helices are stabilized by hydrophobic amino acids (*20*). However, it has been shown that glutenin has more nonpolar amino acids available for intermolecular hydrophobic binding with lipids than does gliadin (*21*).

Thus far, studies on amino acid composition of cereals have been rather disappointing because of their failure to explain differences in breadmaking characteristics of wheat varieties. However, numerous studies have shown that both ionic and nonionic groups govern the unique viscoelastic properties of wheat gluten (*22*). When the amide groups of amino acids in gluten and its

principal fractions (glutenin and gliadin) were methylated, solubility, intrinsic viscosity, and cohesion were changed significantly (*23*). When deuterium oxide instead of water was used in dough mixing, gluten strength and elasticity were increased (*24*). If deuterium is allowed to replace hydroxyl protons of proteins and carbohydrates in a dough that is allowed to stand for an hour, gluten strength is further increased. This result indicates that hydrogen bonds are involved in stabilizing dough structure.

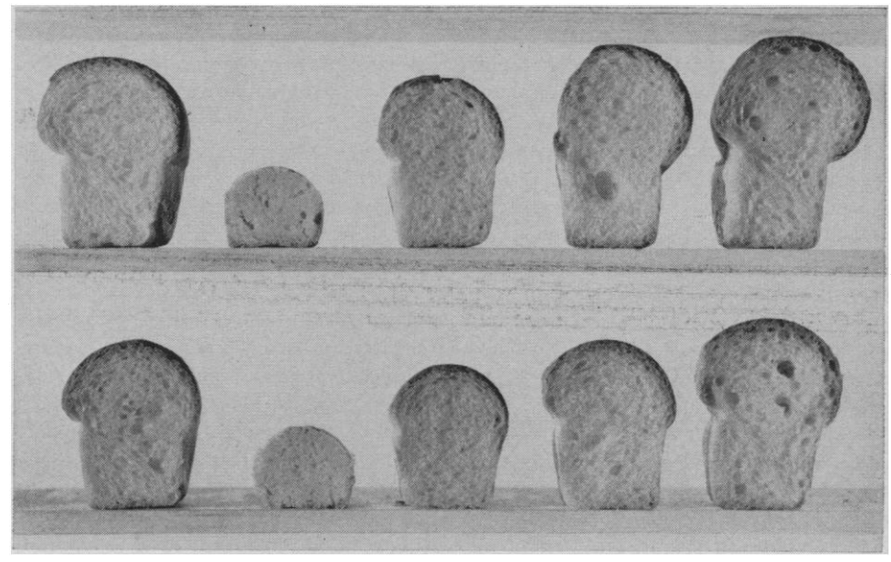

Fig. 5. Microloaves (10 grams of flour) baked from untreated flour (top row) and flour extracted with petroleum ether (bottom row). From left to right: bread from original flour (13 percent protein); from a mixture of starch and water solubles; and from a mixture of starch and water solubles reconstituted with gluten proteins to give 10, 13, and 16 percent protein, respectively (from *31*).

Effects of Oxidants

The role of thiol and disulfide bonds in wheat flour proteins was demonstrated in studies with sulfhydryl-blocking reagents, oxidants, and reducing agents. Rheological properties of wheat dough are impaired dramatically by minute amounts of reducing agents or sulfhydryl-blocking reagents. However, performance of a flour in breadmaking can be improved significantly by adding small amounts (about 20 to 50 ppm) of oxidizing agents (for example, potassium bromate). Oxidation requirements of flours are related to total protein contents and to protein thiol groups and disulfide linkages (*22*). Work of Stahmann and co-workers (*25*) indicated a correlation between oxidation requirements and dehydrogenase activities of wheat flours. Tsen and Hlynka (*26*) presented evidence for peroxidic lipids affecting oxidative improvement.

It has been shown that continuous interchange reactions between sulfhydryl and disulfide groups (*27*) and reactivity of protein sulfhydryl groups (*28*) affect oxidation requirements. Some studies (*29*) indicate that certain aspects of protein quality may be largely governed by the ratio of disulfide to sulfhydryl groups.

Lipids

Wheat flour contains about 0.8 percent free lipids (extractable with petroleum ether) and 0.6 percent bound lipids (that can be extracted with more polar solvents such as water-saturated butanol). In the free lipids, about 0.6 percent are nonpolar components (mainly triglycerides), and 0.2 percent are polar components (glycolipids and phospholipids). The bound lipids are a mixture of phospholipids and glycolipids. Differences in the lipid content and composition of different wheat varieties do not account for differences in baking quality (*30*).

The role of lipids in breadmaking is clearly indicated by fractionating defatted flour. Gluten was prepared from either untreated flour or flour extracted with petroleum ether and added at various ratios to a mixture of starch and water solubles. This provided a comparison between absence and presence of lipids, as gluten washed from untreated flour contains practically all the polar and most of the nonpolar components of lipids. While loaf volume depended primarily on the protein content, loaf volume at each protein concentration was higher and crumb texture was better in bread baked from untreated flour than from flour extracted with petroleum ether (Fig. 5) (*31*).

The role of lipids also was demonstrated by following changes that take place in mold-damaged wheat or flour. Damp wheat or wheat flour is attacked in storage (especially at elevated temperatures) by storage fungi. The attack results in impaired breadmaking quality. Decrease in breadmaking potentialities of mold-damaged wheat flour was accompanied by almost complete breakdown of free flour lipids and by a substantial decrease of bound lipids (*32*). Starch-gel electrophoretic patterns indicated that proteins of storage-damaged flour had undergone only minor changes. Fractionation and reconstitution studies showed that the damage in early stages of fungal attack resulted from breakdown of lipids (mainly polar components) rather than changes in gluten proteins or starch and water solubles.

Both in sound flour and in mold-damaged flour, small amounts of polar lipids substantially improve, and nonpolar lipids impair, bread baked from flour extracted with petroleum ether. Preliminary investigations indicated that the improvement was mainly from glycolipids (*33*). The role of glycolipids in breadmaking was confirmed by studies with synthetic glycosylglycerides (*34*). Availability of methods to synthesize glycolipids would seem of general interest in view of their ubiquitous occurrence in biological systems and their fundamental role in cell membranes and in the photosynthetic apparatus.

Breadmaking experiments with synthetic glycolipids indicate that both hydrophobic and hydrogen bonds are important for the improving effect of glycolipids (*35*). Hydrogen-donating (hydroxyl) groups are essential because acetylated glycolipids cannot replace the free glycolipids. Glycolipids containing a disaccharide were superior as improvers to corresponding monosaccharide derivatives. Insofar as the hydrophobic moiety of the glycolipids is concerned, there is an optimum fatty acid chain length for bread improve-

ment. For monogalactosylglycerides it is octanoic acid (or shorter); for cellobiosyl derivatives it is decanoic acid. Linoleoyl derivatives are more effective derivatives than stearoyl derivatives, though double bonds are not essential for the effect.

Commercially available, synthetic glycolipids (of the sucroester type) can be used to counteract the highly deleterious effects on loaf volume of high concentrations of soy flour in nutritionally improved bread (*36*). The effects of synthetic glycolipids increase with an increase in hydrophilic-lipophilic balance (with decrease in numbers and chain lengths of fatty acids attached to the carbohydrate molecule). Natural and synthetic glycolipids also improve loaf volume and crumb grain of bread baked from wheat flour enriched with defatted cottonseed flour, fish protein concentrate, sesame seed flour, or food grade yeast (*37*).

Macromolecular Interactions of Glycolipid and Wheat Flour

Most free flour lipids become inextractable with petroleum ether during dough mixing; some triglycerides and all polar lipids are bound (*38*). The binding generally increases with increased mixing speed, mixing time, and moisture contents of the dough (*39*). However, fractions rich in glycolipids are bound even if the moisture content of flour is reduced to about 4 percent. It has been postulated that a protein-lipid complex is formed during dough mixing or gluten preparation (*40*).

Studies based on differences in solubility of gluten proteins have shown that polar wheat flour lipids (principally glycolipids) are bound to the glutenin protein by hydrophobic and to gliadin protein by hydrogen bonds (*21*). Results indicated that in unfractionated gluten, the lipid apparently is bound to both protein groups at the same time and forms a complex. The complex was pictured as units of gliadin and glutenin protein bound together by polar lipids.

To study interaction of glycolipids with wheat flour macromolecules, we investigated by infrared and nuclear magnetic resonance (NMR) spectroscopy complexes between galactosylglycerides and starch, gliadin, or glutenin (*41*). Infrared spectroscopy indicated hydrogen bonds between glycolipids and gelatinized starch and between glycolipids and gluten components and van der Waals bonds between glycolipids and gluten components. The NMR spectra showed an inhibition of the methylene signal of glycolipid (at 8.7τ) by glutenin, indicating hydrophobic bonding (Fig. 6).

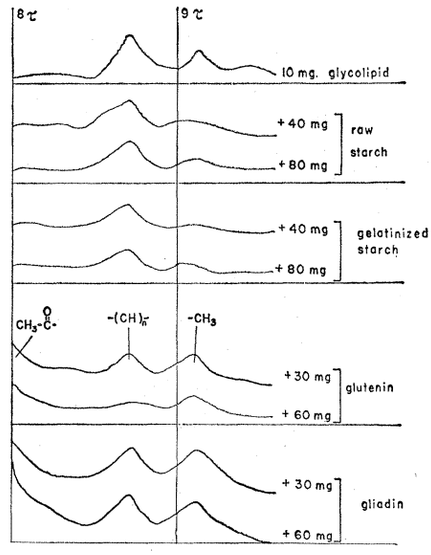

Fig. 6. The NMR spectra of galactosylglyceride (10 mg) complexed with varying amounts of starch, glutenin, or gliadin in 1 ml of D_2O (from *41*).

Two studies (*21*, *41*) concerned interaction of glycolipids with isolated starch and gluten. Additional studies were made on interactions that take place in dough and bread containing both starch and proteins (*42*). Tritium-labeled galactosyldidecanoylglycerol was synthesized. Sections prepared from dough and bread containing the labeled galactolipid were studied by autoradiography. In dough, the galactolipid was distributed in the gluten and, to some extent, in the starch; in the bread, most of the galactolipid was in gelatinized (by oven heat) starch granules.

The findings on macromolecular interaction between glycolipid and wheat flour are summarized in Table 1. The results indicate that glycolipid in dough interacts with gluten protein, according to the scheme based on differences in solubility. Limited interaction with starch granules is also indicated. Basically, increase in loaf volume during breadmaking can be attributed to the formation of a complex between glycolipids and gluten proteins. In bread, a complex between glycolipids and starch seems to be of primary importance and could be responsible for the improved retention of freshness in bread baked with glycolipids.

Table 1. Bonds in glycolipid and wheat flour macromolecule complexes.

Method of study	Type of bond between glycolipid and		
	Starch	Gliadin	Glutenin
Solvent extraction of gluten proteins		Hydrogen	Hydrophobic
Lipid binding in starch dough	Hydrogen		
Infrared	Hydrogen	Van der Waals, hydrogen	Van der Waals, hydrogen
Nuclear magnetic resonance	Hydrogen, some induced dipole interaction		Hydrophobic and hydrogen
Autoradiography	Strong interaction in bread		Interaction in dough
Baking test	Hydrophobic and hydrogen bonds are essential for improvement in breadmaking		

Wheat Maturation and Protein Biosynthesis

Useful information on the role of wheat components in breadmaking was obtained in studies on protein biosynthesis in maturing wheat. Synthesis of gluten proteins begins about 3 weeks before hard red winter wheat is ripe. Optimum loaf volume potential is reached as early as 2 weeks before wheat ripens (*43*). The increase in loaf volume potential is accompanied by a decrease in free amino acids (*44*) and by increases in the size and complexity of the proteins (*45*).

Radioactive tracer studies (*46*) suggest that gliadin reaches maximum rate of biosynthesis later than glutenin, albumin, or globulin. Bran proteins showed markedly increased radioactivity with late injection of labeled compounds, suggesting that they form at later stages of maturation. The distinctive labeling pattern found for the pro-

tein fractions strongly suggests that each possesses a biosynthetic individuality rather than representing a somewhat continuous spectrum of molecules. Later radioactive tracer studies (*47*) indicated that different parts of gliadin are synthesized at different rates and that formation of a disulfide bond is one of the later steps in formation of wheat kernel proteins.

The form in which proteins are present in the endosperm was studied by microscopy. Electron microscopy of immature wheat sections showed (*48*) that endosperm protein was concentrated in discrete bodies supported by a lipoprotein network. Isolated protein bodies were similar to gliadin (according to starch-gel electrophoresis and amino acid assay). Proteins outside the protein bodies were mainly albumins and globulins. With maturation of the grain, the matrix proteins and protein bodies form a continuous network in which developing starch granules are embedded.

Genetic Control of Endosperm Characteristics

Fluctuations in composition and functional properties of wheat varieties are generally greater from environmental factors than from known genetic differences (*49*). However, many investigations show that genetic factors influence differences in composition and functionality.

Protein differences of less than 1 percent between varieties and selections grown in a common environment have discouraged plant breeding efforts to increase protein content, as has the general negative correlation between yield and protein content. Interest in breeding for increased protein content was stimulated by the report of Middleton *et al.* (*50*). They found that when the South American wheat varieties Fronteira [Cereal Investigation (C.I.) 12019] or Frondoso (C.I. 12078) were used as parents, the progenies consistently contained more protein than other varieties grown under comparable conditions. The increased protein content was not obtained at the expense of yield, and numerous experiments throughout the Great Plains of the United States have shown that the genetic barrier to increased protein content has been broken. Recently, agronomists have developed new varieties of wheat with increased protein which is functional in breadmaking (*51*).

Genetic Analysis of Quality Components

Common bread wheats contain 42 chromosomes and produce sex cells of half that number. Conventional wheat breeding and genetic analyses in common wheat are complicated by the polyploid chromosome constitution. Sears (*52*) developed monosomic wheat plants with 20 pairs and one single chromosome. This opened a new era of genetic studies in wheat. Based on the stocks developed by Sears, two techniques, the monosomic (*53*) and chromosome substitution (*54*), have been used to study dominant genes in wheat. The latter seems superior if a characteristic is under the control of many genes (*55*). It has been possible to associate specific chromosomes with certain agronomic factors (disease and insect resistance) and functional (breadmaking) properties. Attempts to establish chromosomal association with gliadin proteins (*56*) and lipid contents and composition (*57*) have thus far been rather inconclusive. The new genetic tool does not permit detection of interaction effects involving genes on different chromosomes. In addition, the single chromosome substitution method creates a different environment for the isolated chromosome in both the nucleus and the cytoplasm because the recipient variety is used as the female parent in backcrossing (*54*). Despite those limitations, the new tool shows promise for identifying the genetic factors that control chemical composition and its various manifestations, including breadmaking potentialities of wheat flour. Finally, the great potential of induced mutations and "isogenic" lines to elucidate nature of genetic differences affecting the critical components, as previously shown for microorganisms and other higher plant systems, merits increased attention for the biochemical genetic analyses of wheat quality components.

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58. This was a cooperative investigation between the Crops Research Division, Agriculture Research Service, U.S. Department of Agriculture and Kansas Agricultural Experimental Station, Manhattan.